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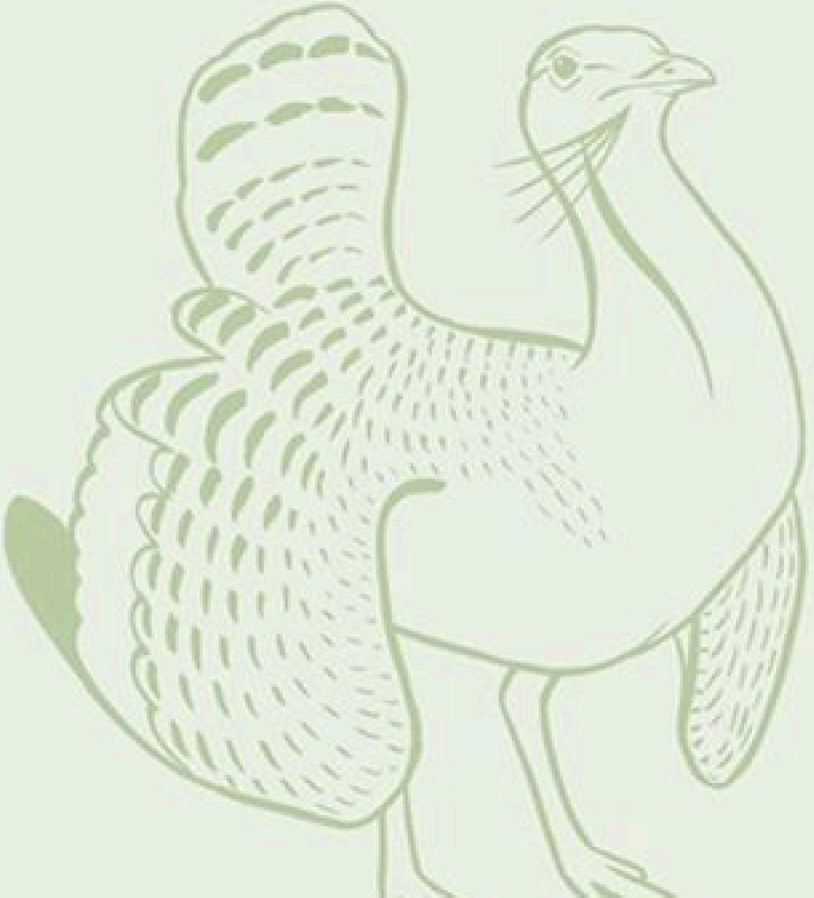

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Review of the development of the Peregrine Falcon *(Falco peregrinus)* population in Hungary between 1997 and 2018

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Abstract Peregrine Falcon *(Falco peregrinus)* populations recovered globally after a dramatic decline experienced between the 1950s and 1980s. The conservation challenge forced the raptor biologist community to co-operate internationally. As a part of the co-operation, four conferences were organised to identify the problem, coordinate conservation efforts including research and to monitor the recovery process of the species' populations worldwide. The line of conferences started in Madison (WI, USA) in 1965 and was followed by two conferences in Sacramento (CA, USA) and Piotrowo/Poznań (Poland) in 1985 and in 2007, respectively. The latest conference was organised in 2017, in Budapest, where Peregrine experts discussed the latest research and monitoring results. The event provides a good occasion to review the development of the Peregrine population in Hungary. The species became extinct in Hungary as a breeding species in the mid-1960s due to the intensive use of pesticides (DDT) and it returned only in 1997, when the first successful breeding was recorded. In 2018, 72 active eyries were recorded. The Hungarian population is the edge of the Carpathian Peregrine population and the birds represent mostly the nominate subspecies *(F. p. peregrinus)*, but individuals showing typical phenotype of the Mediterranean subspecies *(F. p. brookei)* were also observed. The northern race of *F. p. calidus* also occurs on migration and in winter. The Hungarian population is sedentary. Natal dispersal of females is biased to males, but in case of both sexes most ring recoveries of adult birds occurred within the Pannonian basin. The increasing Peregrine population expanding to the lowland may cause conservation conflict on medium term by competing with the endangered Saker Falcon *(Falco cherrug)* for the nest sites. The conservation status of the Peregrine Falcon in Hungary is good in general, but threats may emerge on local scale in some regions. No specific conservation measures are taken, research and monitoring focus on population changes and threats posed on and caused by Peregrines.

Keywords: population recovery, subspecies, diet, movements, *Falco cherrug*

Összefoglalás Az 1950-es és az 1980-as évek közötti időszakban tapasztalt összeomlás után a vándorsólyom *(Falco peregrinus)* világszerte regenerálódott. A természetvédelmi kihívás nemzetközi összefogást kényszerített ki a ragadozómadarakkal foglalkozó biológusok között. Ennek az összefogásnak a részeként négy konferencia került megrendezésre a probléma feltárásának, a kutatások és a védelmi erőfeszítések összefogásának, valamint az állományok regenerációjának világszerte történő nyomon követésének érdekében. A konferenciasorozatban az első az 1965-ös madisoni (Wisconsin állam, USA) konferencia volt, amelyet két konferencia követett Sacramentoban (Kalifornia) és Pietrowo/Poznańban (Lengyelország), 1985-ben és 2007-ben. A sorozat legutóbbi konferenciája 2017-ben Budapesten került megrendezésre, ahol a vándorsólyommal foglalkozó szakemberek megvitathatták a legfrissebb kutatási és monitoring eredményeket. Az esemény jó alkalmat kínált arra, hogy áttekintsük a vándorsólyom állományának változását Magyarországon. Mint fészkelő faj kipusztult Magyarországról a hatvanas évek közepén, az intenzív növényvédőszer-használatnak (DDT) köszönhetően, és csak 1997-ben tért vissza. Akkor figyelték meg ismét sikeres fészkelését az országban. 2018-ban 72 aktív revírt ismerünk. A magyar állomány a Kárpátokban fészkelő állomány peremének tekinthető, és túlnyomórészt a törzsalakhoz *(F. p. peregrinus)* tartozik. Megfigyeltek azonban fészkelésben a mediterrán alfajhoz *(F. p. brookei)* tartozó egyedeket is. Az északi alfaj *F. p. calidus* is előfordul vonuláskor, illetve télen. A magyar költőállomány állandó. A diszperzió a tojóknál nagyobb, mint a hímeknél, de mindkét ivar esetében az ivarérett madarak gyűrűzési megkerülései túlnyomórészt a Kárpát-medence területéről származnak. A növekvő és az alföldi területek felé terjeszkedő vándorsólyom állomány természetvédelmi problémát jelenthet középtávon, amennyiben a veszélyeztetett kerecsensólyom *(Falco cherrug)* fészekkompetítora lesz. A vándorsólyom természetvédelmi helyzete Magyarországon általában jó, de helyi szinten merülhetnek fel problémák bizonyos régiókban. Nincs szükség specifikus védelmi intézkedésre. A kutatás és a monitoring az állomány változásait, valamint a veszélyt jelentő tényezőket vizsgálja. Emellett figyelmet szentel a vándorsólyom által okozott problémáknak is.

Kulcsszavak: állománynövekedés, alfaj, táplálék, elmozdulások, *Falco cherrug*

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Introduction

The recovery of the Peregrine Falcon is a conservation success story: during a few decades the global – more accurately Eurasian and North American – population recovered beyond any expectation. The species' population came back from a devastating decline caused by DDT and other pesticides in the early 2nd half of the 20th century. The road to success, however required international cooperation, which can be best characterized by the four conferences dedicated to the species. The conference held in Madison, Wisconsin, U.S. in 1965 aimed to unveil the possible causes of the disastrous population decline in North America and Europe. The international effort was successful and the so far widely used DDT has been banned in most countries in the world. Three other conferences followed the historic Madison Conference: in Sacramento, USA (1985), in Piatrowo/Poznań, Poland (2007) and in Budapest, Hungary (2017). They summarized the latest knowledge on the species including follow-up of the recovery process, monitoring populations, describing behaviour, introducing new challenges in conservation and proposing conservation management methods.

The last conference confirmed again that the species has well recovered, and the population has been stable or grown even in the last ten years (Beran *et al.* 2018, Brunelli & Saccoro 2018, Zuberogoitia *et al.* 2018). Apart from natural expansion to ancient nesting sites, re-introduction programmes aim to bring back the tree-nesting populations in the plains of Poland (Sielicki & Sielicki 2017) and Russia (Pazhenkov *et al.* 2018). In other cases, populations are stable (Pasquier *et al.* 2018) or follow the changes of distribution patterns of prey species (Nygård & Reinsborg 2017). In some parts of the European distribution range, however, the recovery process was followed recently by a decline (Kéry *et al.* 2018, Monneret *et al.* 2018).

The rapidly growing, viable Peregrine populations may also cause conflicts with other species as they occupy new habitats (Prommer *et al.* 2017, De Rosa *et al.* 2018) and outcompete other large falcons of which diet spectre narrowed down to avian prey (Bondì *et al.* 2017). Of course, conservation problems were also at stake like deliberate poisoning (Inderwildi *et al.* 2018).

The Budapest Peregrine conference gave us the possibility to summarize also the information about the Hungarian population with special regard on the period since the last internationally published article (Bagyura *et al.* 2009, Prommer 2009).

Dynamics of Peregrine Falcon population in Hungary

Monitoring of falcon populations started in the late 10th century when the first Hungarian tribes – practicing falconry – arrived in the Carpathian Basin. Names of geographic locations, cliffs, settlements, medieval poems and trading agreements prove the importance of falcons up to the Modern History (Csőre 1996). Traditional hunting methods like falconry became outdated with the spread of firearms and instead of allies, hunters started to see competitors in birds of prey, which resulted in a long-lasting persecution of raptors. As a result, only a fragment of the original raptor populations remained in Hungary and even them withdrew into the hills and mountains, where large game keepers were uninterested in them. It was only in 1949–1950, when Pátkai and Bástyai carried out a countrywide survey, where they found only 18 Peregrine Falcon eyries in Hungary (Pátkai 1951). DDT, however, took its toll also in Hungary and the last recorded successful breeding was in 1964, when nestlings were removed from the nest to be taken to the Budapest Zoo and Saker Falcons *(Falco cherrug)* occupied the empty Peregrine eyries (Bagyura *et al.* 2009, Prommer *et al.* 2009).

Through 33 years, Peregrine was absent from Hungary as a breeding species. From the early 1990s' observations, Peregrines became more frequent and finally the first breeding took place in Pilis-Visegrádi Hills in 1997: the Peregrine Falcon returned to Hungary (Bagyura 1997). They have gradually taken back the ancient eyries in the hills and mountains. The number of Peregrine pairs remained low in the first ten years, but in 2007 the population started to grow rapidly, and increased to sixfold by 2017 from 12 (2007) to 72 (2018) occupying pairs *(Figure 1)*, but the population growth slowed down in 2015. The recovery process was similar to the recovery of Peregrine populations for example in the Czech Republic (Beran *et al.* 2018) or in Denmark (Andreasen *et al.* 2018). The reasons of decreasing growth rate of the Hungarian population is not exactly known. One possible reason is

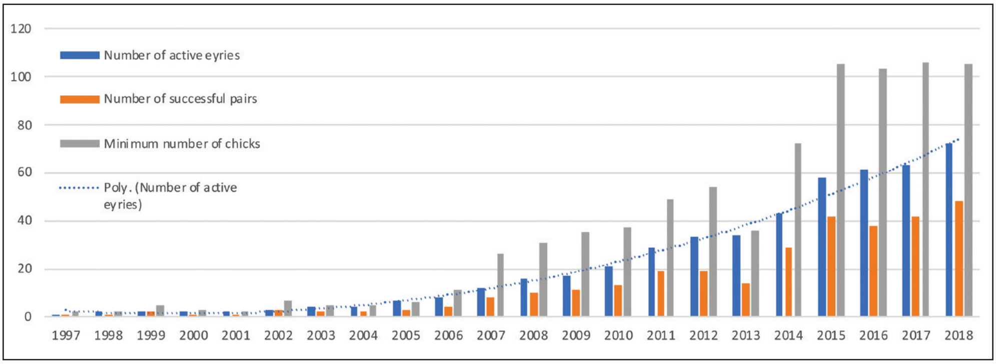

Figure 1. The dynamics of Peregrine Falcon population in Hungary between 1997–2018
1. ábra A magyarországi vándorsólyom-állomány változása 1997 és 2018 között

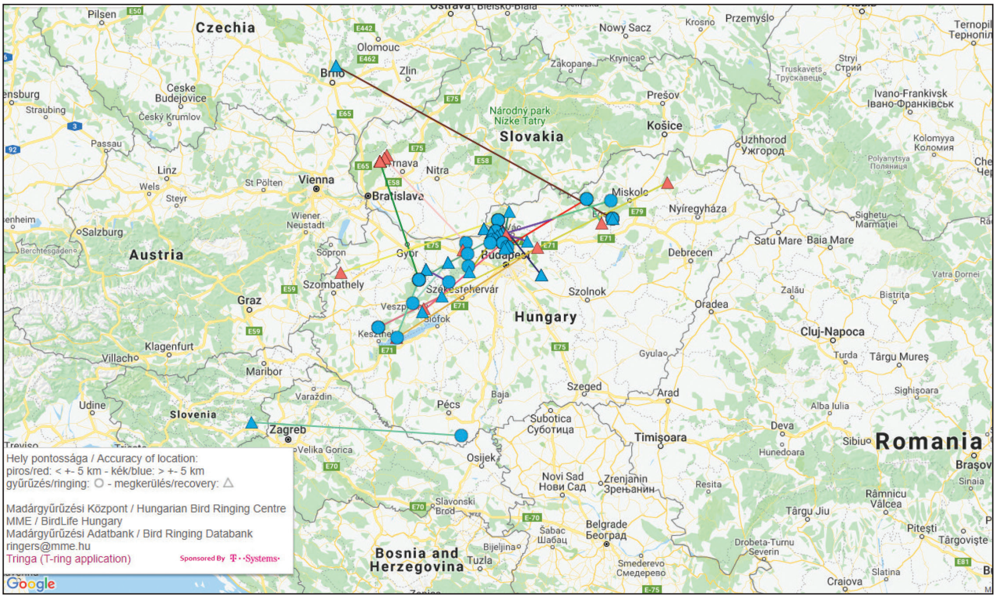

Figure 2. Ring recoveries of Hungarian-ringed (breeding adult – triangles, pullus – dots) Peregrine Falcons

2. ábra A Magyarországon fiókaként gyűrűzött (kör) és költésben megkerült (háromszög) vándorsólymok megkerülései

that Hungary is not very rich in natural cliffs and quarries, and the best quality ones have already been taken by Peregrines or Eagle Owls *(Bubo bubo)*. It can also be an indication of a population decline in the coming years as it occurred in Northern Spain (Zuberogoitia *et al.* 2018), in Switzerland (Kéry *et al.* 2018) and in France (Monneret *et al.* 2018).

The bulk of the Hungarian population distributed across the Transdanubian and Northern Hills represents the *F. peregrinus peregrinus* subspecies and can be considered as the edge of the Carpathian population (Slovakia) as ring recoveries proved *(Figure 2)*. We suspect however, that in South and West Hungary, individuals belonging to *F. peregrinus brookei* may also occur (Bagyura *et al.* 2008). It is likely that Hungary falls in the range where the two subspecies mix, similarly to northern Spain, where typical *F. p. peregrinus* and *F. p. brookei*, as well as many forms of intermediate phenotypes can be observed in a few hundred kilometre broad zone (Zuberogoitia *et al.* 2009). Genetic analyses also confirm and explains phenotypical diversity in those zones (Mengoni *et al.* 2018).

Habitats

Peregrines do not build their own nest but occupy nests of other species or they simply lay their eggs on ledges of cliffs. In addition to natural cliffs and rock formations, they occupy also abandoned or operating quarries. They prefer nest sites close to open areas like large water bodies or arable land, and they need forested areas hosting breeding passerine species.

According to their preferences, Peregrines can be found mostly in hills and mountainous areas in Hungary. As the population expanded however, new pairs appeared also on the edges of the Hungarian plains, in new habitats, where Peregrines were not present earlier as breeding species. They learnt to use nest boxes on pylons of high voltage power lines installed for Saker Falcons (Prommer & Bagyura 2017). We closely monitor all pairs breeding on pylons by using camera traps to identify any colour ringed individuals. Photos of camera traps showed that in all pairs there is at least one colour-ringed individuals fledged from cliff nests in Hungary. That shows a high plasticity of the species in choosing nest site. In 2018, there were seven known pairs on pylons and five of them bred successfully fledging thirteen juveniles.

The next phase of population growth is expected when Peregrines start to occupy cities in Hungary. Unlike in most European and North American cities, there are no record of Peregrine breeding in Budapest or in any other Hungarian city. The first city breeding Peregrines are expected to settle in Budapest, considering available food, nesting possibilities, as well as the dense Peregrine population in its neighbourhood. The Hungarian capital alone could host a minimum of 3-4 breeding pairs. Other cities close to areas with saturated Peregrine populations are potential areas of expansion. Wintering falcons regularly use cities, proving that the habitat can maintain falcons, thus we could expect that Peregrine will inhabit cities. At the same time, wintering falcons – staying in Hungary as long as untill April – may prevent local Peregrines to occupy the best quality habitats in cities in late winter – early spring and form new pairs. The interactions between the two populations still unknown and require more research.

Migrating and wintering Peregrines form a separate population in Hungary (Prommer 2005, Prommer *et al.* 2009). Satellite-tracking studies (Dixon *et al.* 2012, Sokolov *et al.* 2018, Váczi unpubl.) suggest that Peregrines migrating across and wintering in Hungary originate from northwest Russia. A few observations (Bagyura pers. comm.) indicate that the subspecies *F. p. calidus* also may occur in Hungary in the migration and wintering period. Observations on Peregrines (birding.hu) show a double-peak – autumn and spring – distribution, which signals that a larger number of birds migrate across Hungary. A number of "foreign" individuals, however winter in larger cities of Hungary using high building, cathedrals, churches and towers, as well as industrial complexes, as perch sites. Almost all city wintering birds are females and they usually remain until late spring (April).

Migration and other movements

According to observations and ring recoveries, most of the breeding pairs are sedentary and stay in their eyries through all year; or move to an area with abundant prey in the vicinity of the nest site. That movement can be best described as short distance altitudinal 'migration' and it covers the movement of the Peregrines descending from the hills (nest site) to foothills or plains (foraging site) within a few kilometres.

Juveniles usually roam across the Pannonian basin and they even may cross the Carpathians *(Figure 3)* as satellite tracking data (Prommer *et al.* 2009) and ring recoveries show.

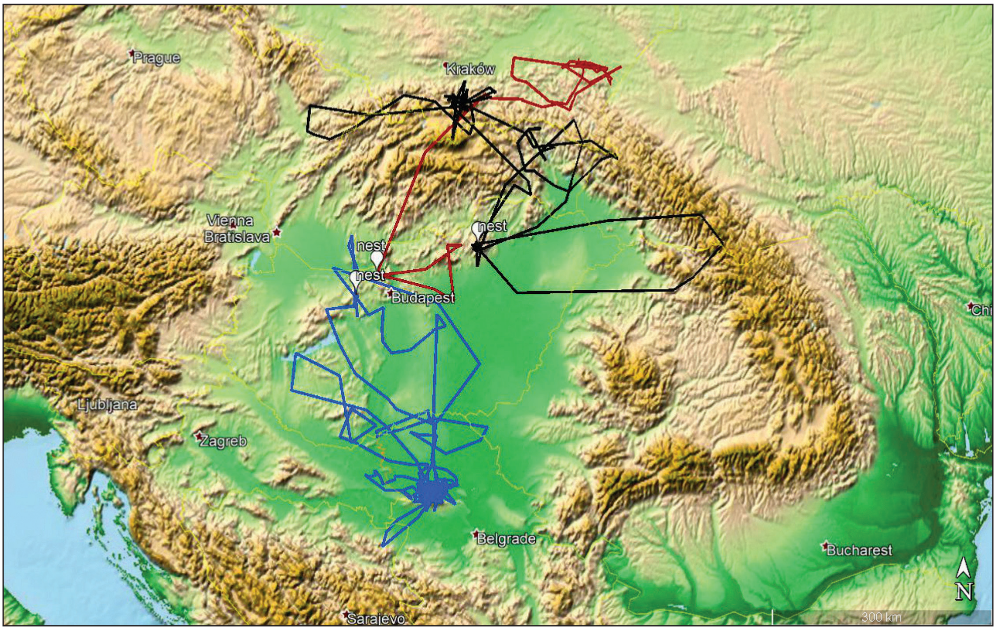

Figure 3. Movements of three satellite tracked juveniles tagged in nest before fledging (2009–2010)
3. ábra Három, kirepülés előtt fészekben jelölt fiatal vándorsólyom mozgásai (2009–2010)

Natal dispersal follows the well-known pattern (Greenwood 1980, Clarke *et al.* 1997, Faccio *et al.* 2013) and males settle closer to the fledging site than females. The values are 177.9 km for males (n = 23) and 212.9 km for females (n = 19) based on the ring recoveries of breeding adults ringed in Hungary (source: Hungarian Bird Ringing Centre). Females of Hungarian origin were identified at nests by their colour rings in Slovakia (3), the Czech Republic (1) and Slovenia (1). Ring recoveries of breeding males restricted so far to Hungary.

Diet

Prey species in Peregrines' diet in the breeding season were identified from remains collected in nests and on photos taken by camera traps set on active nests. Despite the fact that Peregrines take avian prey almost exclusively, their diet is diverse, and many bird species can be found in the species list (Ratcliffe 1993, Rockenbauch 1998). The absolute favourite prey is the Feral Pigeon *(Columba livia f. domestica)*, followed by Starling *(Sturnus vulgaris)* and Hawfinch *(Coccothraustes coccothraustes)*. The presence of latter in the diet however, noticeably decreased in the last few years. Apart from those species, remains of Great Woodpeckers *(Dendrocopos major)*, Green Woodpeckers *(Picus viridis)*, Grey-headed Woodpeckers *(Picus canus)*, Blackbirds *(Turdus merula)* can be regularly seen in nests, but sometimes rarities like Golden Oriole *(Oriolus oriolus)* or even escapees like Budgerigar *(Melopsittacus undulatus)* were found. Apart from birds, a bat species, the Common Noctule *(Nyctalus noctula)* were also relatively common prey. Unsurprisingly, forest-dwelling species dominate the list beside pigeons, which reflects the habitats, in which most Peregrines nests can be found. The prey list is certainly longer, however, no species list is available on preys of Hungarian Peregrines caught outside of the breeding season. In comparison, a northern Peregrine wintering through eleven years in Hungary lists 34 prey species (Kocsis & Prommer 2017). An important difference in diet between local and northern, wintering Peregrines that in the diet of latter wetland birds – waders and waterfowl – can be found in higher proportion (Prommer *et al.* 2009). The difference resulted from the different habitat they use: wintering birds usually establish their wintering eyries near or in wetland areas, where local birds are more tied to hills and forests. As opportunistic predators, Peregrines use available food sources highly efficiently, as recent studies suggest (Dixon & Drewitt 2018, Dixon *et al.* 2018).

Threats

We found sharpened wires twisted around pigeons' legs in Peregrine nests signalling someone's intention to kill birds of prey. Several sources also confirmed that some pigeon-fanciers use illegal methods to kill Peregrines and other birds of prey hunting on pigeons. A differentiation must be made between Homing Pigeons and high-flyers. Homing Pigeons are being released in large numbers when training or in competition and Peregrines, Saker Falcons, Goshawks *(Accipiter gentilis)* and Sparrowhawk *(Accipiter nisus)* target them. High-flyers, however, have been bred for flying circles in close flocks high above their home and remain up in the air for long time. Ideal targets for Peregrines. While most of the raptor attacks on Homing Pigeons remains unseen for obvious reasons, attacks on high-flyers are regularly seen by breeders inducing strong emotional reactions. It must be noted, however, that the main problem of breeders is not the loss of a pigeon, but that Peregrines spoil the competition, in which they invested considerable money, because the flock disintegrates, and the pigeons land much earlier than they suppose to. As Peregrine population evolved, pigeon-fanciers ceased breeding high-flyers in some parts of Hungary. In other areas, they still use illegal methods to eliminate falcons attacking their flocks (Inderwildi *et al.* 2018).

Accidental or deliberate human disturbance is a major threat on breeding success. As Hungary does not have many cliffs, the few ones are tourist destinations with a visitors' peak in spring. Established pairs are usually very tolerant, but volunteer nest guarding is organised for the most sensitive sites.

Illegal take of chicks from nest are officially recorded only in 2018, when a camera trap set on a nest recorded a man climbing down to the nest and taking away two nestlings. Indirect signs however, suggested that similar actions were done at other nests as well in the previous years.

Electrocution and collision to wires or buildings must be also counted as a threat on Peregrines, which affects mostly the inexperienced juvenile birds.

Every year one or two juvenile Peregrines are reported to be caught in pigeon houses or in the loft. They followed the pigeons there and could not make their way out. The real number is probably higher and not all the birds survive the mistake they made.

Conservation and research

The Peregrine population in Hungary is growing and also considering international trends, no extra conservation measures are necessary apart from local measures to protect endangered breeding. We do annual monitoring of recent and former breeding sites, we follow the changes in the population, ring and colour ring the chicks, install camera traps on nests, make problematic nest sites safe and organise nest guarding where it is necessary.

We closely follow the evolution of pylon-nesting pairs especially that those type of population expansion may conflict the Saker Falcon conservation interests.

Public awareness raising is also part of the work, e.g. Peregrine Falcon was the "*Bird of the Year*" in 2018 and the species was highlighted in the media.

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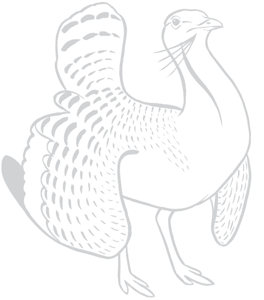

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Genetic variability in Peregrine Falcon populations of the Western Palaearctic region

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Abstract We analysed variation in ten polymorphic microsatellite loci and a portion of cytochrome b gene of mitochondrial DNA in 65 samples from four populations of Peregrine Falcon (*Falco peregrinus peregrinus* and *F. p. brookei*) breeding in Northern and Southern Italy, Northern Spain and the Czech Republic to assess genetic diversity in the poorly investigated Western Palearctic region. We added to our cytochrome b sequences a dataset of previously published mtDNA sequences of other populations and subspecies to outline genetic variation in the region on a worldwide basis. Regarding mtDNA we identified 12 haplotypes from our 65 Peregrine Falcon samples, nine of which were new and three already known. The 52% of our samples, including all Italian and Czech specimens, belonged to the previously identified HI haplotype, another 22% of the samples, most of which were from Sicily, showed the new H1 haplotype, while the remaining 26% of the sample partitioned among the other 10 haplotypes. Allelic patterns and genetic structuring of microsatellites were similar to those of other European populations. Genetic differentiation in both mtDNA and microsatellites loci is almost absent and it is not possible to distinguish geographical groups according to taxonomic designation at the subspecies level.

Keywords: Genetic structuring, *Falco peregrinus brookei,* microsatellites, mitochondrial DNA, Peregrine Falcon

Összefoglalás A kevéssé kutatott Nyugat-Palearktikus régióban vizsgáltuk a vándorsólyom két alfajába (*Falco peregrinus peregrinus* and *F. p. brookei*) tartozó négy populáció (Észak-, és Dél-Olaszország, Észak-Spanyolország, Cseh Köztársaság) genetikai diverzitását. Ehhez tíz mikroszatellit lókusz variabilitását és a mitokondriális DNS citokróm b génjének szekvenciáit elemeztük 65 mintában, négy populációból, melyek az észak-és dél-olaszországi, az észak-spanyol és a cseh populációkból származtak. Az általunk szekvenált citokróm b szekvenciákat együtt elemeztük a már korábban publikált más populációk és alfajok szekvenciáival, hogy a genetikai diverzitást a teljes elterjedési területen tudjuk vizsgálni. A saját 65 vándorsólyom mintákból 12 haplotípust azonosítottunk, melyek közül kilenc volt új és három már ismert. A mintáink 52%-a, beleértve az összes olaszországi és csehországi egyedet, a már korábban publikált HI haplotípusba tartozott, a minták egy másik 22%-a, amik főleg Szicíliából származtak, az új H1 haplotípusba, míg a maradék 26% megoszlott a többi 10 haplotípus között. A mikroszatelliták vizsgálata alapján találtunk különbségeket az allélek megoszlásában, így van egyfajta genetikai mintázat más európai populációkkal összehasonlítva, ennek ellenére sem a mikroszatellit lókuszok, sem pedig a mitokondriális DNS alapján nem lehet egyértelmű földrajzi csoportokat elkülöníteni a taxonómiai besorolás szerinti alfaji szinten.

Kulcsszavak: genetikai térképezés, *Falco peregrinus brookei,* mikroszatelliták, mitokondriális DNS, vándorsólyom

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Introduction

The Peregrine Falcon *(Falco peregrinus)* is a nearly-cosmopolitan species with a large phenotypic variability, currently described in 19 subspecies across the world (White *et al*. 2013a). After a massive decline and several regional extinctions in the second half of the 20th century, the ban of organochlorine pesticides coupled with greater protection, reintroduction programmes and restrictions of illegal trading have stopped the species' decline and have boosted up the Peregrine Falcon populations of the Northern Hemisphere (Cade *et al*. 1988, White *et al*. 2013a).

The use of molecular markers that can be easily amplified by polymerase chain reaction (PCR) and then sequenced is nowadays a widespread tool for the reconstruction of phylogenetic relationships among avian taxa (Sibley 1994). The nucleotide sequence of the mitochondrial cytochrome b gene was one of the first markers used in this field, and original contributes related to the phylogeny of Peregrine Falcon and its allied species in the Falconiformes group have been reported in Helbig *et al.* (1994) and Wink *et al*. (1998, 2000). Microsatellites, referred to as tandem repeats of short DNA sequences, are genetic markers that show a high level of variation and have been employed for studying avian population structure and systematics (Ellegren 1992, Bruford & Wayne 1993, Nesje *et al*. 2000a). Actually, there are available several developed microsatellite markers specifically for the Scandinavian Peregrine Falcons, which were used to compare the population structure and genetic variability of *F. p. peregrinus* populations breeding in north Europe with some subspecies present in North America and Tasmania (Nesje *et al*. 2000b).

Molecular analyses of variable microsatellite markers and mitochondrial DNA supported the conservation actions taken in North Europe and North America (Nesje *et al*. 2000a, Tordoff & Reding 2001, Jacobsen *et al*. 2008, Johnson *et al*. 2010, Ponnikas *et al*. 2017), and the investigation of the genetic relationships among many subspecies, including some of remote oceanic islands (Nesje *et al*. 2000b, Talbot *et al*. 2011, White *et al*. 2013b, Bell *et al*. 2014). In Mediterranean areas of Western Palaearctic region, corresponding to most of *F. p. brookei* range, the past population collapse was less extended. For instance, both in Italy (Schenk *et al*. 1985, Allavena & Brunelli 2003) and Spain (Gainzarain *et al*. 2002) large populations (826–1048 breeding pairs in Italy, and 2384–2690 in Spain) fluctuated or increased locally and were threatened mostly by nest despoliation for illegal trading of eggs and chicks, and direct human persecution. As consequence, population structure and genetic variability of Peregrine Falcons living in these areas were poorly investigated. In this study, we characterize the genetic composition and structure of four populations breeding in North and South Italy, North Spain and the Czech Republic by using ten polymorphic microsatellites and a portion of cytochrome b gene of mitochondrial DNA. The Spanish population breeds in the *F. p.*

brookei/F. p. peregrinus contact zone (Zuberogoitia *et al*. 2009), both the North Italian and the Czech populations breed within the *F. p. peregrinus* range, while the South Italian breeds within the *F. p. brookei* range (Bryndová *et al*. 2012, White *et al*. 2013a).

Material and Methods

We genotyped quills of nuchal feathers (e.g. Horváth *et al.* 2005) and muscle tissues of documented nest-site origin coming from 65 specimens: 9 from Northern Spain (Biscay), 8 from the Czech Republic, 5 from Northern Italy (Piedmont and Emilia), and 43 from Southern Italy (1 from Campania, continental Italy; 42 from the island of Sicily). One nestling from each nest site was used *(Table 1).* Feather samples were obtained from wild nestlings (Spain, Sicily, and the Czech Republic), while muscle tissues came from adult individuals found dead in different and well separated localities of North and continental Southern Italy. The sample from the Czech Republic is a subsample of wild Peregrine Falcons DNA already used in Bryndová *et al.* (2012).

We used ZR Genomic DNA II Kit™ for solid/liquid samples (Zymo Research) to extract and purify genomic DNA from samples. DNA samples were genotyped across 10 microsatellite markers originally designed for *Falco peregrinus* (Nesjie *et al.* 2000a): Fp13, Fp31, Fp46_1, Fp54, Fp79_4, Fp86_2, Fp89, Fp92_1, Fp107; and for *Accipiter gentilis* (Topinka & May 2004): Age5. We carried out two independent PCR replicates to check the absence of Allelic Drop Out (ADO) or false alleles (FA). Furthermore, we amplified and sequenced a 960 bp long fragment of cytochrome b gene in mtDNA using a combinations of primer pairs (L14841-H15149, L15132-H15516, L15489-H15915) according to protocols described in Bell *et al*. (2014), to which refer for further details. In both cases we used the following PCR protocol: a first denaturation step at 94 °C for 3 min; 35 cycles at 94 °C for 40 s, 55 °C for 40 s, 72 °C for 40 s; and a final step at 60 °C for 30 min. PCR products were then processed in an ABI 3130XL sequencer. We used Genalex 6.1 (Peakall & Smouse 2006) to estimate the allele frequencies by locus and population, mean number of alleles per locus (NA), observed (H_o) and expected unbiased (UH_e) heterozygosity and the related chi-square test for deviations from Hardy-Weinberg equilibrium (HWE). Pairwise F_{ST} (Weir & Cockerham 1984), which is a measure of among-population variance in allelic frequencies, and principal coordinate analysis (PCoA), which gives an ordination of all data points based on a covariance matrix with microsatellite data standardization, were calculated using GENETIX 4.05 (Belkhir *et al.* 1996–2004) and FSTAT (Goudet 2001). We aligned the mtDNA sequences of our samples together with 17 haplotype sequences of *F. peregrinus*, and one Sharp-shinned Hawk *(Accipiter striatus)* sequence retrieved from GenBank and published by Bell *et al.* (2014). The latter was used as outgroup as in Bell *et al.* (2014). We aligned the mtDNA sequences with Bioedit (Hall 1999), then we identified the haplotypes using Dnasp 5 (Librado & Rosas *al.* 2009). We clustered a Tamura and Nei genetic distance matrix using the neighbour-joining procedure in Mega 5 (Tamura *et al.* 2011) with internode bootstrap values determined after 1000 resampling steps. Eventually, we reconstructed the phylogenetic relationships among the mtDNA haplotypes using median-joining networks in Network 4.6 (Bandelt *et al.* 1999).

Table 1. List of specimens considered in the study of genetic diversity of the Western Palaearctic Peregrine Falcons. Sample: MU = muscle tissue, FE = feather; mtDNA haplotypes HE (GeneBank Accession No. KP863007), HI (KP863006) and HL (KP863014) described in Bell *et al*. 2014, while haplotypes H1-H9 found in the present study (MH837632-MH837640)

1. táblázat A vándorsólyom egyedek táblázata, amelyek mintáit használtuk a genetikai diverzitás felmérésére a nyugat-paleakrtikusi elterjedési területen. Sample: MU = izomszövet, FE = toll; Bell *et al.* (2014) által publikált mtDNS haplotípusok: HE, HI és HL, ebben a vizsgálatban talált új haplotípusok: H1-H9

Id Lab	Taxon	Area	Region	Sampling year	Sex	Age	Sample	Mt DNA haplotype
FPE62	*F. p. brookei*	South Italy	Campania	2005	M	NA	MU	HI
FPE63	*F. p. brookei*	North Italy	Emilia	2010	M	NA	MU	HI
FPE66	*F. p. peregrinus*	North Italy	Piedmont	2012	M	SAD	MU	HI
FPE69	*F. p. peregrinus*	North Italy	Piedmont	2007	M	JUV	MU	HI
FPE71	*F. p. peregrinus*	North Italy	Piedmont	2010	F	AD	MU	HI
FPE72	*F. p. peregrinus*	North Italy	Piedmont	2010	M	NA	MU	HI
FPE76	*F. p. peregrinus*	Czech Republic	Central	2011	M	JUV	FE	HI
FPE77	*F. p. peregrinus*	Czech Republic	Central	2011	F	JUV	FE	HI
FPE78	*F. p. peregrinus*	Czech Republic	Ústí nad Labem	2010	M	JUV	FE	HI
FPE79	*F. p. peregrinus*	Czech Republic	Central	2011	F	JUV	FE	HI
FPE80	*F. p. peregrinus*	Czech Republic	Hradec Králové	2011	F	JUV	FE	HI
FPE81	*F. p. peregrinus*	Czech Republic	Central	2010	M	JUV	FE	HI
FPE83	*F. p. peregrinus*	Czech Republic	Ústí nad Labem	2010	F	JUV	FE	HI
FPE85	*F. p. peregrinus*	Czech Republic	Central	2011	F	JUV	FE	HI
FBI19	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	H1
FBI6	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	HI
FBI7	*F. p. brookei*	South Italy	Sicily	2017	M	SAD	FE	H1
FPE1	*F. p. brookei*	South Italy	Sicily	2017	F	JUV	FE	H1
FPE102	*F. p. brookei*	South Italy	Sicily	2017	F	JUV	FE	H1
FPE105	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	H1
FPE13	*F. p. brookei*	South Italy	Sicily	2016	M	JUV	FE	H6
FPE15	*F. p. brookei*	South Italy	Sicily	2016	M	JUV	FE	H1
FPE16	*F. p. brookei*	South Italy	Sicily	2016	F	JUV	FE	HE
FPE20	*F. p. brookei*	South Italy	Sicily	2016	M	AD+	FE	H7
FPE47	*F. p. brookei*	South Italy	Sicily	2017	M	AD+	FE	HI
FPE48	*F. p. brookei*	South Italy	Sicily	2017	F	SAD	FE	HL
FPE49	*F. p. brookei*	South Italy	Sicily	2017	M	AD+	FE	HI
FPE5	*F. p. brookei*	South Italy	Sicily	2016	F	JUV	FE	H3
FPE50	*F. p. brookei*	South Italy	Sicily	2017	F	AD+	FE	HI

Id Lab	Taxon	Area	Region	Sampling year	Sex	Age	Sample	Mt DNA haplotype
FPE51	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	HE
FPE52	*F. p. brookei*	South Italy	Sicily	2017	F	SAD	FE	HL
FPE53	*F. p. brookei*	South Italy	Sicily	2017	F	SAD	FE	H4
FPE54	*F. p. brookei*	South Italy	Sicily	2017	F	JUV	FE	HL
FPE55	*F. p. brookei*	South Italy	Sicily	2017	M	SAD	FE	HI
FPE56	*F. p. brookei*	South Italy	Sicily	2017	F	JUV	FE	H8
FPE57	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	HI
FPE58	*F. p. brookei*	South Italy	Sicily	2017	M	SAD	FE	H5
FPE59	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	HI
FPE6	*F. p. brookei*	South Italy	Sicily	2016	F	JUV	FE	HI
FPE60	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	H1
FPE61	*F. p. brookei*	South Italy	Sicily	2016	M	JUV	FE	H9
FPE64	*F. p. brookei*	South Italy	Sicily	2016	F	AD+	FE	HI
FPE65	*F. p. brookei*	South Italy	Sicily	2016	F	JUV	FE	H9
FPE67	*F. p. brookei*	South Italy	Sicily	2005	F	AD+	FE	HI
FPE68	*F. p. brookei*	South Italy	Sicily	2005	F	–	FE	H1
FPE70	*F. p. brookei*	South Italy	Sicily	2017	F	SAD	FE	HI
FPE74	*F. p. brookei*	South Italy	Sicily	2016	M	SAD	FE	H1
FPE75	*F. p. brookei*	South Italy	Sicily	2017	F	JUV	FE	HI
FPE86	*F. p. brookei*	South Italy	Sicily	2017	F	JUV	FE	HI
FPE88	*F. p. brookei*	South Italy	Sicily	2017	–	JUV	FE	H1
FPE89	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	H1
FPE9	*F. p. brookei*	South Italy	Sicily	2016	M	JUV	FE	H1
FPE94	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	H6
FPE96	*F. p. brookei*	South Italy	Sicily	2017	M	JUV	FE	H1
FPE98	*F. p. brookei*	South Italy	Sicily	2017	F	JUV	FE	HI
FPE99	*F. p. brookei*	South Italy	Sicily	2017	F	JUV	FE	H1
FPE21	*F. p. brookei*	Spain	Biscay	2016	F	JUV	FE	HI
FPE25	*F. p. brookei*	Spain	Biscay	2016	M	JUV	FE	HI
FPE27	*F. p. brookei*	Spain	Biscay	2016	M	JUV	FE	HI
FPE30	*F. p. brookei*	Spain	Biscay	2016	F	JUV	FE	HI
FPE32	*F. p. brookei*	Spain	Biscay	2016	F	JUV	FE	HE
FPE33	*F. p. brookei*	Spain	Biscay	2016	F	JUV	FE	HE
FPE35	*F. p. brookei*	Spain	Biscay	2016	M	JUV	FE	HI
FPE37	*F. p. brookei*	Spain	Biscay	2016	F	JUV	FE	HI
FPE41	*F. p. brookei*	Spain	Biscay	2016	M	JUV	FE	H2

Results

Mitochondrial DNA

The analysis of the four populations of Peregrine Falcons revealed a low inter-population genetic variability between the considered subspecies (*peregrinus* and *brookei*), albeit an insular effect can be observed based on the genetic pattern of Sicilian population. We identified 12 haplotypes from the 65 Peregrine Falcon samples, nine of which were new haplotypes found for the first time and coded from H1 to H9, while the other three have been already described by Bell *et al*. (2014) *(Table 1)*. The 52% of our samples (n = 34) belonged to the previously published HI haplotype, and another 22% (n = 14) of the samples showed the new H1 haplotype, while the remaining 26% of the samples partitioned among the other 10 haplotypes. Both the whole Italian and the Czech samples belonged to the HI haplotype, while the Spanish Peregrine Falcons split up among two Bell's haplotypes HI (n = 6) and HE (n = 2), and one new H2 haplotype (n = 1). The Sicilian Peregrine Falcons showed the largest haplotype diversity as the 42 individuals split up among Bell's and new haplotypes unique for this population. The already identified Bell's haplotypes found in Sicily are: HI (n = 14), HL (n = 3) and HE (n = 2), whereas the new ones are: H1 (n = 14) and from H3 to H9, all these latter with n = 1, but H6 and H9 with n = 2 individuals.

The neighbour-joining network of the haplotypes found in a 960 bp fragment of cyt b mtDNA gene and considered in this study *(Figure 1)* reproduces the large heterogeneity between the geographic origin and the taxonomic designation of Peregrine Falcons. For instance, haplotype HI, the most shared among individuals, occurs across Canada *(tundrius)* and Europe *(peregrinus, brookei)*. Yet, in our sample this haplotype assembles Sicilian and South Italian Peregrines expected to be *brookei*, together with Spanish specimens from the *brookei/peregrinus* border zone of Biscay, plus two more Spanish *brookei* samples present in Bell *et al*. (2014). Such a *brookei* group of samples anyway cluster with North Italian and Czech Republic individuals expected to belong to the nominate subspecies *peregrinus*. 14 Sicilian samples were grouped in the new haplotype H1, which indeed was the second in order of frequency among the found haplotypes. Third in order of frequency comes the haplotype HQ, which is separated by one mutational step from H1, and is definitely the most cosmopolitan one, as groups together some Sicilian and Biscay Peregrine Falcons with the Australian *(macropus)*, the Argentinian *(cassini)*, the American *(tundrius, anatum)*, the African *(minor)* and others subspecies with unknown geographic origin *(babilonycus*, *pelegrinoides)*.

Microsatellites

The genetic intra-population diversity based on microsatellite analysis of 65 unrelated specimens (42 from Sicily, 9 from Spain, 8 from the Czech Republic, 6 from Italy) has been reported in *Figure 2* and *Table 2*. All loci were polymorphic. The number of alleles per locus ranges from 1 to 11 (in Spain: 2–8, in the Czech Republic: 2–7, in Italy: 1–8, in Sicily: 2–11) with a total mean±SE of 3.65 ± 0.319 alleles over the four populations, the highest number of different alleles was found in Sicily *(Figure 2)*. Average of allelic richness in the four population was 3.24, ranging from the minimum 3.03 in the Czech Republic to the maximum

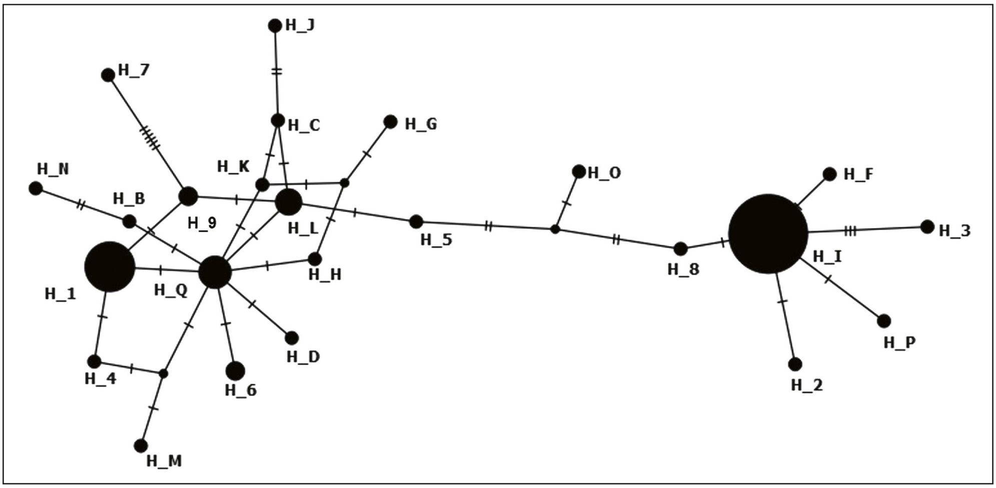

Figure 1. Haplotype neighbour-joining network of 960 bp segment of cytochrome b gene of mtDNA based on the 65 Peregrine Falcons considered in this study (the 9 new haplotypes are marked from H1 to H9) and the Bell *et al.* (2014) samples (15 haplotypes marked with H followed by letter) retrieved from GenBank. Three Bell's haplotypes (HI, HL and HE) were also found in our sample. The size of the nodes indicates the relative frequency of the corresponding haplotype in the dataset, as listed in *Table 1*. Small tracts show the mutational steps occurring between adjacent haplotypes

1. ábra A mtDNS citokróm b génjének 960 bázispár hosszú része alapján készült haplotípus hálózat. H1-H9: a 65 vándorsólyom minta alapján általunk talált haplotípusok, H-betűkkel jelölve: Bell *et al.* (2014) által közölt haplotípusok a GenBank-ból származó szekvenciái alapján. A mintáinkban a Bell *et al.* (2014) által közölt haplotípusok közül hármat találtunk meg (HI, HL and HE). A nóduszok méretei megfelelnek a haplotípusok relatív gyakoriságainak az *1. táblázat*ban közölt mintákban. Az ágakon lévő kicsi vonalak a mutációs lépések számát jelölik a haplotípusok között

3.40 in Italy. All populations have a comparable mean of different alleles with a frequency ≥ 5%, as well as of effective alleles, indeed the mean of these latter is slightly lower in the Czech Republic than in the other populations *(Figure 2)*. Contrariwise, Sicily has the highest mean of unique alleles with respect to the other populations *(Figure 2)*, depending from the absolute number of exclusive alleles (n = 10) found in the island, with respect to the Czech Republic (n = 3), Spain and Italy (both n = 2). Besides, Shannon diversity index, the observed (H_o), expected (H_e) and unbiased expected heterozygosity (UH_e) values were comparable among the four populations, with a relatively lower Shannon diversity value, and UH_e of the Czech population *(Table 2)*. Fixation index values are negative for Italy and the Czech Republic and positive for Spain and Sicily. This latter has the relatively higher reduction in heterozygosity when compared to Hardy-Weinberg expectations *(Table 2)*. As a matter of fact, none of the populations shows significant differences from Hardy-Weinberg equilibrium, with a fixation index ranging around a zero average value (–0.031).

As regards to genetic structuring, we have found a low amount of non-random mating in all populations, which shows F_{IS} values (after 1000 allelic permutations averaged over the ten loci in each population) negative in Czech Republic (–0.056) and positive in the others three areas (Spain = 0.082, Italy = 0.071, Sicily = 0.053). P-values were not significant for all pairwise comparisons between the F_{IS} values.

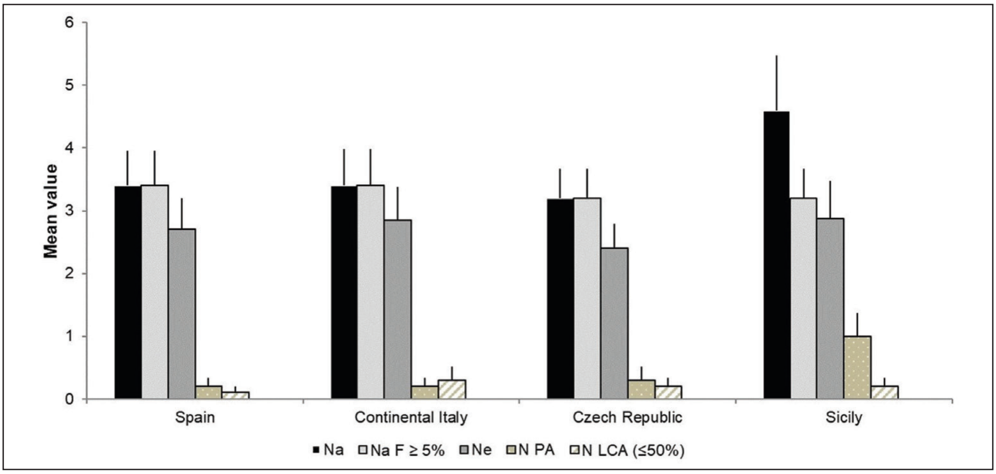

Figure 2. Allelic pattern across populations of Peregrine Falcon in areas of the Western Palaearctic. Na = N of different alleles; Na (F≥ 5%) = N of different alleles with a frequency ≥ 5%; Ne = N of effective alleles; N PA = N of alleles unique to a single population; N LCA (≤50%) = N of locally common alleles with a frequency of ≥5% found in 50% or fewer populations

2. ábra Vándorsólyom-populációk allél-mintázatai a Nyugat-Palearktiszban. Na = különböző allélek száma; Na (F≥ 5%) = különböző allélek száma, melyek gyakorisága ≥ 5%; Ne effektív allélek száma; N PA = csak egy populációban előforduló egyedi allélek száma; N LCA (≤50%) = lokálisan azonos allélek száma, melyek gyakorisága ≥5% csak a populációk 50%-ban, vagy kevesebben megtalálható

Table 2. Intra-population diversity and heterozygosity mean (± SE) values based on microsatellite analysis of 65 unrelated Peregrine Falcons. Mean over loci for each Peregrine Falcon population. SI = Shannon index; H_o = Observed Heterozygosity; H_e = Expected Heterozygosity; UH_e = Unbiased expected Heterozygosity; FI = Fixation index

2. táblázat Populáción belüli diverzitás és átlagos heterozigócia (átlag (mean) ± standard hiba (SE)) értékek a 65 nem rokon vándorsólyom mintáinak mikroszatellita elemzése alapján. A táblázat a lókuszok átlagos értékeit mutatja az egyes populációkban (Spain-spanyol, Continental Italy-kontinentális olasz, Czech Republic-cseh, Sicily-szicíliai, Total-összes). SI = Shannon index; H_o = megfigyelt heterozigócia; H_e = várt heterozigócia; UH_e = torzítatlan várt heterozigócia; FI = fixációs index

		SI	**Ho**	**He**	**UHe**	**FI**
Spain	Mean	0.973	0.533	0.546	0.578	0.011
	SE	0.146	0.079	0.061	0.065	0.091
Continental Italy	Mean	0.994	0.567	0.556	0.606	–0.004
	SE	0.161	0.097	0.073	0.079	0.096
Czech Republic	Mean	0.902	0.580	0.517	0.552	–0.162
	SE	0.123	0.048	0.051	0.055	0.081
Sicily	Mean	1.079	0.549	0.572	0.579	0.035
	SE	0.154	0.048	0.050	0.051	0.037
Total	Mean	0.987	0.557	0.548	0.579	–0.031
	SE	0.071	0.034	0.029	0.031	0.040

Pairwise values of F_{ST} statistics, as obtained from FSTAT (above diagonal values) and GENETIX (below diagonal values) software have been reported in *Table 3*. We reported results from both software for a careful approach as GENETIX implements a permutation-based procedure alternative to jack-knifing used in FSTAT to calculate statistical inference. According to both software, differences among populations are small and only the values between the Czech Republic and Sicily are statistically significant (marked with asterisk in *Table 3*), while only GENETIX recorded significant values also between Spain and the Czech Republic.

The analysis of molecular variance (AMOVA) shows that differences between the four populations are marginal as they explained only 3.3% of the total genetic variation, while intra-population difference was the 96.7% of the total genetic variation *(Table 4)*.

Eventually, the scatter of Principal Coordinates Analysis *(Figure 3)* shows how all the specimens spread across the first two factor axes (F1 and F2) that give a measure of the variance accounted for by the corresponding coordinates (eigenvectors), evidencing the lack of genetic structuring among the four studied Peregrine Falcon populations. Such a lack of genetic structuring keeps even considering the third axis (F3). The cumulative percentage of variance explained by the first 3 axes is equivalent to 31.36%.

Table 3. Pairwise F_{ST} statistics comparison between populations, as obtained from FSTAT (above diagonal values) and GENETIX (below diagonal values) software. Values marked with asterisk are statistically significant ($P \leq 0.05$)

3. táblázat Páronkénti F_{ST}-értékek a populációk (Spain-spanyol, Continental Italy-kontinentális olasz, Czech Republic-cseh, Sicily-szicíliai) összehasonlítására az FSTAT (diagonális feletti értékek) és a GENETIX (diagonális alatti értékek) programmal számolva. A csillagozott értékek statisztikailag szignifikánsak ($P \leq 0.05$)

	Spain	**Continental Italy**	**Czech Republic**	**Sicily**
Spain	–	–0.0173	0.0299	0.0151
Continental Italy	0.4083	–	–0.0022	0.0092
Czech Republic	0.0083*	0.1333	–	0.0317*
Sicily	0.0250	0.0750	0.0083*	–

Table 4. Analysis of molecular variance table showing the low differentiation among the populations with respect to the large individual variability. The related PhiPT statistics is = 0.033, with P = 0.022. The probability P (random ≥ data) for PhiPT is based on standard permutations across the full data set

4. táblázat A molekuláris variancia analízis táblázata, ami kevés variabilitást mutat a populációk között (Inter-population), összehasonlítva a nagy variabilitással a populációkon belül (Intra-population). A PhiPT érték = 0.033, és a hozzátartozó P-érték = 0.022. A PhiPT P-értkétt (random ≥ adat) standard permutációval számítottuk ki a teljes adathalmazra. df: szabadsági fok, SS: eltérés-négyzetösszeg, MS: eltérés-négyzetösszeg átlaga, Estimated Variance: becsült variancia

Source	**df**	**SS**	**MS**	**Estimated Variance**	**Estimated Variance (%)**
Inter-population	3	25.688	8.563	0.207	3.3
Intra-population	61	374.405	6.138	6.138	96.7
Total	**64**	**400.092**		**6.345**	**100**

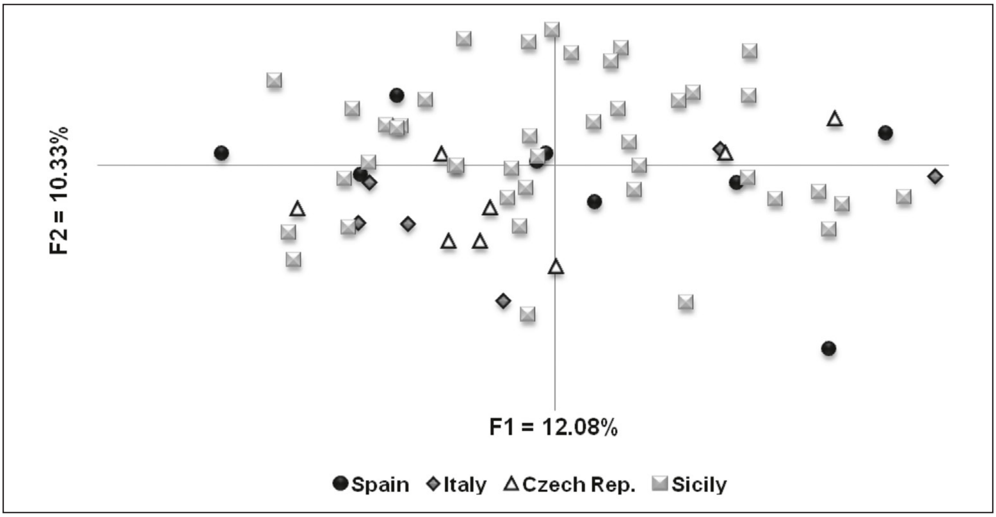

Figure 3. Scatter of the ordination method (Principal Coordinates Analysis by covariance matrix with data standardization) used to detect similarities of microsatellite data among the 65 unrelated Peregrine Falcons breeding in the four populations of Western Palaearctic. F1 and F2 are the factor axes that account for percentage of variation among specimens. No geographic grouping emerges from the scatter

3. ábra Főkomponens-analízis eredménye (PCoA) kovariancia mátrix alapján 65 nem rokon vándorsólyom minta adatait standardizálva a négy nyugat-palearktikus populációból

Discussion

We reported here for the first time molecular data from wild Peregrine Falcons living in Sicily, continental Italy and Northern Spain (Biscay). Low sample sizes in some of the considered populations might affect some results, as likely occurs for the higher Shannon diversity index of the Sicilian population, which had also the larger sample size. Despite this limitation, the estimation of intra-population diversity and allelic patterns provided an adequate genetic condition in the Spanish and Italian studied populations as the low-medium number of alleles and medium level of observed heterozygosity values were observed, but coupled with statistically not significant F_{IS} values and departure from HW equilibrium. These data fall within the species' variability range as they are consistent to other Peregrine Falcon populations. For instance, Nesje *et al.* (2000a) found 2–11 alleles per locus with a mean ± SE of 4.25 ± 0.81, mean ± SE H_o value was equal to 0.452 ± 0.080 and H_e was 0.512 ± 0.073 when examining genetic relationships among Peregrine Falcon populations in Southern Norway. In a much larger comparison of subspecies across the world, Nesje *et al*. (2000b) found 3–18 alleles per locus with H_o ranging from 0.405 to 0.490 in all populations (except the Tasmanian with H_o = 0.146). Jacobsen *et al.* (2008) comparing Southern Scandinavian and Northern Fennoscandic populations with different origin have found the H_o to decrease from 0.53 ± 0.07 in the historical population to 0.46±0.08 in the reintroduced population. Likewise, the H_e value's range was from 0.56 ± 0.07 in the historical to 0.50 ± 0.07 in the reintroduced population, anyway both heterozygosity decreases were not statistically significant.

The complete dataset (n = 30) of wild Peregrine Falcons that Bryndová *et al.* (2012) have analysed gave slight different values with respect to the subsample (n = 8) considered here *(Table 2)*. For instance, the mean H_o was 0.546, while the mean H_e was 0.632, and the allelic richness per locus ranged from 2.69 to 6.51 in the complete dataset. In addition, the whole Czech sample showed deviation from Hardy-Weinberg equilibrium in the form of heterozygote excess in the locus fp31, besides to a significant higher inbreeding coefficients F_{IS}.

As regard the genetic structuring, we have found a low amount of non-random mating comparable to the historic Scandinavian population (F_{IS} = 0.08 in Jacobsen *et al.* 2008) and quite less than contemporary reintroduced wild populations (F_{IS} = 0.14 in Jacobsen *et al.* 2008 and F_{IS} = 0.139 in Bryndová *et al.* 2012). The relatively higher F_{IS} value in our samples was found in the Biscay population from Spain. It is enquiring that the signal of non-random mating among individuals, although low, is larger in a continental than in the insular population of Sicily. Interchange of adults in the Biscay population was documented within a radius of about 360 km (Zuberogoitia *et al.* 2009), a value that would maintain genetic connections with other Spanish and South-western French populations. It remains an open question whether such a non-random mating signal could be depending by chance from the specific sample here used, or from the peculiar condition of the Biscay population, at the border between the Spanish '*brookei*' and the French '*peregrinus*' ranges (Zuberogoitia *et al.* 2009). Otherwise, first investigation on natal dispersal has not yet recorded emigration from Sicily (see Bondì *et al.* 2018), though we cannot still exclude immigration from continental Italy. This condition goes hand in hand with the large number of exclusive alleles found in the Sicilian falcons, so to allow supposing a quite close population. If this would be the case, the population of Peregrine Falcons in this island, currently estimated at 240–250 pairs (see Bondì *et al.* 2018), would be large enough to limit non-random mating among individuals.

Despite the significant F_{ST} differences between the Sicilian and the Czech populations, and also between the Spanish and the Czech based on only the GENETIX results, the AMOVA showed no differentiation among populations, with only a 3.3% of inter-population genetic variation. Similarly, Jacobsen *et al.* (2008) showed that differences between their four Scandinavian populations explained only 5% of the total genetic variation.

The low differentiation among populations is confirmed yet by the analysis of cytochrome b mitochondrial DNA sequences that produced a haplotype network, which was not concordant with geographic origin and taxonomic designation of the specimens. Previous works (White *et al.* 2013a, Bell *et al.* 2014, Johnson *et al.* 2017) have already noted such a discrepancy, suggesting that historical and recent dispersal, combined with rapid morphological evolution, could have contributed to the lack of phylogenetic concordance between mitochondrial DNA variation and geographic origin of the Peregrine Falcon. Both the Biscay and Sicilian populations could well describe this situation. The former has been suggested to show a character introgression with the close French *F. p. peregrinus* population that would produce variable phenotypes (Zuberogoitia *et al.* 2009) and the signals of non-random mating would stabilize pairs maintaining phenotypical variation (*Figure 4)*. While the Sicilian population appears to be quite isolated as judging from the presence of an exclusive and highly frequent H1 haplotype and the lack of dispersal (see Bondì *et al.* 2018). Despite this presumed insular condition, Sicilian Peregrine Falcons show quite large deviation from the expected *brookei*

Figure 4. Individual phenotype variability of Biscay Peregrine Falcons. Above, a male *brookei* phenotype which is paired to a female *peregrinus* phenotype (below). Photo by Iñigo Zuberogoitia

4. ábra Egyedi fenotípusos változatosság a Biscay-i vándorsólymokban. Felül: hím *brookei* fenotípusú egyed, ami párt alkot egy tojó *peregrinus* (alul) fenotípusú egyeddel. Fotó: Iñigo Zuberogoitia

Figure 5. Individual phenotype variability of Sicilian Peregrine Falcons. Four adult females collected in different years and localities of Sicily arranged from the most *F. p. peregrinus* (left) to the most *F. p. brookei* (right) similar phenotype, above in ventral and below in dorsal view. Courtesy of Carmagnola Museum, Turin. Photo by Giovanni Boano

5. ábra Egyedi fenotípusos változatosság a szicíliai vándorsólymokban. Négy öreg tojó, amelyek különböző években és helyeken lettek gyűjtve Sziciliában *F. p. peregrinus* (bal) és *F. p. brookei* (jobb) jellegeket mutat. Felül hasi, alul háti nézetben. Carmagnola Museum, Torinó. Fotó: Giovanni Boano phenotype *(Figure 5)* and mitochondrial sequences consistent with continental populations that would admit gene flow with *peregrinus* populations. Further genomics analyses (e.g. Johnson *et al*. 2017) of both the Biscay and Sicilian and their neighbouring populations, together with natal dispersal studies may further clear these aspects.

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Phylogeny of Falconidae and phylogeography of Peregrine Falcons

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Abstract We first examine how falcons can be integrated into avian tree of life. Then we go one step further and investigate the position of Peregrine Falcons in a comprehensive phylogeny of the falcons (genus *Falco*), which was reconstructed on the basis of DNA sequences. Whether the 19 subspecies of the Peregrine Falcon can be identified genetically is examined in the next step. Recently, the question of Peregrine Falcon's genetics in Central Europe has become of wider interest. Which subspecies was present before the collapse of populations and which currently after various reintroduction projects? Evidence is provided, that Central Europe constitutes a (natural) hybrid zone between *F. p. brookei* from the Mediterranean and *F. p. peregrinus* of northern Europe.

Keywords: molecular phylogeny, Falconiformes, *Falco*, Peregrine subspecies

Összefoglalás Első lépésként áttekintjük, hol helyezkednek el a sólymok a madarak törzsfáján. Következő lépésként megvizsgáljuk a vándorsólyom filogenetikai helyzetét a sólymok (*Falco* nemzetség) átfogó filogenetikáján belül, DNS szekvenciák összehasonlításával. Ezt követően a vándorsólyom 19 alfajának genetikai azonosítására törekszünk, ugyanis a közép-európai populációk genetikája egyre inkább az érdeklődés középpontjába került az utóbbi időben. Kérdés, mely alfajok voltak jelen a populációk összeomlásakor, illetve melyek kerültek be a visszatelepítési programokkal? Bizonyítékok vannak arra vonatkozóan, hogy Közép-Európa a mediterrán *F. p. brookei* és az észak-európai *F. p. peregrinus* alfajok természetes hibridzónája.

Kulcsszavak: molekuláris filogenetika, sólyom-alakúak, *Falco*, vándorsólyom alfajok

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Where are falcons in avian tree of life?

Falcons belong to the family Falconidae, which is divided into two subfamilies Falconinae and Herpetotherinae. The subfamily Falconinae is further divided into two tribes Polyborini and Falconini. While the Polyborini are limited in their distribution to the New World, representatives of the Falconini live on all continents (del Hoyo & Collar 2014, del Hoyo *et al.* 2014). Falcons have traditionally been placed in the common order Falconiformes with other birds of prey due to their appearance and lifestyle as predators (Sibley & Monroe 1990). However, recent genomic DNA studies (Hackett *et al.* 2008, Jarvis *et al.* 2014, Prum *et al.* 2015) show that this classification is not correct and that similarities in appearance and behaviour are convergent characters. While Cathartidae (New World vultures), Pandionidae (Osprey), Accipitridae (eagles, buzzards, hawks, kites, harriers) and Sagittariidae (Secretarybird) have a common ancestor and are united as Accipitriformes, the falcons fall into a more distant grouping, which includes falcons, parrots and passerine birds (the "Eufalconimorphae" clade) (Hackett *et al.* 2008, Suh *et al.* 2011, Wink 2012, 2013, 2015, Jarvis *et al.* 2014, Prum *et al.* 2015, Kraus & Wink 2015). Therefore, the order Falconiformes today comprises only the family Falconidae *(Figure 1)*. In the evolution of birds, the specialisation as a predator apparently occurred repeatedly and convergently, e.g. in birds of prey (Accipitriformes sensu stricto), owls (Strigiformes) and falcons (Falconiformes). But also seagulls and skuas exhibit many elements of birds of prey in their hunting behaviour.

Phylogeny of the genus Falco

Almost 25 years ago, we started to investigate the phylogenetic relationships within birds of prey using DNA markers (Seibold *et al.* 1993, Wink 1995, 2000, Wink & Ristow 2000, Wink & Sauer-Gürth 2000, 2004, Wink *et al.* 1996, 2000, 2004, 2010). As marker genes, we have selected the nucleotide sequences of the mitochondrial cytochrome b gene, which is very well suited for family and genus level analysis, and the nuclear gene RAG-1. The methods have been described in detail in Wink and Sauer-Gürth (2000, 2004) and Storch *et al.* (2013). *Figure 2* shows a molecular phylogeny of falcons of the genus *Falco* with 35

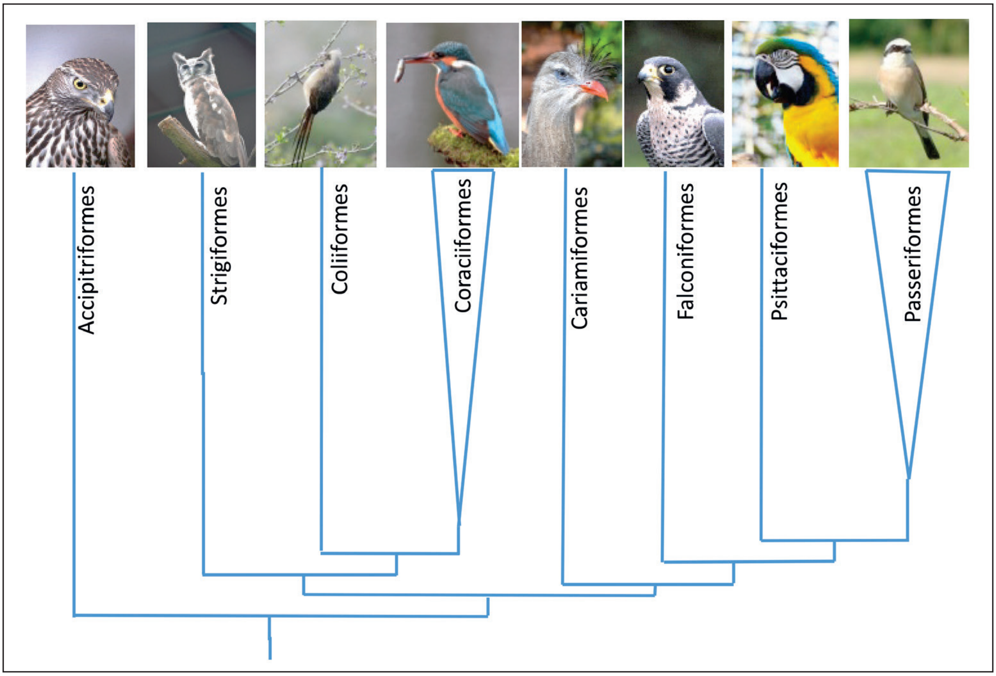


Figure 1. Position of falcons in the avian tree of life (simplified after Prum *et al.* 2015). The original phylogeny comprises genome sequences of 198 species (259 nuclear genes with 390 000 nucleotides for each taxon). (Photos: M. Wink)

1. ábra A sólymok filogenetikai elhelyezkedése a madarak életfáján (Prum *et al.* 2015 nyomán leegyszerűsítve). Az eredeti filogenetikai elemzés 198 faj genom szintű szekvenciáit tartalmazza (259 nukleáris gén, fajonként 390 000 nukleotiddal). (Fotók: M. Wink) of the 38 known falcon species (only *F. moluccensis, F. rufigularis, F. severus* are missing in this phylogeny), which was created on the basis of DNA sequences of the cytochrome b gene. As one can easily see, most falcon species are grouped as it would have expected due to morphological characteristics (Weick 1980, del Hoyo *et al.* 1994). Important results are:

Three major clades are apparent in falcons (family Falconidae) *(Figure 2)*. The subfamily Herpetotherinae at the base, followed by the tribes Polyborini and the Falconini *(Figure 2)*. Within the tribe Falconini Falconets and Pygmy Falcons of the genera *Polihierax* and *Microhierax* cluster at the tree base and as a sister group to the monophyletic genus *Falco*. Within the genus *Falco*, some monophyletic groups are clearly identified.

The Peregrine Falcon *(F. peregrinus)* is differentiated into various subspecies, which are genetically only slightly distinct; i. e. the branch lengths in the phylogram are very short. *F. pelegrinoides*, formerly separated as Barbary Falcon, is clearly a Peregrine Falcon and should therefore be considered as a subspecies with *F. peregrinus*. The Taita Falcon *(F. fasciinucha)* from Africa is very closely related to the Peregrine Falcon (Bell *et al.* 2014) and might be regarded as a subspecies of the Peregrine Falcon rather than an independent species.

The lineage of Hierofalco, which comprise *F. rusticolus, F. cherrug, F. biarmicus,* and *F. jugger*, form the sister group to the Peregrine complex. Its members are also genetically more closely related to each other than falcons in other species complexes (see Hobbys, Merlins) (Wink *et al.* 2004, 2010, Nittinger *et al.* 2005, 2007). However, they are usually recognized as separate species. Interestingly, the Australian Black Falcon *(F. subniger)* is a member of the Hierofalcons. It apparently represents the group of large falcons in Australia.

The Prairie Falcon *(F. mexicanus)*, formerly counted among the Hierofalcons, forms a sister taxon to the Peregrine – Hierofalco clade similar to the Grey Falcon *(F. hypoleucos)*.

The kestrel group forms a monophylum with many species (Common Kestrel, Australian Kestrel, Madagascar Kestrel, Seychelles Falcon, Mauritius Falcon, Greater Kestrel, Fox Kestrel and Lesser Kestrel). The American Kestrels *(F. sparverius)* behave like kestrels, but they fall basal in the family trees and outside the "kestrel" group from the Old World.

Also Hobbys and their relatives fall into a clearly defined monophylum with Australian and African Hobbys, Sooty Falcons and Eleonora's Falcons. Depending on the calculation, the Orange-breasted Falcon *(F. deiroleucus)* also falls into this group.

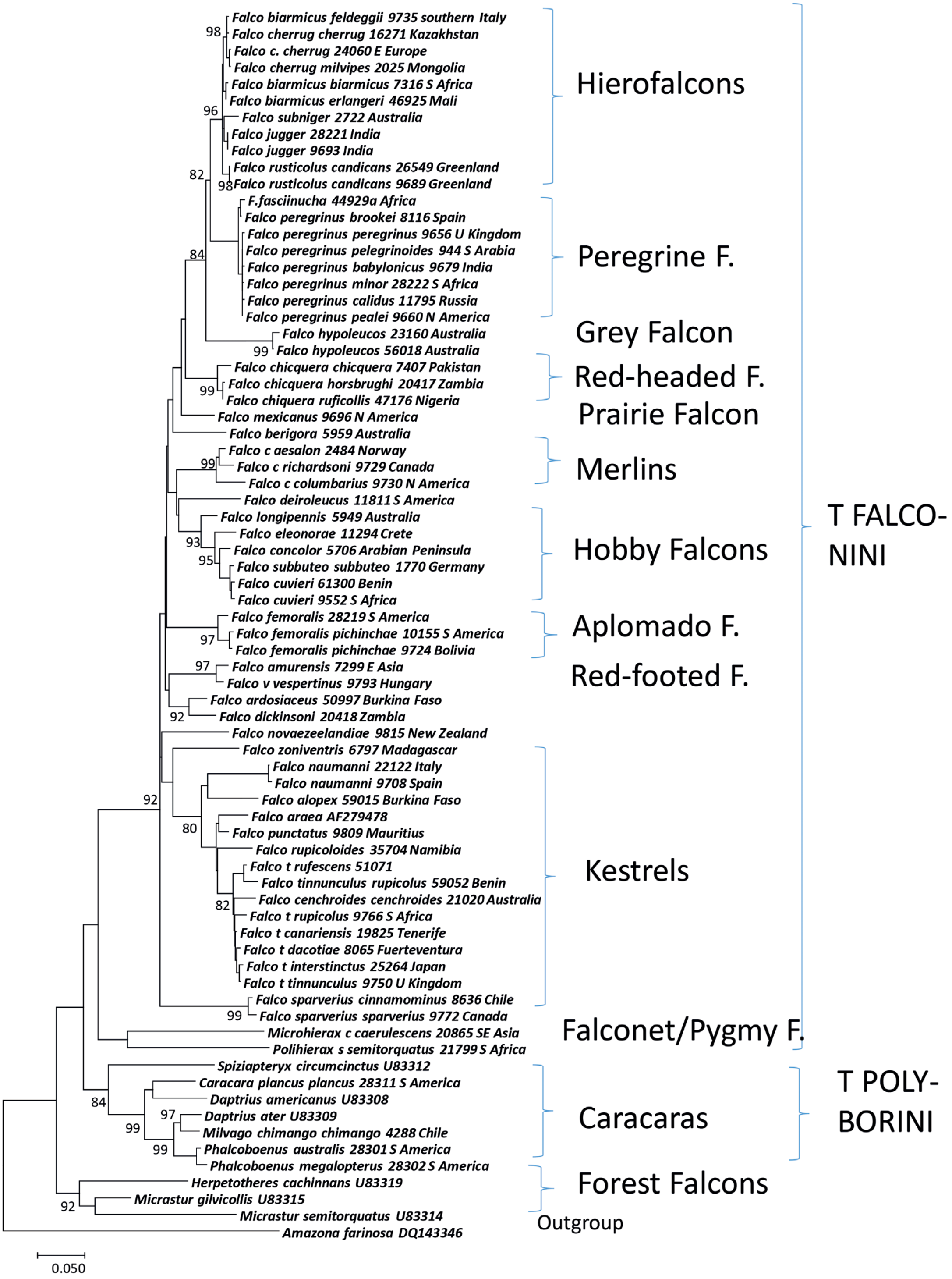
The Red-footed Falcon *(F. vespertinus)* is closely related to the Amur Falcon *(F. amurensis)*; both species breed in Eurasia and winter in sub-Saharan Africa.

The Merlin *(F. columbarius)* is subdivided into several subspecies that are genetically highly differentiated and may have already reached species status.

The Red-headed Falcons *F. chiquera* form a monophylum that can be divided into three species *F. horsbrughi, F. ruficollis* and *F. chiquera* due to their distribution (India or Africa).

The African Grey Falcons *(F. ardosiacus)* and Dickinson's Kestrels *(F. dickinsoni)* are grouped as sister species.

The phylogenetic position of some Old World, New World and Australian species is unclear (i.e. not supported by significant bootstrap values); they do not form monophyla.


Falco biarmicus feldeggii 9735 southern Italy
Falco cherrug cherrug 16271 Kazakhstan
Falco c. cherrug 24060 E Europe
Falco cherrug milvipes 2025 Mongolia
Falco biarmicus biarmicus 7316 S Africa
Falco biarmicus erlangeri 46925 Mali
Falco subniger 2722 Australia
Falco jugger 28221 India
Falco jugger 9693 India
Falco rusticolus candicans 26549 Greenland
Falco rusticolus candicans 9689 Greenland
F.fasciinucha 44929a Africa
Falco peregrinus brookei 8116 Spain
Falco peregrinus peregrinus 9656 U Kingdom
Falco peregrinus pelegrinoides 944 S Arabia
Falco peregrinus babylonicus 9679 India
Falco peregrinus minor 28222 S Africa
Falco peregrinus calidus 11795 Russia
Falco peregrinus pealei 9660 N America
Falco hypoleucos 23160 Australia
Falco hypoleucos 56018 Australia
Falco chicquera chicquera 7407 Pakistan
Falco chicquera horsbrughi 20417 Zambia
Falco chiquera ruficollis 47176 Nigeria
Falco mexicanus 9696 N America
Falco berigora 5959 Australia
Falco c aesalon 2484 Norway
Falco c richardsoni 9729 Canada
Falco c columbarius 9730 N America
Falco deiroleucus 11811 S America
Falco longipennis 5949 Australia
Falco eleonorae 11294 Crete
Falco concolor 5706 Arabian Peninsula
Falco subbuteo subbuteo 1770 Germany
Falco cuvieri 61300 Benin
Falco cuvieri 9552 S Africa
Falco femoralis 28219 S America
Falco femoralis pichinchae 10155 S America
Falco femoralis pichinchae 9724 Bolivia
Falco amurensis 7299 E Asia
Falco v vespertinus 9793 Hungary
Falco ardosiaceus 50997 Burkina Faso
Falco dickinsoni 20418 Zambia
Falco novaezeelandiae 9815 New Zealand
Falco zoniventris 6797 Madagascar
Falco naumanni 22122 Italy
Falco naumanni 9708 Spain
Falco alopex 59015 Burkina Faso
Falco araea AF279478
Falco punctatus 9809 Mauritius
Falco rupicoloides 35704 Namibia
Falco t rufescens 51071
Falco tinnunculus rupicolus 59052 Benin
Falco cenchroides cenchroides 21020 Australia
Falco t rupicolus 9766 S Africa
Falco t canariensis 19825 Tenerife
Falco t dacotiae 8065 Fuerteventura
Falco t interstinctus 25264 Japan
Falco t tinnunculus 9750 U Kingdom
Falco sparverius cinnamominus 8636 Chile
Falco sparverius sparverius 9772 Canada
Microhierax c caerulescens 20865 SE Asia
Polihierax s semitorquatus 21799 S Africa
Spiziapteryx circumcinctus U83312
Caracara plancus plancus 28311 S America
Daptrius americanus U83308
Daptrius ater U83309
Milvago chimango chimango 4288 Chile
Phalcoboenus australis 28301 S America
Phalcoboenus megalopterus 28302 S America
Herpetotheres cachinnans U83319
Micrastur gilvicollis U83315
Micrastur semitorquatus U83314
Amazona farinosa DQ143346
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Hierofalcons
Peregrine F.
Grey Falcon
Red-headed F.
Prairie Falcon
Merlins
Hobby Falcons
Aplomado F.
Red-footed F.
Kestrels
Falconet/Pygmy F.
Caracaras
Forest Falcons
Outgroup
T FALCO-NINI
T POLY-BORINI

Figure 2. Molecular phylogenetic analysis of falcons based on DNA sequences of the cytochrome b gene by Maximum Likelihood method. The evolutionary history was inferred by using the Maximum Likelihood method based on the General Time Reversible model. The tree with the highest log likelihood (–11683.84) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 1.0640)). The rate variation model allowed for some sites to be evolutionarily invariable ([+I], 41.68% sites). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 74 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. There were a total of 1143 positions in the final dataset. Evolutionary analyses were conducted in MEGA7 (Kumar *et al.* 2016)

2. ábra A sólymok molekuláris filogenetikai elemzése a citokróm-b gén szekvenciája alapján. A csoport evolúciós történetisége a GTR modell alapján, maximum likelihood módszerrel lett meghatározva. Az ábrán a legmagasabb log-likelihood értékkel (–11683,84) rendelkező fa látható. Az ágakon található számok annak a százalékos arányát mutatják, hogy az egyes taxonok milyen mértékben kerültek ugyanabba a pozícióba a különböző fákon. A távolságmátrixon alkalmazott maximális összetett likelihood (Maximum Composite Likelihood – MCL) képezte annak a heurisztikus keresésnek az alapját, mely Neighbor-Join és BioNJ algoritmusok alapján határozta meg a kiindulási fát/fákat, kiválasztva azt a topológiát, amelyik a legmagasabb log-likelihood értéket kapta. A bázisokban bekövetkező változások evolúciós frekvenciájának becslésére egy diszkrét Gamma-eloszlást feltételező modell szolgált (5 kategória (+G, paraméter = 1,0640)). Egyes pozíciók változatlanságát egy újabb modell biztosította ([+I], 41,68%). A kapott fa ághosszai az egyes pozíciókban bekövetkező változások számával arányosan skálázottak. Ebben az elemzésben 74 nukleotid szekvencia szerepelt. Első+második+harmadik és nem kódoló kodon helyek lettek megkülönböztetve. A végső adatbázisban összesen 1143 pozíció szerepelt. Az elemzések a MEGA7 programban készültek (Kumar *et al*. 2016)

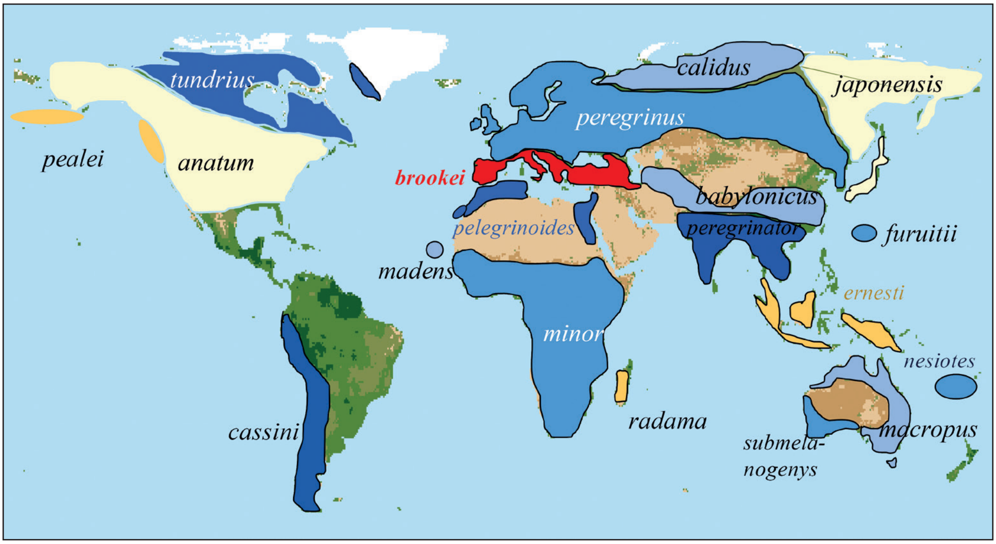

Figure 3. Distribution of the subspecies of the Peregrine Falcon

3. ábra A vándorsólyom alfajok földrajzi eloszlása

Figure 4. Molecular phylogenetic analysis of peregrine and Hierofalcons by Maximum Likelihood method. (Details as in *Figure 2*)

4. ábra A vándorsólyom és a Hierofalco alnemzetség molekuláris filogenetikai elemzése maximum likelihood módszerrel. (Részleteket lásd: *2. ábra*)

Systematics and phylogeography of Peregrine Falcons

The Peregrine Falcon *(F. peregrinus)* is one of the few species of birds of prey with a cosmopolitan distribution. Presumably, many distribution areas of the Northern Hemisphere have only been populated after the end of the last glaciation period; thus the Peregrine Falcons form young populations in geological terms. A total of 16 to 19 subspecies are distinguished with differing distribution areas *(Figure 3)*. These subspecies were defined due to differences in size, coloration and distribution, albeit obvious clinal patterns. When interpreting the distribution map, it is important to note that wide contact zones must exist between the defined subspecies in which natural mixing should take place. Furthermore, it is possible that the existing subspecies and local populations are mixed with Peregrine Falcons of other genetic origin, as genetically not clearly defined Peregrines have been released in many places in North America and Europe as part of reintroduction projects.

We have succeeded in genetically characterizing 11 subspecies of the Peregrine Falcon by sequencing their cytochrome b gene. As shown in *Figure 4*, all Peregrine Falcon subspecies are closely related. The genetic distances within the subspecies range between 0.01 and 0.8%, indicating differentiation within the last 5000 to 400000 years. Our findings are confirmed by Bell *et al.* (2014), whose genetic distances in the cyt-b gene within Peregrine Falcons were between 0.001 and 1%.

Only a few well-defined subgroups can be identified *(Figure 4)*: *F. p. brookei* from the Mediterranean clusters as a basal group and is one of the few clearly differentiated subspecies. *F. p. macropus* from Australia, *babylonicus* from SE Asia and *minor* from Africa presumably form their own phylogenetic lines. The *peregrinus* cluster includes all other subspecies of the Peregrine Falcon. Even the Barbary Falcon *(F. p. pelegrinoides)*, which was previously considered a species of its own, does not differ more than the other peregrine subspecies, so it is appropriate to consider it as a subspecies of the Peregrine Falcon.

In addition to our studies, the phylogeny of Peregrine Falcons has also been investigated in two further research groups (White *et al.* 2013, Bell *et al.* 2014). Bell *et al.* (2014) investigated sequences of the cyt b gene of 41 Peregrine Falcons and 11 subspecies. They identified 16 haplotypes, which do not show any correlation with distribution and subspecies status. They found, however, that the Taita Falcon *(F. fasciinucha)*, which occurs in Africa, is closely related to the Peregrine Falcons, but suggest that it is probably a species of its own. This is also apparent in our data *(Figure 2, 4)*. *F. p. brookei* also showed (as in our work) a haplotype different from the other Peregrine Falcons. White *et al*. (2013) analyzed the more variable control region of 219 Peregrine Falcons, which included 12 subspecies (but not *brookei*). The result corresponds to the data from Bell *et al*. (2014) and our data, and implies that the subspecies cannot be defined genetically unambiguously and that a strong gene flow has taken place and probably still takes place.

Genetic classification of Peregrine Falcons in Germany

We have identified the cytochrome b haplotypes of meanwhile more than 300 young Peregrine Falcons, which had hatched between 2000 and 2015 in southern Germany (especially Baden-Württemberg; few from Rhineland Palatinate, Hesse, North Rhine-Westphalia and eastern Germany). According to their distribution range, they should theoretically belong to the subspecies *F. p. peregrinus*. However, 62% of the studied Peregrine Falcons show the clearly recognizable mitochondrial haplotype of *F. p. brookei*, which should only occur in the Mediterranean region *(Figures 2, 4)*. Since the mtDNA is inherited maternally, the mothers of the *brookei* falcon chicks must also have the *brookei* haplotype. These can be pure *brookei* or, alternatively, *peregrinus* × *brookei* hybrids. Since the *brookei* and *peregrinus* haplotypes are often found in neighboring nests, we have to assume that the population of Central Germany consists of a mixture of *brookei* × *peregrinus* throughout. Nevertheless, pure *brookei* and *peregrinus* individuals are also expected (Wink *et al.* 2010).

This hybridization hypothesis was supported by a first microsatellite analysis (Wink *et al.* 2010). Five alleles were detected in the microsatellite locus NVH fp89. AT12 and AT13 are alleles characteristic of pure *brookei* from the Mediterranean region; these alleles are not found in peregrines of northern Europe with the haplotype *peregrinus*. But peregrine falcons from the German *brookei* cluster also have these alleles. This means that we are able to detect *brookei* not only via the maternal mtDNA, but also via the biparentally inherited nuclear DNA. The allele AT6 is only found in *peregrinus*, but also in the German *brookei* haplotypes. Accordingly, they must be – at least in part – hybrids.

Probably similar contact zones exist between the other subspecies of the Peregrine; no clear demarcations are expected for subspecies in theory either.

Where do the *brookei* haplotypes come from?

It would be naive to assume that there is a strict geographical separation of the two subspecies *peregrinus* and *brookei.* A more or less large contact zone would also theoretically be expected. Our current data indicates that the whole of Central Europe is such a contact zone. By examining almost 60 Peregrine Falcon skins from different museums from the period before 1960, we were able to establish that a contact zone with *brookei* haplotypes already existed before the population collapse (Rockenbauch 1998, 2002) and release measures in Central Europe; 42 *peregrinus* haplotypes were found in addition to 17 *brookei* haplotypes *(Table 1)*. Compared to the current situation, the share of the *brookei* haplotype before the collapse of the Peregrine Falcon's population was lower than today, after recovery of stocks and reintroduction measures.

Already in the 1950s, German falconers dealt with the challenge of captive Peregrine breeding. Inspired by the success of the Peregrine breeders and reintroduction programs in the USA, breeding programs were initiated in Germany and between 1977 and 2010 a total of 1099 Peregrine Falcons were released in Germany (C. Saar, pers. comm.). Of 31 blood samples of breeding falcons provided by Prof. Dr. C. Saar, 29 carried the *brookei* haplotype. These falcons are descended from Peregrine Falcons from Scotland, which theoretically belong to the subspecies *peregrinus*. Our data indicate that *brookei* haplotypes are also found in the UK and the contact zone is even larger than expected. Therefore, it cannot be completely ruled out that the *brookei* haplotypes present in northern and eastern Germany are also descended from reintroduced falcons. The high proportion of *brookei* haplotypes in southern Germany, where no peregrine falcons have been released, indicates that a natural mixed population occurs here.

Table 1. Haplotypes of Peregrine Falcons from Germany, which were sampled between 2000 and 2015 and of Peregrine Falcons from museum collections collected before 1960

1. táblázat A németországi vándorsólymok haplotípusai 2000 és 2015 közötti mintákból, valamint 1960 előtti múzeumi gyűjteményekből

Region	Falcons with *brookei* haplotype	Falcons with *peregrinus* haplotype
2000–2015		
Baden-Württemberg	113	80
Rhineland-Palatinate	5	7
Nordrhein Westfahlen	5	0
Hesse, Bavaria	2	0
Niedersachsen	0	4
East Germany	48	18
Switzerland	17	6
Total	**190 (62%)**	**115 (38%)**
Before 1960		
Baden-Württemberg	4	4
Baveria	9	7
Saxony	1	21
Norway	3	10
Total	**17 (29%)**	**42 (71%)**

It was speculated that the Peregrine Falcons, which today populate more and more buildings, would be descendants of the reintroduced falcons. Since the *brookei* haplotypes of our study originate in part from building breeders from southern Germany, where no reintroduction or immigrants took place, it seems to be an ecological adaptation to urban life, similar to the way we know it from Blackbird, Wood Pigeon or Goshawk.

In conclusion; for the Peregrine Falcon a natural mixture between the subspecies is widespread phenomenon, which is also supported by the results of White *et al.* (2013) and Bell *et al.* (2014).

Outlook

The Peregrine Falcon seems to be one of the young species that only differentiated within the last 200,000 years during cycles of glaciation and adapted to different habitats and biomes. Variations in size and coloring are therefore to be seen as adaptive characters and as adaptations to the different environments. Since a strong mixing of haplotypes can be demonstrated, a systematic differentiation into clearly defined subspecies (except for *F. p. brookei*) must be regarded with some caution. It should not be forgotten, that the differentiation and global spread of modern man *(Homo sapiens)* also follows a similar pattern without genetically definable subspecies.

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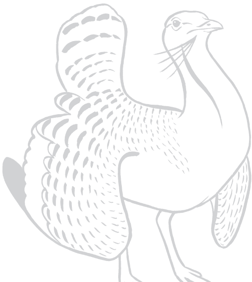

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Extreme weather affects Peregrine Falcon *(Falco peregrinus tundrius)* breeding success in South Greenland

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Abstract In order to better understand the potential effects of climate change on the Peregrine Falcon, we investigated the relationship between extreme weather events and Peregrines' breeding success in South Greenland. We defined three variables – number of days with extremely low temperatures, extreme precipitation, consecutive rainy days – and an additive variable, total days with extreme weather, and tested their relationship with Peregrines' breeding success (measured as young per site and nest success) over a 33 year study period. Breeding success was negatively influenced by the number of days with extreme weather and extremely low temperature. The strongest relationship found was total days with extreme weather in the entire breeding season, which explained 22% and 27% of the variation in nest success and young per site, respectively. The number of days with extreme weather in our study related to fluctuations in the North Atlantic Oscillation (NAO). Thus, with a strengthening of the NAO, linked to climate change, more extreme weather may occur in the Arctic and induce increased variation in Peregrines' breeding success. Our data did not allow us to pinpoint when in the breeding cycle inclement weather was particularly harmful, and we recommend finer-scale research (e.g. automated nest cameras) to better monitor the species-specific effects of rapidly changing climate.

Keywords: Arctic, climate change, productivity

Összefoglalás A klímaváltozás vándorsólymokra gyakorolt lehetséges hatásainak jobb megértése érdekében a faj költési sikerének és a szélsőséges időjárási események kapcsolatát vizsgáltuk Dél-Grönlandon. Négy változót határoztunk meg – szélsőségesen alacsony hőmérsékletű napok száma, túlzott csapadékmennyiség, egymást követő esős napok száma – kiegészítve a szélsőséges napok teljes számával, melyeket a vándorsólymok költési sikerével (fiókák száma és a fészek sikeressége) vetettünk össze, egy 33 évet felölelő adatsor alapján. A költés sikeressége egyaránt negatív összefüggést mutatott a szélsőséges időjárású, valamint az alacsony hőmérsékletű napok számával. A legerősebb összefüggést mutató változó a fészek sikerességében és a fiókák számában mutatkozó változatosság 22, illetve 27%-át magyarázta. A szélsőséges időjárású napok száma összefüggést mutat az Észak-atlanti Oszcillációs Rendszerrel (NAO). Ezért a NAO erősödésével, mely a klímaváltozáshoz szorosan kapcsolódik, egyre szélsőségesebb időjárás várható a sarki régióban, amely egyre inkább befolyásolhatja a vándorsólymok költési sikerét. Adataink nem tették lehetővé azt, hogy pontosabban meghatározzuk, hogy a költési időszak melyik szakaszában különösen fenyegetőek ezek a változások, ezért finomabb skálán kivitelezett kutatások (pl. fészekkamerák alkalmazása) javasolt a gyorsan változó klíma különböző fajokra gyakorolt hatásának vizsgálatára.

Kulcsszavak: Sarki-öv, klímaváltozás, költési siker

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Introduction

Past and current climate change, caused by anthropogenic emissions, has led to increasing surface temperatures, more frequent and intense temperature extremes as well as increased variability in precipitation (Parmesan 2006, Stocker *et al.* 2013). For much of the Arctic, climate change scenarios predict higher precipitation levels and increased and more varied temperatures, which in turn will cause more precipitation to fall as rain (Stocker *et al.* 2013). In addition, the North Atlantic part of the Arctic is affected by a strengthening of the North Atlantic Oscillation (NAO). The NAO is caused by fluctuations in atmospheric sea-level pressure differences between the subtropical region (centered in the Azores) and the subpolar region (centered in Iceland). This might result in more extreme weather events due to the disruptive influence of NAO on temperature and precipitation patterns (NOAA 2018). This drastic change in the Arctic climate destabilizes species' communities in the region. Examining how Arctic species respond to weather variability can help predict how species composition may change in the future (Cleasby *et al.* 2017). The Peregrine Falcon *(Falco peregrinus)* is a suitable study species since it is a well-studied Arctic top predator with long term monitoring data on productivity and occupancy from different regions, and sensitive to inclement weather during critical stages of the breeding cycle (Olsen & Olsen 1988, Anctil *et al.* 2014).

Falco peregrinus tundrius, (further the Peregrine) arrives in May to the subarctic southern parts of Greenland from its wintering locations in Latin America (Vorkamp *et al*. 2017). Its nesting sites are often located on sheltered ledges on steep cliff walls, for protection from predatory mammals and harsh weather (Falk *et al*. 1986, Wightman & Fuller 2005). In South Greenland the Peregrine's breeding season starts in mid-May and, on average, chicks hatch in early July (Falk & Møller 2017). However, over the past three decades the Peregrine's breeding success has been highly variable in South Greenland. This may be explained by variations in the frequency of extreme weather events related to climate change and the increased manifestation of the NAO. Over the same period, the breeding has been starting slightly earlier which might indicate a response to a warming climate (Parmesan 2006, Fletcher *et al.* 2013). Even the NAO may or may not affect the Peregrine's shift towards earlier arrival and may consequently result in earlier breeding and hatching (review in Haest *et al*. 2017). The long-term consequence of earlier breeding and hatching may be a mismatch between the Peregrine's highest food demand during the breeding season and peak prey abundance, which may lead to reduced breeding success (Parmesan 2006, Sullivan *et al.* 2015).

Although the Peregrine Falcon is a well-studied top predator in the Arctic, only a few works have identified how and if weather events – and possible interannual variation linked to the NAO – may affect the breeding populations. However, Anctil *et al*. (2014) found that number of days with extreme rainfall had increased in Arctic Canada, negatively affecting Peregrine productivity. Breeding success depends on food supply from the moment the adult birds arrive at their nesting sites, and even the body reserves the female is carrying when she arrives from her wintering and migration foraging sites (Franke 2017). Harsh weather may inhibit the breeding pair from efficiently hunting their swift avian prey, since avian prey may be less active and available during heavy rains (and strong winds). Rainfall and extreme temperature may further increase movement costs, complicate foraging, and disrupt egg incubation (Öberg *et al.* 2015). After the chicks hatch, extreme weather may even directly affect nestling survival. During their first 21 days, nestlings are vulnerable to wet and cold, due to lack of thermoregulation (Bradley *et al.* 1997, Anctil *et al.* 2014, Pipoly *et al.* 2013). In addition to these direct weather effects, starvation among nestlings due to parents' limited foraging success, may be an indirect consequence of harsh weather. Therefore, studying how breeding success is influenced by variability in rainfall and temperature is important for understanding how future climate changes and weather extremes may affect the population of this bird of prey.

In order to understand the potential effects of climate change on the Peregrine, we investigate whether NAO affects the frequency and duration of extreme weather events in South Greenland, and whether these extreme weather events in turn affect the breeding success of the Peregrine Falcon population in this region. This study will answer the four following questions:

1. Does strengthening of the NAO during the breeding season influence number of days with extreme weather during this period?
2. Does an increased number of days with extremely low temperatures influence breeding success?
3. Do extreme precipitation and consecutive rainy days influence breeding success?
4. Is there any period during the breeding season when extreme weather events are particularly linked to breeding success?

Materials and methods

Study Species and Area

The Peregrine is a top predator with few enemies (Mearns & Newton 1988, Wightman & Fuller 2005) with a distribution across all major land masses, except New Zealand and Antarctica, and with many subspecies adapted to different climate regimes around the globe (White *et al*. 2013). Peregrines can reach a maximum age of 12–15 years, have an average generation time of 6.8 years, and females normally lay 2–4 eggs (Park *et al.* 2011, White *et al.* 2013). The worldwide population of the Peregrine Falcon is estimated at 140,000 individuals (subspecies included) and is listed as least concern (LC) on the IUCN Red List of

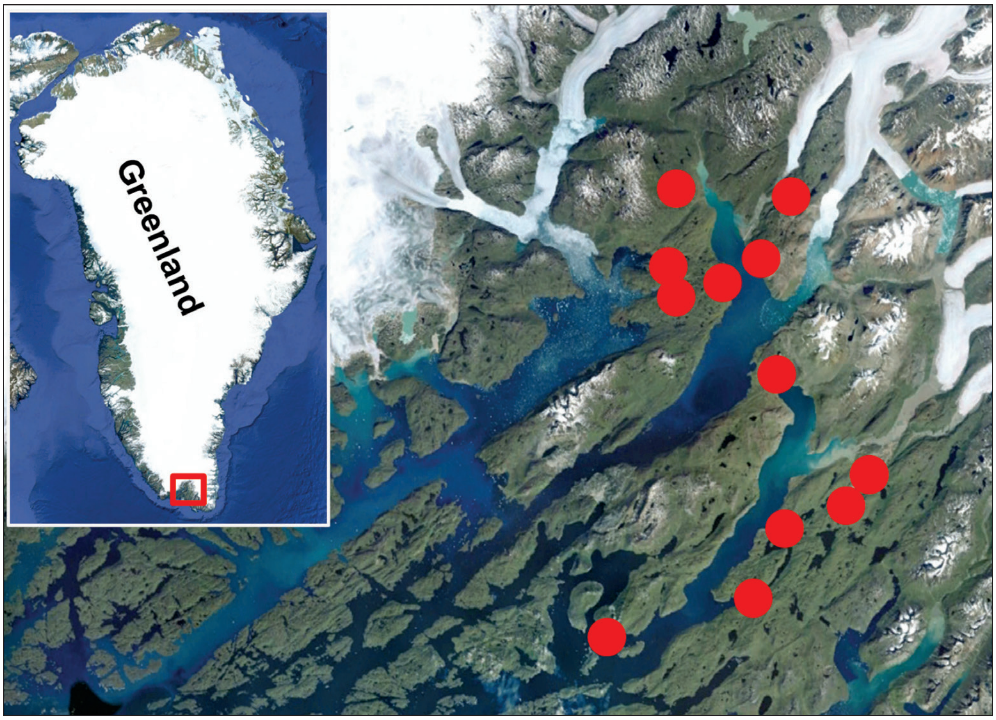

Figure 1. The 12 sample sites along Tunulliarfik and Igaliku fjords, each site may hold a territorial pair of Peregrines, some of which will produce young in any given year. Data was collected between 1981 and 2015. Picture modified after Google maps

1. ábra A 12 mintavételi pont elhelyezkedése Tunulliarfik és Igaliku fjordok mentén. Minden mintapont egy-egy vándorsólyom pár területére esik, amely párok az adott évben neveltek fiókákat. Az adatok 1981 és 2015 között lettek gyűjtve. A képek a Google térképek felhasználásával készültek

Threatened Species (BirdLife International 2016). Greenland holds 100–500 breeding pairs (Falk & Møller 1988, Boertmann 2008). In South Greenland, the Peregrine feeds almost exclusively on migratory passerines (Falk *et al.* 1986). The survey area is located in Southwestern Greenland and the Peregrine monitoring sites are distributed across the coastal and inland areas of Tunulliarfik and Igaliku fjords *(Figure 1)*.

Known Peregrine breeding sites were surveyed 1 to 3 times per year in June and/or July, sometimes also in August. During surveys of active nests, the number of eggs and/or young was recorded and the timing of breeding estimated based on age of nestlings (Clum *et al.* 1996) or on the developmental stage of eggs (White *et al*. 2002).

For this study, we defined three periods of the breeding cycle. Firstly, the pre-laying period, which begins in May when the Peregrines arrive to their breeding grounds in South Greenland and (re)occupy territories and mate. Secondly, the approximately 33-day long incubation period roughly corresponding to the month of June. Thirdly the nestling period lasting throughout July (Falk *et al.* 1986). The mean hatching date is the 3rd of July (Falk *et al.* 1986, Falk & Møller 2017).

NAO and Weather Data

NAO-index data for 1981–2015 were downloaded from NOAA/Climate Prediction Center (NOAA 2012) for the months of May, June and July (Peregrine breeding season). Local weather data collected from weather stations in Qaqortoq and Narsarsuaq were available from The Danish Meteorological Institute (Cappelen 2016). We calculated mean daily temperature and total precipitation (for the 24-hour period) for the three breeding cycle periods: pre-laying (May), incubation (June) and nestling period (July). Missing precipitation values in the data set were estimated based on mean values of surrounding measurements; if precipitation and temperature values were missing for more than 24 hours, values for that day were omitted from analyses.

In order to test whether extreme weather events are particularly harmful for the Peregrines breeding success during any particular period of the breeding season (pre-laying, incubation or nestling period), we estimated the extreme weather variables for each period (i.e. May, June and July) as well as for the breeding season as a whole (May–July). We calculated four extreme weather variables 1) extreme low temperatures, 2) extreme precipitation, 3) consecutive rainy days and 4) total days with extreme weather (cumulative variable), based on Bradley *et al.* (1997), Fisher *et al.* (2015) and Pipoly *et al.* (2013). Extreme low temperatures were defined as all values under the 10th percentile of the average daily mean temperature (pre-laying between [–9.7 °C and 10.3 °C], incubation between [1.5 °C and 5.5 °C] and for nestling period between [4.9 °C and 8.1 °C]). Extreme precipitation was defined by adding the standard deviation (SD) to the average mean precipitation for each period (only days with rain over 0.1 mm included) as follows: pre-laying (mean + SD = 5.8 mm + 8.0

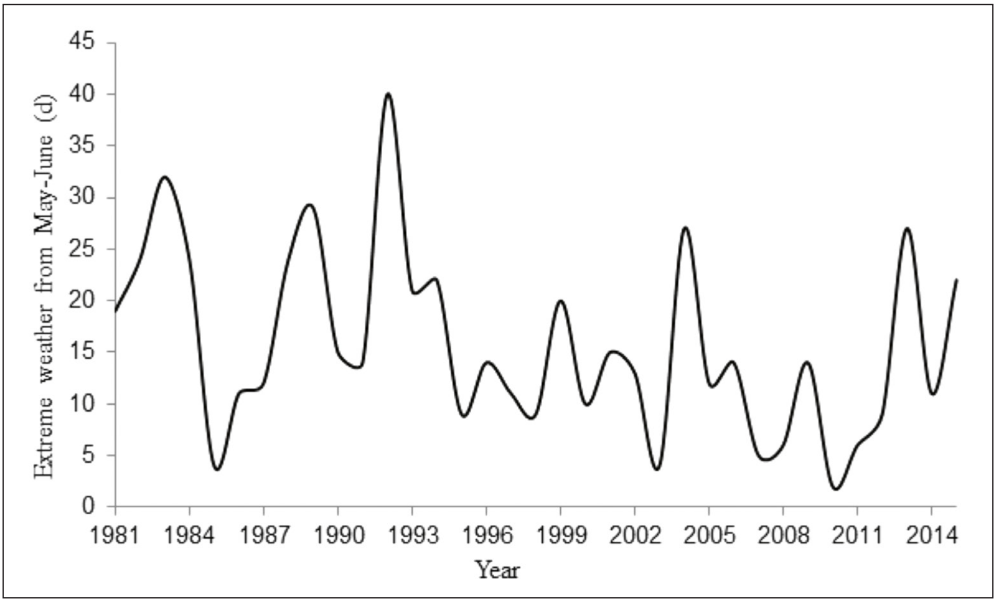

Figure 2. Variation in days with extreme weather over the study period 1981–2015
2. ábra A szélsőséges időjárású napok megoszlása az 1981–2015 közötti vizsgálati időszakban

mm), incubation (mean + SD = 6.5 mm + 10.0 mm) and nestling period (mean + SD = 7.0 mm + 9.9 mm). Approximately 10% of all days with rain were extreme. Two or more days with continuous rain and with equal or higher than mean precipitation were defined as consecutive rainy days. In order to understand the overall *additive* effect of all extreme weather events on breeding success we added up all days with extreme weather events into one variable: total extreme days. This variable showed high inter-annual fluctuation but no overall change over time *(Figure 2)*.

Response Variables

We used two response variables in this study to represent the Peregrine's breeding success, (1) young per site and (2) nest success. Young per site is the total number of young divided by the monitored sites (known territories) for each monitored year (n = 33). Nest success is the proportion of territorial pairs (in %) producing young during each monitored year (n = 33).

Data analyses

Due to the small data set (n = 33), we used a statistical approach where each of our hypotheses was directly tested with univariate or multiple linear regressions. With a larger data set, we could have used a more comprehensive approach, such as analyzing the predictive power of a large number of potential weather-related predictor variables (main effects and interactions) in conjuncture with a model simplification approach according to Aikaike's Information Criterion to determine the best model. However, this approach could not be used here since extreme weather variables are often strongly correlated, such as extremely low temperature with extreme precipitation in July ($R^2 = 0.43$, in our data set), and they can therefore not be used together in the same model.

We thus proceeded as follows: In order to answer question 1, linear regression analyses for each period (pre-laying [May], incubation [June] and nesting period [July]) tested whether extreme weather was connected to the strength of the NAO. In order to answer question 2 and 3, we used further linear regression analyses to test the effects of extremely low temperature, extreme precipitation, consecutive rainy days and total days with extreme weather on young per site and nest success for each of the different breeding seasons, as well as for the breeding season as a whole. In order to test question 4, whether breeding success was more sensitive to the different extreme weather events during any particular breeding period; R^2-values from all regression analyses, conducted separately for each period (May, June and July) were compared to each other as well as to the R^2-values for the breeding season as a whole. We used the statistical software IBM SPSS Statistics 24 for all statistical analyses. Significance levels were set at $\alpha = 0.05$ and data were log10(x) transformed to achieve a normal distribution.

Results

We found a significant positive relationship between total extreme days and NAO during all three defined periods of the breeding season: the pre-laying period in May ($P < 0.001$, $R^2 = 0.32$), during the incubation period in June ($P < 0.001$, $R^2 = 0.44$) and during the nestling period in July ($P = 0.005$, $R^2 = 0.18$).

We also found significant relationships between several of the extreme weather variables and the breeding success of the Peregrine *(Table 1, Figure 3, 4)*. When analyzing the entire breeding season, nest success was significantly negatively related to extreme precipitation

Table 1. Relationship between extreme weather overall and during the different periods of the breeding season (May, June or July) and Peregrine breeding success (nest success and young per site). R^2 represents the proportion of variation explained by the predictor variable, P represents the P-value and the relationship whether the relationship between the variables is positive or negative

1. tábla A szélsőséges időjárási tényezők és a vándorsólymok költési sikerének (fészek sikeressége és fiókák száma) kapcsolata, összességében és a költési időszak egyes periódusaiban (május, június és július). R^2 – a független változó magyarázó ereje, P – szignifikancia érték. A változók közötti összefüggés irányát + vagy – jelöli

	Nest Success			**Young per site**		
	Relationship (+ or –)	R^2	P-value	Relationship (+ or –)	R^2	P-value
Breeding Season (May – July)						
Extreme low temperature (d)	–	0.207	**0.004**	–	0.202	**0.004**
Extreme precipitation (d)	–	0.090	**0.045**	–	0.129	**0.020**
Consecutive rainy days (d)		0.002	0.405		0.015	0.250
Total extreme days (d)	–	0.221	**0.003**	–	0.271	**0.001**
Pre-laying period (~ May)						
Extreme low temperature (d)	–	0.098	**0.038**	–	0.177	**0.007**
Extreme precipitation (d)		0.035	0.150		0.039	0.136
Consecutive rainy days (d)		0.001	0.439		0.024	0.194
Total extreme days (d)	–	0.099	**0.037**	–	0.184	**0.006**
Incubation period (~ June)						
Extreme low temperature (d)	–	0.155	**0.012**	–	0.155	**0.012**
Extreme precipitation (d)		0.064	0.077		0.083	0.052
Consecutive rainy days (d)		0.015	0.250		0.040	0.132
Total extreme days (d)	–	0.199	**0.005**	–	0.224	**0.003**
Nestling period (~ July)						
Extreme low temperature (d)		0.051	0.104		0.021	0.210
Extreme precipitation (d)		0.007	0.325		0.020	0.218
Consecutive rainy days (d)		0.005	0.343		0.018	0.227
Total extreme days (d)		0.028	0.178		0.013	0.266

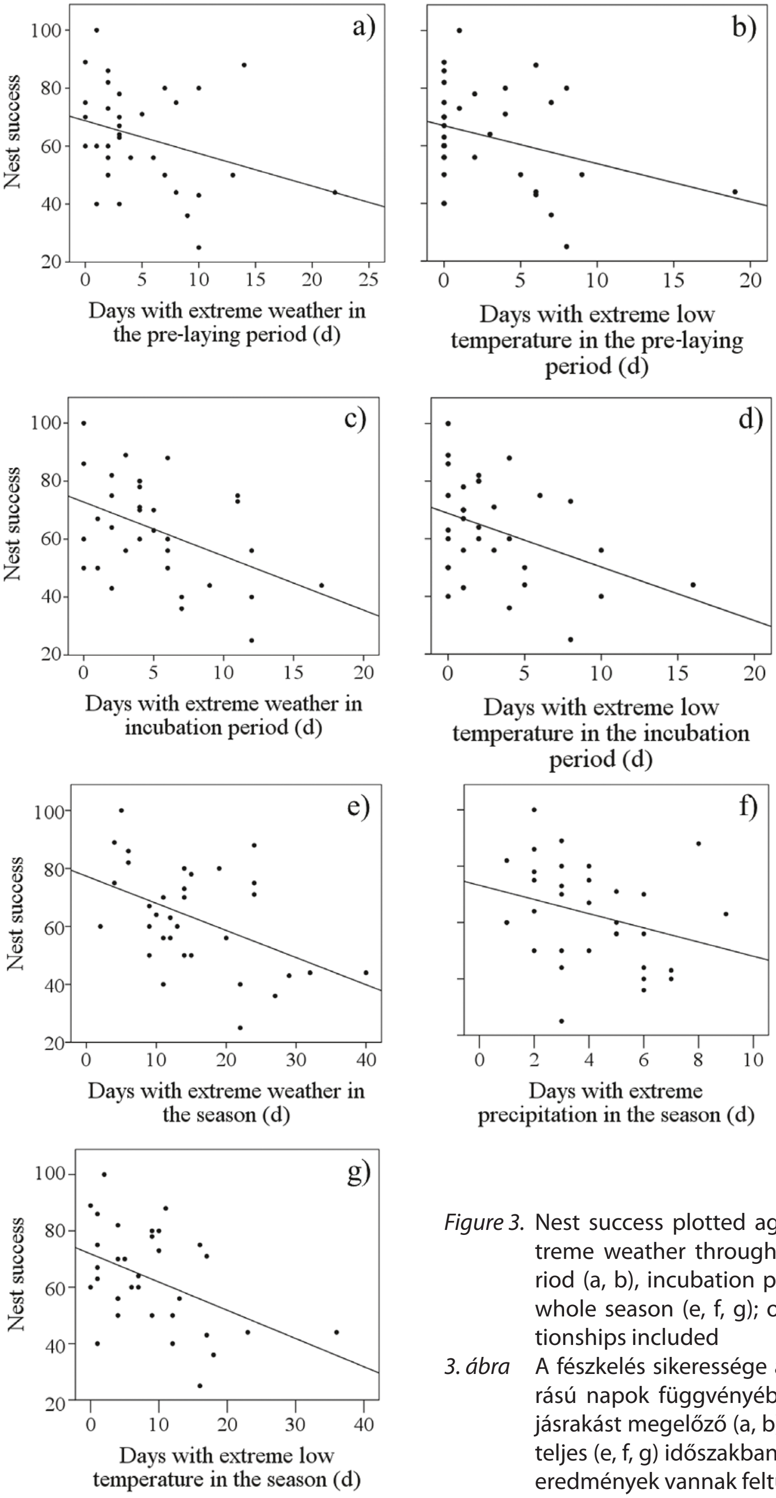

Figure 3. Nest success plotted against days with extreme weather through the pre-laying period (a, b), incubation period (c, d) and the whole season (e, f, g); only significant relationships included

3. ábra A fészkelés sikeressége a szélsőséges időjárású napok függvényében ábrázolva, a tojásrakást megelőző (a, b), a kotlási (c, d) és a teljes (e, f, g) időszakban. Csak a szignifikáns eredmények vannak feltüntetve

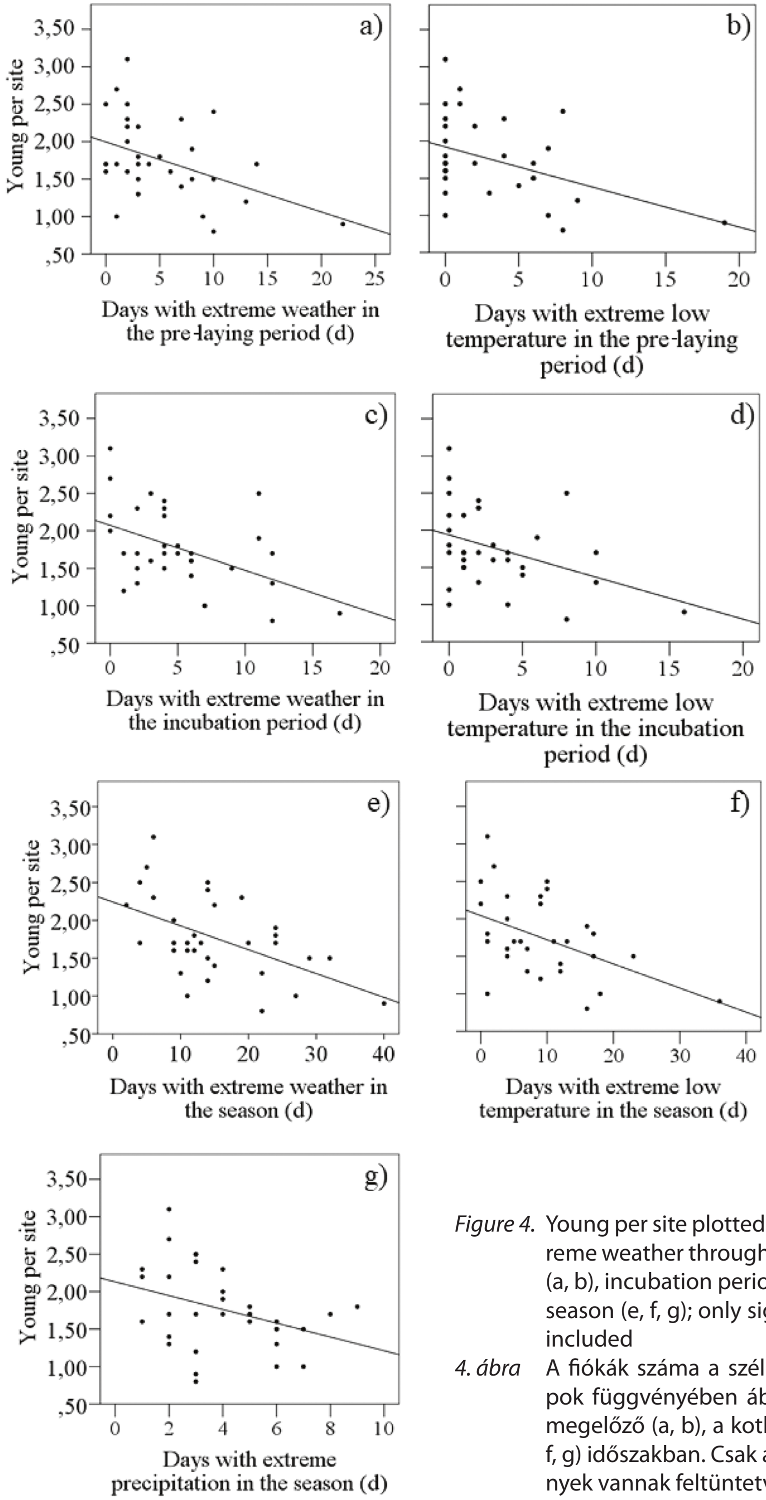

Figure 4. Young per site plotted against days with extreme weather through the pre-laying period (a, b), incubation period (c, d) and the whole season (e, f, g); only significant relationships included

4. ábra A fiókák száma a szélsőséges időjárású napok függvényében ábrázolva, a tojásrakást megelőző (a, b), a kotlási (c, d) és a teljes (e, f, g) időszakban. Csak a szignifikáns eredmények vannak feltüntetve

(Figure 3f), extreme low temperatures, *(Figure 3g)* as well as the additive variable (including temperature and rain) total days with extreme weather *(Figure 3e)*. Young per site was dependent on extreme precipitation *(Figure 4g)*, extreme low temperatures *(Figure 4f)* and total days with extreme weather *(Figure 4e)* in the breeding season *(Table 1)*. However, we found no significant relationship between breeding success and the predictor variable consecutive rainy days ($P > 0.05$).

When considering weather in the three defined periods of the breeding season separately, extreme low temperature and total extreme days emerged as factors with significant relationships with both the dependent variables in the pre-laying period and the incubation period *(Table 1)*; no significant relationships with weather in the nestling period was found. Total extreme days in the incubation period was the strongest predictor of nest success as well as of young per site.

Our results showed that the breeding success of the Peregrines is linked to extreme weather events *(Figure 2, 3)* and the strongest predictor for overall breeding success the additive weather variable “total extreme days in the season”, explains 22% and 27% of the variation in nest success and young per site, respectively.

Discussion

The total number of extreme days in all breeding periods (May, June and July) significantly correlated with the NAO index (answering question 1). The number of days with extreme low temperature negatively affected breeding success during the whole breeding season, as well as separately for the pre-laying and the incubation period, but not the nestling period (answering question 2). Extreme precipitation (but not consecutive rainy days) negatively affected breeding success during the whole breeding season. However, no significant relationship was detected for extreme precipitation or consecutive rainy days on breeding success during any of the separate breeding periods (May, June or July) (answering question 3). Last, we found that extreme weather events early during the breeding season (pre-laying and incubation) had stronger effects on breeding success than extreme weather during nestling period (answering question 4).

We found the strongest relationship between Peregrine breeding success and the additive weather variable “total number of extreme days” measured over the whole breeding season. This is not surprising for several reasons. Firstly, rain events are usually associated with cold days in the study area (although cold, dry days do occur), so the combined factor total number of extreme days captures the combined power of days with bad weather. Secondly, the response variables on Peregrine productivity (young per site and nest success) are annual means only and, thirdly, overall breeding success measures reproduction and survival integrated over the whole breeding period and does not include any information on *when* in the breeding season the breeding attempt failed. Contrary to expectations from other studies, where rainfall has been identified as a cause for avian mortality during the nestling period, including Peregrines (Mearns & Newton 1988, Bradley *et al.* 1997, Anctil *et al.* 2014, McDermott & DeGroote 2016), extreme precipitation in our study showed a significant relationship for the entire breeding period and not for a specific period.

Since South Greenland can experience several consecutive days of wet, foggy weather, presumably affecting Peregrine food accessibility and thus posing a risk of exposure to eggs and young, we expected to find a negative effect of consecutive rainy days on the Peregrines' breeding success. We found no such effect which may be because we applied too conservative criteria for consecutive rainy days: we only included days with mean precipitation or above. In addition, there is local spatial variations in weather, which are not well captured in our data since there are only two weather stations in the area.

The effect of weather on productivity is mediated by the parents' selection of a suitable protective nest ledge and Peregrines frequently return to successful nest sites and desert nesting sites that are exposed to direct rainfall or that have become wet or flooded already during the pre-laying period (Olsen & Olsen 1988, Bruggeman *et al.* 2016). However, there is a limit to how effective this strategy is (Olsen & Olsen 1988, McDonald *et al.* 2004): an experimental Arctic study reduced nesting mortality through rain events by installing nest boxes (Anctil *et al.* 2014). This shows clearly that nest mortality is, at least partly, caused by exposure to rain. Especially small nestlings in the Arctic are at risk from hypothermia caused by low temperatures and humidity due to their lack of thermoregulation (Fletcher *et al.* 2013, Lehikoinen *et al.* 2013, Pipoly *et al.* 2013, Anctil *et al* 2014), but even in temperate regions a single daylong intensive rainfall event can kill 2 week-old young (P. Lindberg and N. P. Andreasen, pers. com.). We conclude that extreme rain events are likely to affect peregrines' breeding success. However, it is not clear under which circumstances and in combination with which other factors extreme precipitation is most detrimental to breeding success. Other weather phenomena besides the NAO may also influence number of days with extreme weather; nevertheless we can conclude that strengthening of the NAO is one factor that is influencing the local weather patterns and that NAO may possibly be used as a predictor for Peregrine productivity.

We have shown that locally extreme weather events are affecting Peregrine productivity negatively in subarctic South Greenland, but our data do not allow finer identification of critical periods of the breeding cycle in order to pinpoint the specific mortality events or the Peregrine's ability to adapt to these extreme weather events. Fine-resolution information on individual nesting failures – timing in the breeding cycle, age of eggs/young – would be needed. This calls for simple upgrades to existing field procedures by upscaling the use of automated recordings by cameras (Anctil *et al.* 2014, Robinson & Prostor 2017) which we would recommend for any long-term studies of raptors, partly in order to monitor the effects of rapidly changing climate.

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Population trends of Peregrine Falcon in Northern Spain – Results of a long-term monitoring project

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Abstract We monitored Peregrine Falcon *(Falco peregrinus)* population in Bizkaia, Northern Spain, during two decades (1998–2017). Our population increased from 34 to 47 territorial pairs, as did other European populations until the first years of the 21st century, and then declined until 34 territorial pairs in 2017. The combination of catastrophic events (Prestige oil spill), increasing rain in winter and spring, and direct and indirect mortality factors significantly affected incubation onset, productivity and population stability, which in turn could impact on the floater population. Rain in February significantly affected incubation onset, which showed a slight positive trend during the last decade. Juvenile females laid 12 days later than adults, and each adult female started incubation in the same dates every year. However, the proportion of juvenile females did not significantly increase as might have been expected. Moreover, productivity was inversely related to incubation onset dates. Rain in April and May also affected productivity, and combined with short term extreme weather events determined a decreasing productivity during the last decade. Moreover, apart from human persecution (which caused 40.30% of the known deaths of Peregrines), we found 18 cases of breeders affected by infectious diseases, also related to weather. The combined effects of these factors, and the low availability of adequate nesting sites, negatively affected (i) territorial populations, (ii) productivity, and (iii) floater population, which in turn also determined territorial population and productivity.

Keywords: productivity, population decline, floater population, incubation onset, repeatability, weather

Összefoglalás A vándorsólyom *(Falco peregrinus)* állományának alakulását két évtizeden keresztül (1998–2017) követtük nyomon Bizkaiaban, Észak-Spanyolországban. Ez idő alatt az állomány 34-ről 47 territoriális párra növekedett, hasonlóan a más európai állományoknál megfigyelt trendekhez, majd 2017-re újra 34 párra csökkent. A növekvő téli és tavaszi csapadék, katasztrófák (pl. Prestige olajkatasztrófa), és a közvetlen és közvetett mortalitási tényezők együttes hatása befolyásolta a költési idő kezdetét, a szaporodási sikert és a populáció stabilitását, ami ennek következtében hatással volt a nem költő állományra. A februári eső jelentősen befolyásolta a kotlás kezdő időpontját, ami az elmúlt időszakban némileg későbbre tolódott. A fiatal tojók 12 nappal később rakták le a tojásokat, mint az adult tojók. Minden egyes adult egyed azonos napon kezdte a kotlást, minden évben. Azonban a fiatal tojók aránya nem nőtt jelentősen, ahogy az várható lett volna. Sőt a költési siker a kotlási időszak eltolódásával ellentétesen alakult. Az áprilisi és májusi eső szintén befolyásolta a költési sikert, és a rövid időtartamú extrém időjárási eseményekkel együtt meghatározta az elmúlt évtized csökkenő tendenciáit. A fő probléma a szándékos pusztítás volt (ami az összes vándorsólyom pusztulás 40,3%-át okozta). Ezen felül 18 esetet találtunk tenyésztőknél, melyeket fertőző betegségek okoztak, és amiket az időjárás is befolyásolt. Ezen tényezők együttes hatása és a megfelelő fészkelőhelyek alacsony száma negatívan befolyásolta a (i) a territoriális populációkat, (ii) a költési sikert és a (iii) nem költők állományát.

Kulcsszavak: költési siker, állománycsökkenés, nem-költő (floater) populáció, kotlási időszak kezdete, megismételhetőség, időjárás

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Introduction

Peregrine Falcon *(Falco peregrinus)* populations increased throughout the 1980s and 1990s in most of their distribution range (White *et al.* 2013). Once populations reach carrying capacity, which is shaped principally by food and nest substrate availability, it is expected that density-dependent regulation starts to operate on each case (Newton 1998, Bruggeman *et al.* 2015), although not always is so evident (Wootton & Bell 2014). Many factors influence population growth, but only density-dependent factors, whose effect increase with crowding, can bring the size of a population under control (Rockwood 2015). As it is often the case, denso-dependent regulations mainly affect productivity and in a lesser extent population growth, which tends to asymptote (see e.g. Heuck *et al.* 2017). However, denso-dependent factors do not explain per se population declines, and other denso-independent factors usually appear to modulate populations (Monneret *et al*. 2018). In fact, poisoning by contaminants, increasing of mortality factors and changes in climate conditions affect survival rates of territorial and non-territorial falcons (Zuberogoitia *et al.* 2006, Smith *et al.* 2015, Newton *et al.* 2016). Moreover, most studies on density dependence in animals have focused primarily on the breeding populations, and have generally ignored the possibility that non-breeder mortality has the potential to affect persistence of populations (1) rescuing small populations from extinction by replacing the breeders that die or disperse out of the populations (Kokko & Shuterland 1998), and (2) buffering the impact of environmental and demographic stochasticity on the viability of the breeding population (Walters *et al.* 2002, Grimm *et al.* 2005, Penteriani *et al.* 2009).

Many populations of territorial species are composed of both territory holders and non-territorial, usually nonbreeding individuals, commonly defined as ‘floaters’ (Sergio *et al.* 2009). Floaters are multifaceted population members that are better understood when considered in three nonexclusive (and frequently interacting) contexts: (1) the ecological scenarios underlying breeding population dynamics; (2) the process of natal dispersal, and (3) the age cohorts contributing to floater pools (Penteriani *et al.* 2011). Newton (1998) observed that, for Peregrine Falcons, a ratio of one or more floaters to one breeder could be expected for healthy populations, and that larger pools of floaters were associated with more stable breeding populations. However, studying floaters has invariably proven difficult because of their elusive behaviour (see e.g. Bondì *et al*. 2018), to the point that they have been referred to as a ‘shadow’ population living in a secretive ‘underworld’ (see Sergio *et al.*

2009). The first indirect evidence for the existence of floaters was the rapid replacement of territorial owners following their experimental removal (Newton 1992).

When mortality is high in floater settlement areas the consequences are diverse. Normally at the beginning of a population decline resulting from a major loss of floaters, the relative stability of breeding performance could generate the false impression that the population is healthy, even if some breeding territories are lost (Penteriani *et al.* 2011). Additionally, when other factors are combined with floater mortality to reduce the income of individuals to the floating contingent, it may be detected an acceleration rate of population decline due to the lack of individuals to replace the loss of territorial owners.

In the present work we investigate and discuss the demographic trends of a Peregrine population in Bizkaia (Northern Spain). Our study population increased as well as other European populations until the first years of the 21st century (White *et al.* 2013, Beran *et al*. 2018), and after that experienced strong decline. Here we show some of the factors explaining this negative trend, and we stress the hidden effect over floater population which actually may be a key argument to explain the observed situation.

Study area

The study area covered the whole administrative territory of Bizkaia (northern Spain; area *ca.* 2,384 km^2; coordinates from 43º11'00" to 43º12'70"N and from 3º12'70" to 2º13'10"W). The landscape is hilly (50 km separate sea level from the highest altitude, at 1,480 m a.s.l.) and characterized by the presence of extensive urban and industrialized areas. More than 50% of the area is dedicated to forestry, at the expense of traditional small-scale farming. The weather is dominated by a wet and warm Atlantic influence and it is included within the rainiest regions of Europe (www.climate-charts.com/World-Climate-Maps.html). The weather is temperate, with an annual rainfall of 1,000–1,300 mm and a mean annual temperature of 11–12 ºC (www.euskalmet.euskadi.eus).

Methods

The Peregrine Falcon population in Bizkaia was systematically surveyed from 1998 to 2017. In each year we started searching for falcons 30 days before the earliest local laying date recorded for the population (20th February, Zuberogoitia *et al.* 2002). At this time of the season, breeding pairs can be readily detected since they frequently engage in courtship displays, and eyries can be located by observing individuals displaying near the crags and sea cliffs where they will eventually breed. During this period we focused our efforts on identifying adult breeders (Zuberogoitia *et al.* 2013, Zabala & Zuberogoitia 2014). Once eggs were laid, we monitored the Peregrine incubation behaviour with telescopes and binoculars. The monitoring points were distant to the eyries (300–1000 m, depending on the surrounding relief and the degree of tolerance to humans) to avoid any undesirable effects of the observer on bird behaviour. In order to gather data on productivity (number of fledglings per nesting attempt) and to ring the nestlings, we visited each nesting site at least twice per breeding season, before the young fledged. We first climbed to the eyrie when the nestlings were 20–30 days old (for more details see Zuberogoitia *et al.* 2013). During the study period we also put a great deal of effort in identifying adult breeders of each territory (for further details see Zuberogoitia *et al.* 2013, Zabala & Zuberogoitia 2015).

Incubation onset is a crucial factor in the biology of a species which, usually, does not receive proper attention, perhaps because it is difficult to collate a reliable date of this event. Scientists normally use indirect proxies obtained during nestling monitoring (age of nestling plus 32 days of incubation, see e.g. Zuberogoitia *et al.* 2002). However, using this method, it results in an overestimation of successful attempts and lack of data regarding those clutches that failed. In order to get a better approximation to incubation onset, we also monitored laying dates and beginning of incubation by direct observation.

Weather data was obtained from three meteorological stations located in the north-eastern coast (Matxitxako), southern mountains (Orozko) and western valleys (Cerroja) which represent climatic variations in the area (www.euskalmet.euskadi.eus). We used the average data of the three stations for each case (rain and number of rainy days per month).

Data analysis

We ran Generalized Linear Mixed Models (GLMMs) with Gaussian (normal) and Poisson distribution on the response variables. First, we used the incubation onset (normal distribution) as response variable and precipitation and rainy days during February and their interaction as predictive factors; age of females (juvenile or adult) was included as a fixed factor, and year as a random factor. Second, we used the productivity (number of fledglings per territorial pair: 0–4, Poisson distribution) as a response variable to determine the effect of incubation onset dates (predictive variable), considering territory as a random factor. And, third, to compare breeding success from different years while controlling for annual variations in breeding success, a Breeding Quality Index (BQI, normal distribution) was used as the response variable. BQI was calculated as the number of fledglings produced by an animal minus the annual mean of fledglings produced by all the monitored animals the same year (Zabala & Zuberogoitia 2014, 2015). We used BQI to analyse the effect of precipitation and number of rainy days in April and May and their interactions. To account for possible non-independence relations, territory identity was included as a random factor.

Models were performed through “glmer” and “Anova” functions implemented in the “lme4” (Bates *et al.* 2015) and “car” (Fox & Weisberg 2011) packages for R (R Core Team 2015).

We used one-way ANOVA entering female as a factor to determine if incubation onset dates of each female resembled each other more than they did the overall population. Further, we calculated repeatability as described by Lessels and Boag (1987) and calculated standard errors associated with the repeatability as described by Becker (1984). Repeatability is the fraction of behavioural variation that is due to differences between individuals. Formally, repeatability (r) is the variance among individuals and s^2 is the variance within individuals over time. Behaviours that show relatively low within-individual variance compared to high among-individual variance are more repeatable. In other words, when individuals

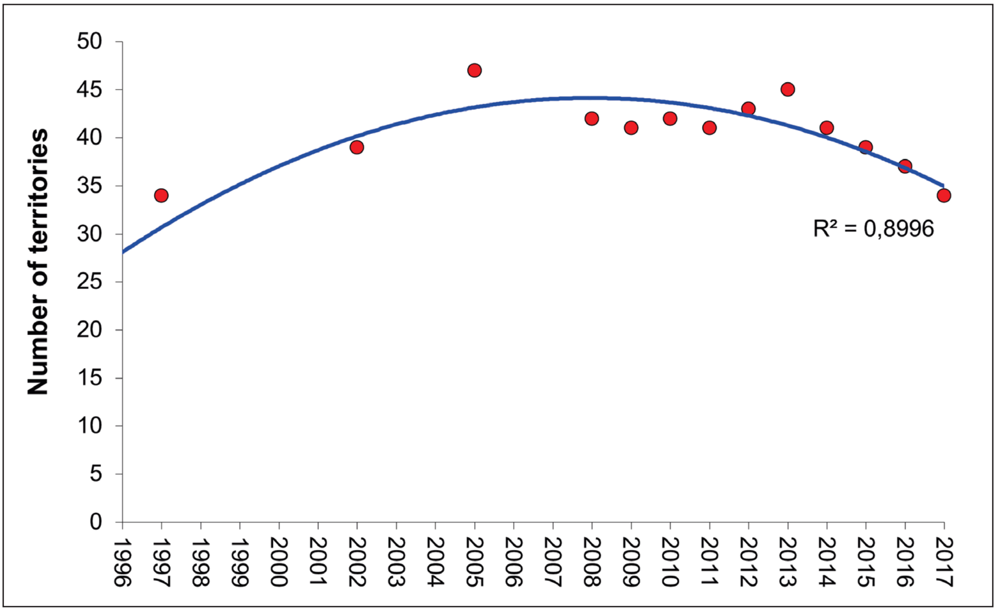

Figure 1. Population trend of Peregrine Falcon in Bizkaia, Northern Spain, during the study period (1997–2017)

1. ábra A vándorsólyom populáció alakulása a vizsgálati időszakban (1997–2017) Bizkaia, Észak-Spanyolország területén

behave consistently through time and when individuals behave differently from each other, then the behaviour is repeatable (Bell *et al.* 2009).

Mean values have been reported with (±) the standard deviation. Statistical significance was set at $P < 0.05$.

Result and Discussion

Population trend

When we started to monitor the Peregrine population we found 34 territorial pairs, just the same number than 21 years later. The population grew steadily to 47 territorial pairs (2005), following the recovery of the population over the European's range (see White *et al.* 2013) and later started a slight decline until 2017 *(Figure 1),* as occurred also in other European populations (Kéry *et al*. 2018, Monneret *et al*. 2018, Prommer & Bagyura 2018).

Reproductive parameters and factors affecting them

Productivity of Peregrine Falcons followed a negative trend ($R^2 = 0.59$, productivity = $-0.08*\text{year} + 2.47$) *(Figure 2)*. This figure was gradually affected by different factors where some of them hide the effect of others.

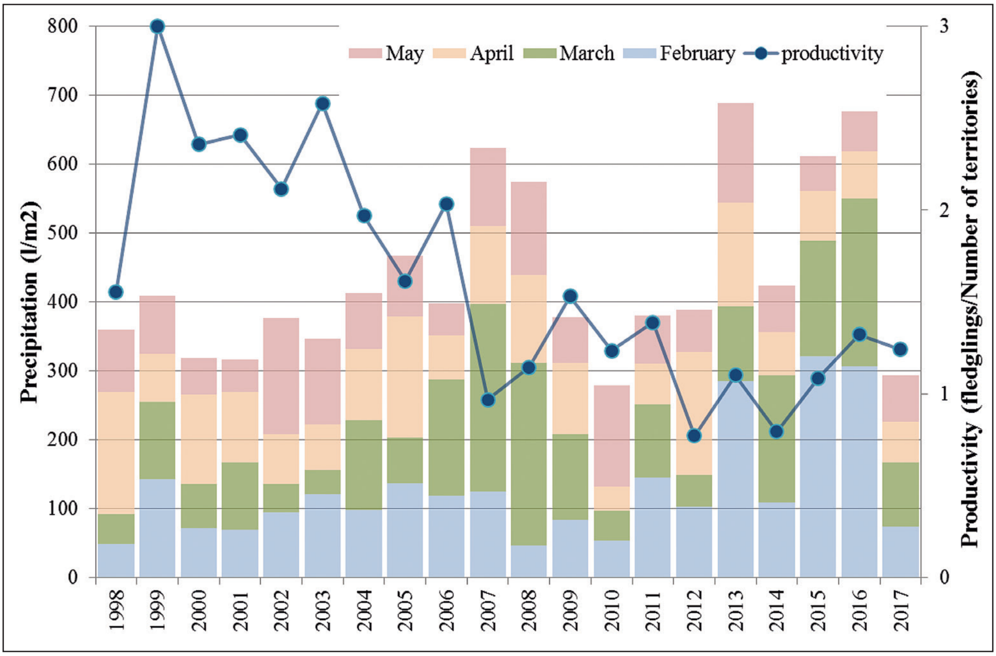

Figure 2. Productivity of Peregrine Falcons and cumulated precipitation during the breeding seasons (February-May) in Bizkaia, Northern Spain, during the study period (1998–2017)

2. ábra A vándorsólymok produktivitása és a csapadék megoszlása a költési időszakban (február-május) Bizkaiaban, Észak-Spanyolországban, a vizsgálati időszakban (1998–2017)

Catastrophic events

On the 13th November 2002, the tanker Prestige sunk off La Coruña (NW Spain) and provoked an oil spill that affected the whole of the Cantabrian Coast and the Southwest of France, including our study area. An undetermined number of adults was affected by lethal oil concentrations through eating polluted prey, increasing the turnover rate of territorial adults from 22% (before Prestige) to 30% (Zuberogoitia *et al.* 2005). Moreover, at the same time, an unknown proportion of the Peregrine Falcons carried sub-lethal levels of pollutants which caused breeding disorders. On the one hand, an evident effect was the loss of clutches, mainly during incubation, due to the death of females and to failures caused by high levels of polycyclic aromatic hydrocarbons in the eggs which killed embryos (Zuberogoitia *et al.* 2005). On the other hand, the bioaccumulation of pollutants caused even more serious long-term effects, affecting the reproductive capacity of males and females which remained in the territory. Further, some sterile birds also remained in the territory during several years, affecting the medium-term productivity rate.

The effect of this catastrophic event was buffered due to the combination of both relative dry springs in the following years, which favored the productivity rate, and previous high reproductive seasons *(Figure 2)*, that produced a large number of floaters. However, we did not know the proportion of floater population affected by lethal and sub-lethal pollution

Table 1. Results of GLMM to evaluate the effect of precipitation (rainfall and number of rainy days and their combined effect) and age of females on the incubation onset of Peregrine Falcons in Bizkaia during the study period (1998–2017). The values of the estimator, standard error, the z value and its corresponding P value probability are shown. Significant values are highlighted in bold

1. táblázat Az általánosított lineáris kevert modell eredményei a csapadék hatásának elemzésére (eső és esős napok száma, illetve ezek együttes hatása), és a vándorsólyom tojók életkora a kotlás kezdetén Bizkaiaban, a vizsgálati időszak alatt (1998–2017). A táblázat a paraméterbecslést, a standard hibát, a z és a P értékeket mutatja. A szignifikáns értékek félkövéren szedettek

Values	**Estimator**	**St Error**	***z***	***P***
Intercept	**19.28**	**4.72**	**4.08**	**< 0.001**
Factor (female age) juvenile	**11.30**	**2.36**	**4.79**	**< 0.001**
Rainfeb	**–0.03**	**0.05**	**–0.68**	**0.015**
Dayfeb	–0.26	0.27	–0.95	0.89
Rainfeb* Dayfeb	0.003	0.002	1.13	0.26

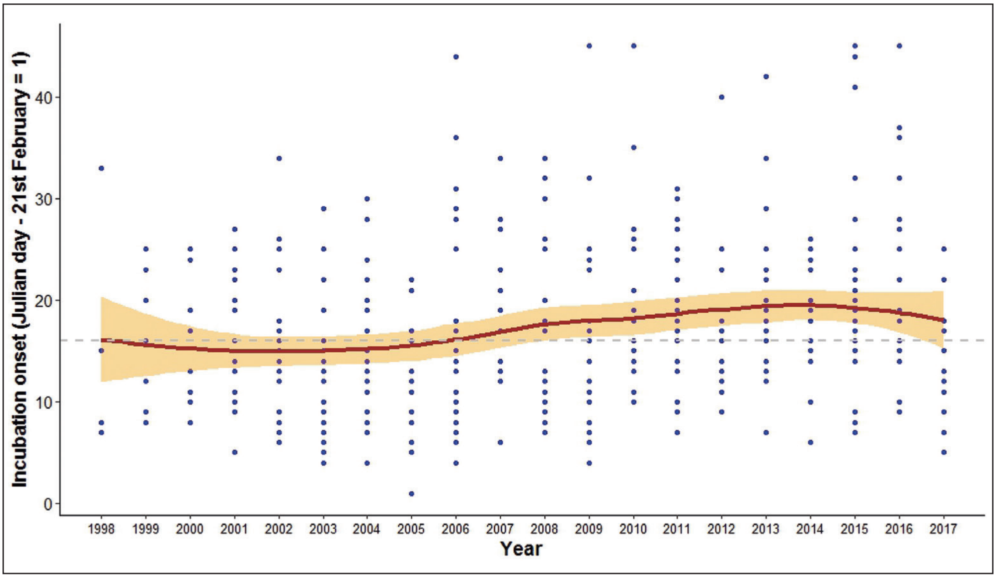

Figure 3. Incubation onset of Peregrines in Bizkaia, Northern Spain, during the study period (1997–2017). Dates were transformed to Julian dates, being 21st February the first day (the earliest incubation onset). Average dates (line) and standard error (shaded area) are represented using a smoothed curve. Dashed line refers to 16th day

3. ábra A vándorsólymok kotlási dátumainak eltolódása Bizkaia, Észak-Spanyolország területén a vizsgált időszakban (1997–2017). A dátumok a Juliánusz-naptár alapján módosított értékek, vagyis február 21 a kezdő dátum (a legkorábbi eltolódás). Az átlagos dátumokat vonal, míg a standard hibát árnyékolt terület jelzi. A szaggatott vonal a 16. napnak felel meg effects, although we suspect that it might have been high, if we consider the effect observed on territorial falcons.

Late winter weather conditions and incubation onset

The incubation onset of Peregrines showed a slight ascendant trend during the last decade *(Figure 3)*. In a first sight, this seems to be due to a direct relationship with rain in February that affects dates of incubation onset *(Table 1)*. Winter weather also determines breeding phenology of Peregrines and their prey species in other latitudes (Bruggeman *et al.* 2015). However, this factor alone does not explain the observed constant trend of delaying dates. It may be expected that incubation onset is affected by the combined effect of other parameters. For example, juvenile females started incubation on average 12 days later than adults (*Table 1, Figure 4)*. Juvenile females lay eggs later than adults due to a delayed maturation (Deeming 2002).

Incubation onset strongly depends on individuals. Females laid clutches approximately in the same dates every year *(Table 2)*. The average range of variability on the laying dates was 13 ± 8.05 days in the study area. Our study suggests that the laying date may be a heritable trait of females, although our estimate of repeatability (0.53) indicates that current heritability may be affected by external factors. Intra-individual variability was linked with factors related

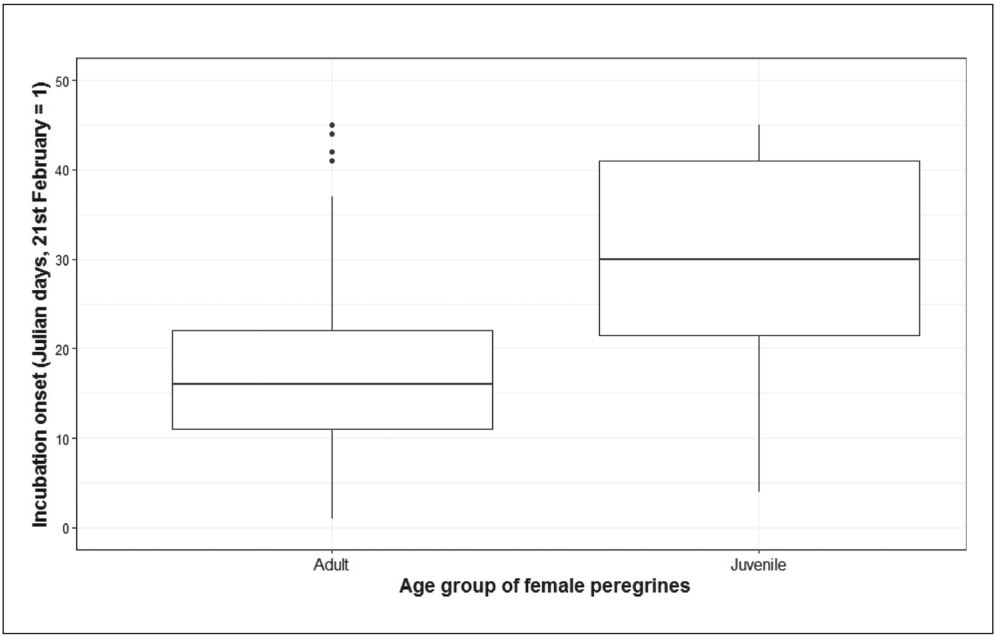

Figure 4. Boxplot showing differences between the incubation onset of adult and juvenile females of Peregrine Falcon in Bizkaia during the study period (1998–2017). Dates were transformed to Julian dates, being 21st February the first day (the earliest incubation onset)

4. ábra A kotlás idejének eltolódásában megmutatkozó különbség öreg és fiatal tojók esetében a vizsgálati időszakban (1998–2017) Bizkaiaban. A dátumok a Juliánusz-naptár alapján módosított értékek, vagyis február 21. a kezdő dátum (a legkorábbi eltolódás)

Table 2. Results of date repeatability analysis of the incubation onset of Peregrine Falcon in Bizkaia (1998–2017), considering first the same female and second the same territory but changing the female

2. táblázat A vándorsólyom költések dátum-eltolódásainak ismételhetőségi elemzésének eredményei Bizkaiaban (1998–2017). Az első esetben ugyanaz a tojó, míg a második esetben ugyanaz a terület, de más tojó figyelembe vételével

	Ri	SE	F	df	P
Same female	0.53	0.47	3.26	212	0.000
Changing female	0.11	0.89	1.238	89	0.239

to the change of mate that always caused delayed laying dates, or body condition of the female (pers. observ.). However, when we analysed repeatability considering the change of the females of each territory, we obtained a very low repeatability index (0.11, juvenile females were not considered in the analysis), which reinforced our previous remark on heritability.

During the first decade of our study, females kept the average incubation onset below the 16th Julian day, but after the declining of the productivity the incubation onset started to delay due to the incorporation of new females that laid eggs later than previous ones.

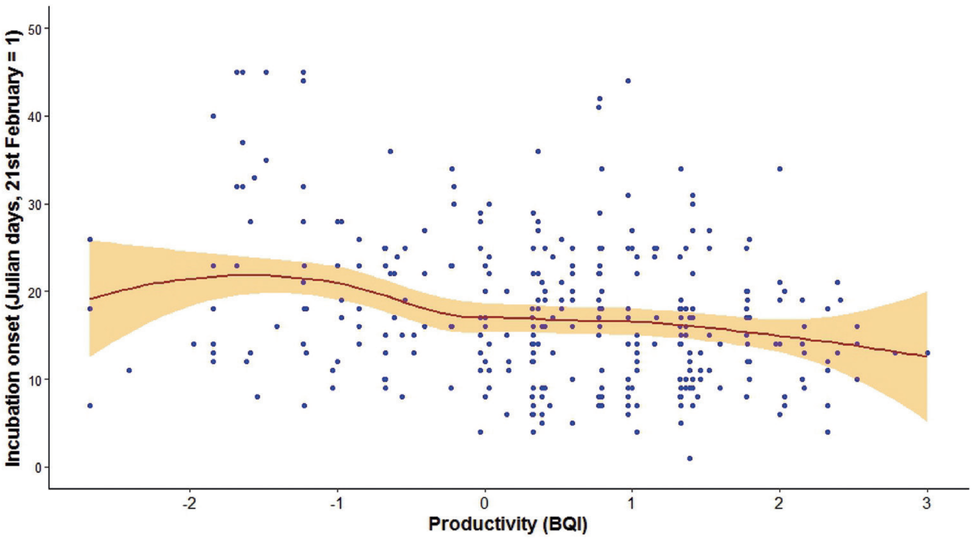

Figure 5. Relationship between productivity, measured as Breeding Quality Index (BQI), and the laying dates of Peregrines in Bizkaia, Northern Spain, during the study period (1998–2017). Dates were transformed to Julian dates, being 21st February the first day (the earliest incubation onset). Average (line) and standard error (shaded area) are represented using a smoothed curve

5. ábra A produktivitás és a mért költés minőségi index (Breeding Quality Index, BQI) kapcsolata, kiegészítve a vándorsólymok tojásrakási dátumaival Bizkaiaban (Észak-Spanyolország), a vizsgálati időszakban (1998–2017). A dátumok a Juliánusz-naptár alapján módosított értékek, vagyis február 21. az kezdő dátum (a legkorábbi eltolódás). Az átlagos dátumokat vonal, míg a standard hibát árnyékolt terület jelzi

As expected, productivity was inversely related to incubation onset dates (GLMM, Estimate = –0.036, SE = 0.007, t = –4.95, P < 0.001) (Tapia & Zuberogoitia 2018). However, the low value of the estimate is due to high variability in the results *(Figure 5)*. This variability is conditioned by other factors as weather during incubation and nestling raising phases.

Juveniles as breeders

During the study period we detected 36 yearling (second calendar year) females in the monitored population *(Figure 6)*. High number of juvenile Peregrines trying to nest implies a high turnover rate due to an increase in breeder mortality (Zuberogoitia *et al.* 2009).

Zabala and Zuberogoitia (2015) showed that yearling females were significantly worse breeders than adults. On the one hand, our results suggest that what makes the difference is not breeding experience or age but maturity, since we found no evidence of reduced success in first time adult breeders. On the other hand, according to Altwegg *et al.* (2014), observed survival estimates showed high juvenile mortality, with survival probability soaring to ≈ 0.75 in the second year and increasing slightly to ≈ 0.79 in older birds. These estimations suggest a strong selection against low quality Peregrines in the first year of life, before the breeding season begins. Therefore, we suggest that the yearling females occupying a territory could be highly successful birds and that territorial and mating displays could be accelerating the maturation process. More interesting is the fact that, with equal survival probabilities for adult breeders and breeding yearlings, individuals that start to breed as yearlings are likely to have a higher lifetime breeding success rate than other birds (Zabala & Zuberogoitia 2015).

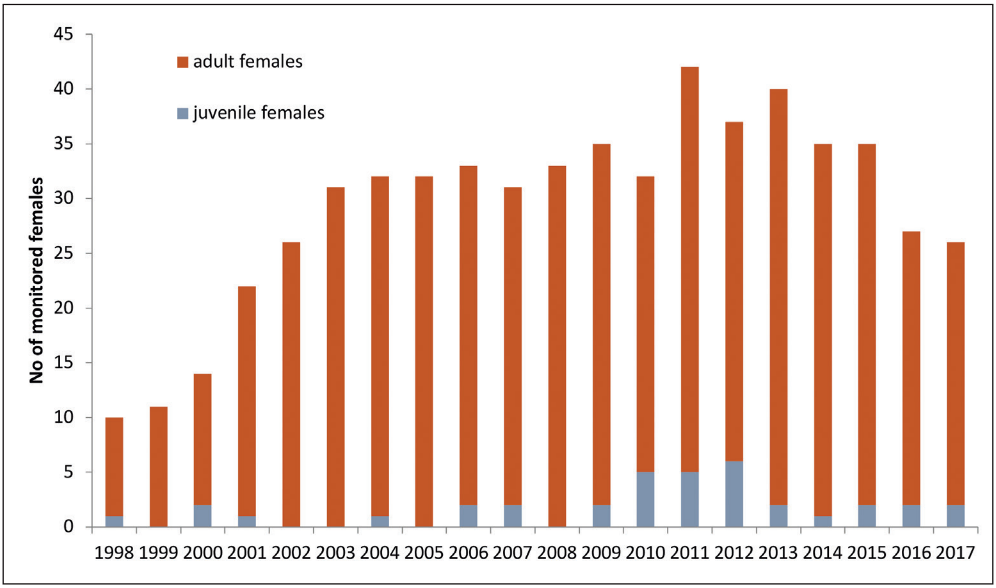

Figure 6. Number of juvenile and adult females in the monitored breeder populations of Peregrine Falcons in Bizkaia during the study period (1998–2017)

6. ábra A fiatal és öreg tojók száma a megfigyelt vándorsólyom populációban Bizkaiaban a vizsgálati időszakban (1998–2017)

Simultaneously, during the study period we only found five yearling breeding males. Two of them did not breed in their first attempt and disappeared, another did not breed in the first year but he did in the subsequent years. The fourth started the breeding season but failed during the laying process, and the fifth male paired in the 2015 breeding season with a fourth calendar year female. They successfully raised two fledglings out of three hatched chicks.

April and May rainfall

Zuberogoitia *et al.* (2015) proved that low April rainfall significantly increased productivity in our study area. The amount of precipitation and duration of rain affected nestlings during their first weeks of life. The affection was different considering eyrie quality and shelter capacity (Zuberogoitia *et al.* 2015), as it has also been reported in other regions (Bruggeman *et al.* 2015). However, the effect of April rainfall on nestling survival varied during the last years due to observed delayed reproduction of Peregrines (see below) and strong effects of short term extreme weather events.

Productivity, considering the whole study period (1998–2017) was negatively affected by rain in April and the combination of amount of precipitation and number of rainy days of April, but also the combination of rain in April and May and the number of rainy days in April and May *(Table 3)*. However, the low value of the estimates suggests that the effect could be masked by other factors not considered in this analysis.

During the last years we detected strong effects of episodic weather events on nestling survival, which agrees with Anctil *et al.* (2013) and Carlzon *et al.* (2018). For example, the

Table 3. Results of GLMM to evaluate the effect of precipitation (rainfall and number of rainy days and their combined effect) during April and May on the Breeding Quality Index (BQI) of Peregrine Falcons in Bizkaia during the study period (1998–2017). The values of the estimator, standard error, the z value and its corresponding P value probability are shown. Significant values are highlighted in bold

3. táblázat Az általánosított lineáris kevert modell eredményei az április és májusi csapadék (csapadék mennyisége és az esős napok száma, valamint ezek kombinációja) a vándorsólyom költés minőségi indexére (Breeding Quality Index, BQI) gyakorolt hatásának becslésére, Bizkaiaban, a vizsgálati időszakban (1998–2017). A táblázat a paraméterbecslést, a standard hibát, a z és a P értékeket mutatja. A szignifikáns értékek félkövéren szedettek

Values	Estimator	St Error	*z*	*P*
Intercept	2.78	2.01	1.28	0.20
Rainapril	**0.05**	**0.01**	**3.79**	**<0.001**
Rainmay	0.01	0.01	1.60	0.11
Dayapril	-0.1	0.11	-1.53	0.13
daymay	**-0.46**	**0.14**	**-3.33**	**<0.001**
Rainapril:rainmay	**-0.01**	**0.00**	**-3.94**	**<0.001**
Dayapril:daymay	**0.02**	**0.00**	**3.26**	**0.001**
Rainapril:dayapril	**-0.01**	**0.00**	**-3.57**	**<0.001**
Rainmay:daymay	0.00	0.00	1.27	0.20

spring of 2017 was being dry *(Figure 2)* and the breeding success of Peregrines was high. However, a polar cyclone affected the study area during the last week of April. There was a combined effect of low temperatures that dropped close to 0 ºC, winds over 80 km/h and strong precipitations (over 20 l/m^2 in two days; www.euskalmet.euskadi.eus). In a period of five days we detected the die of all the nestlings of ten eyries out of 23 monitored nesting events. Most of the affected cases were related with exposed eyries, but not all, and unlikely some exposed eyries survived. The cyclone differentially affected the nestlings according to their age. Most of the affected nestlings were between 10 and 20 days old, whereas nestlings younger than 10 days and older than 20 days survived. Little nestlings were covered by their mothers, keeping warm and dry conditions, and nestlings over 20 days were able to thermoregulate and they were also attended by their parents. However, nestlings between 10 and 20 days old do not thermoregulate yet and their size caused that females were not able to cover them completely, which caused a continuous loss of heat and the progressive weakening occurred.

Similar events also occurred, for instance in the third week of April 2012, when the study area was strongly affected by an extra-tropical cyclone (which was called “Petra”), and during the second week of April 2016 or the last week of April 2014. All of these particular adverse weather events caused significant declines in the productivity of Peregrines *(Figure 2)*. Hence, the impact of weather in few days hides the above mentioned relationship between productivity and monthly weather statistics, making it the most difficult to find a significant relationship.

Mortality causes

The main cause of mortality of Peregrine Falcons in our study area was direct persecution *(Table 4)*. Actually, killing is still the first cause of death for birds of prey in Spain (Real *et al.* 2001, Martínez *et al.* 2006, 2016, González *et al.* 2007, Margalida *et al.* 2008). Notwithstanding their protected status, Peregrines are intentionally shot every year, even during the breeding season. Direct persecution has a double effect. First, productivity is affected due to the death of territorial birds and its effect related to the differential quality and experience of new breeders respect to older birds which stay in the same territory for years (Zabala & Zuberogoitia 2014). Second, direct persecution affects both territorial falcons and floaters. Therefore, floater population is reduced due to (1) direct mortality, (2) a lower than expected number of incomers, because of reduced productivity, and (3) the number of floaters that enter in empty territories. The floating population could become exhausted through increased recruitment to the breeding population (Franklin 1992).

Con-specific attacks during territorial conflicts caused six known deaths in our study population (8.96%) *(Table 4)*. This cause is not normally considered in scientific publications but it should be taken in mind for future researches. Killing by other Peregrines may be an important denso-dependent factor regulating populations.

Mortality caused by diseases is also difficult to monitor because weak birds normally die in cliffs, far from people. During the study period we collected eight dead Peregrines with evident signs of disease and starvation *(Photo 1)*. The first record was found during the

Table 4. Causes of death of Peregrine Falcons in Bizkaia, Northern Spain, during the study period (1998–2017). Information about the number of affected Peregrines, considering the gender, and how many of them died is also attached for "disease"

4. táblázat A vándorsólyom pusztulás okai a vizsgálati időszakban (Bizkaia, Észak-Spanyolország). A „betegségek" kategória esetén az érintett egyedek száma, neme és a pusztulások száma részletezve

Causes of death	N	Percentage (%)
Shoot	27	40.30
Collision		
Electric line	5	7.46
Fence	3	4.48
Wind mill	2	2.99
Others	8	11.94
Electrocution	3	4.48
Disease	8	11.94
Drowned	2	2.99
Oil	1	1.49
indet?	2	2.99
Peregrine attack	6	8.96
total	**67**	

	N of cases	Mortal consequence
Females	10	2
Males	8	6

Photo 1. Male breeder dead due to infectious disease. It results evident the effect of swollen and lachrymose eyes. In fact, orbital cerum was broken due to the amazing swollen. © Photo credit: Iñigo Zuberogoitia

1. fotó Egy fertőző betegségben elpusztult költő hím. Ennek egyértelmű jele a duzzadt és csipás szem. © Fotó: Iñigo Zuberogoitia

Image 2. The female (right), dry, came to the eyrie to relieve the male, that was totally drenched. Male was incubating eggs during intense rain while female was resting in a shelter place, recovering after suffering the same situation. © Photo credit: Avis Producciones

2. fotó A tojó (jobb oldalon) száraz, épp akkor érkezett a fészekhez, hogy segítsen a hímnek, aki addigra teljesen elázott. A hím heves esőben kotlott a tojásokon, amíg a tojó ugyanebből a helyzetből regenerálódott egy védett helyen. © Fotó: Avis Producciones

rainy, breeding season of 2007, when some territorial Peregrines appeared with clear symptoms of being suffering a fatal disease (Zuberogoitia 2010). Affected Peregrines showed swollen and lachrymose eyes and apathetic behaviour. It seems that in those wet and cold breeding seasons the disease was more virulent and affected more individuals. Females were first affected while incubating eggs or little nestlings. Our hypothesis here is that during adverse weather conditions females must spend more energy heating eggs and nestlings and they become weaker because of the contact between the incubating patch and wet substrates. During the first days the eyes of the affected females started to swell up until they were almost closed. Although females still incubated, males had to invest more time and effort incubating and feeding females and nestlings *(Photo 2)*. During the last years we detected ten females with evident signs of this disease, from which two died or at least suddenly disappeared (carcasses were not found). The other 80% survived thanks to male care. The other side of the coin was that while males attended females, they (males) were infected with the disease. Not all were severely infected, but we detected eight cases (some, but not all, of them were paired with previously affected females) in which males suffered the same symptoms. In such cases males were not able to hunt and stayed by their females. Six of the affected males (75%) disappeared. Therefore, in addition to habitual mortality causes, hidden infectious diseases could be behind the adult turnover rate.

Other problems

We have to consider also the loss of breeding sites caused by human activities. The main factor was the alteration of old abandon quarries, albeit the knowledge of the problem and the protection status of the species (Castillo *et al.* 2008). In the last years we have registered the actual loss of five territories after actuations to filling abandon quarries.

Conclusion

Our results reveal that Peregrine Falcons in our study area are suffering a combined effect of different factors affecting finally to the population structure. One of the main factors is the weather conditions during the last weeks of winter, before the laying dates, and during incubation and nestling raising period. This factor negatively affected productivity, but also adult survival due to higher prevalence of fatal diseases during rainy springs. This, in turn, caused low numbers of juveniles incoming to the floater population due to such a low productivity. Peregrines could be "trying to correct" the negative effect of adverse weather, delaying incubation onset. We suspect that the observed trend in laying dates might be an adaptive response of the population, since some late breeders could be recompensed with higher breeding success.

Floaters occupy territorial vacancies after the death of owners. The changeover rate also increased after catastrophic events (Zuberogoitia *et al.* 2009) and due to other mortality causes. However, the reduction of floater population is becoming evident since some vacancies are not covered by new birds, mainly in low quality territories which finally disappear (Penteriani *et al.* 2005).

In summary, the combined effect of rainy events during winter and springs, direct and indirect mortality factors, and reduced availability of adequate nesting sites, affects (1) territorial populations, (2) productivity and (3) floater population, which in turn determine territorial population and productivity.

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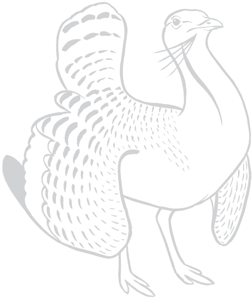

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The Peregrine population study in the French Jura mountains 1964–2016: use of occupancy modeling to estimate population size and analyze site persistence and colonization rates

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Summary We summarize key results of the first 53 years of one of the longest-running avian population studies in the world, on the Peregrine Falcon *(Falco peregrinus),* in the French Jura mountains (12,714 km^2), launched in 1964. A total of 449 cliff sites in 338 potential Peregrine territories were surveyed: 287 (85%) of these territories were occupied by an adult pair at least once, while in 51 (15%) we never detected an adult pair. Most sites were visited several times during a breeding season to survey occupancy and later fecundity, but the proportion of sites visited was highly variable over the years. We highlight the power of the Bayesian implementation of site-occupancy models (MacKenzie *et al.* 2002, 2003) to analyze data from raptor population studies: to correct population size estimates for sites not visited in a given year and for the biasing effects of preferential sampling (when better sites are more likely to be checked). In addition, these models allow estimation and modeling of the site-level persistence and colonization rates, which can provide important clues about drivers of population dynamics, even without individually marking any birds. Changes in the dynamics rates may serve as early-warning signals for subsequent population declines.

Since 1964, the observed number of adult pairs varied between 17 in 1972 and 196 in 2008, but the proportion of sites visited increased from 43% in 1964 to 80–90% after 2002. Hence, this raw population total must be an underestimate. We found strong evidence for preferential sampling in our study. Correcting for this, we estimated 56 pairs in 1964, after which the population dropped to a minimum of 18 in 1972, but then recovered rapidly, leveling off somewhat around 1995 and reaching a maximum of 200–210 adult pairs during 2000–2012. This was then followed by a decline to 170–190 pairs. In any one year, the raw counts underestimated the true population size by 5–39% (mean 11%), due to sites not being visited (this correction ignores imperfect detection though). Site persistence rates declined from 78% to less than 60% during 1967–1972, and then increased rapidly to over 90% during 1980–1990, suggesting that once pesticide effects vanished, individual survival probability increased rapidly and as a consequence also site persistence. Since the 1990s, persistence has declined slowly, which may indicate decreasing adult survival. In contrast, colonization rates increased steadily from about 3% in the early years to maxima of 46–49% during 1994–2001, but declined thereafter and currently reach about 33%. Taller cliffs had greater persistence and colonization rates than medium or small cliffs.

Both the decline in colonization and in persistence rates during the last 15 years may reflect density-dependence, predation by the expanding European Eagle Owl *(Bubo bubo)* population, human persecution or any as yet unknown factors. Importantly, we note that both persistence and colonization rates began to decline many years before the recent population decline became apparent. Thus, analysis of population studies using dynamic occupancy models can provide early-warning signals for future population declines. Our study demonstrates the benefits of modern analytical methods that can correct for several key deficiencies in probably all raptor population studies: incomplete coverage of sites and imperfect detection (though we only dealt with the former here). Occupancy models, possibly accounting for preferential sampling, appear to represent the logical analytical framework for abundance in raptor population studies.

Keywords: Bayesian, BUGS, Dynamic occupancy model, colonization, detection probability, extinction, JAGS, Peregrine Falcon, persistence, territory

Összefoglalás Jelen dolgozat foglalja össze a kulcsfontosságú eredményeit annak az 53 évet átfogó vizsgálat-sorozatnak, amely az egyik leghosszabb populációdinamikai kutatás a világon, és amely a francia Jura-hegységben (12 714 km^2) indult 1964-ben, a vándorsólyom *(Falco peregrinus)* állományának felmérésére. Mintegy 449 szirtet vizsgáltunk 338 lehetséges vándorsólyom territóriumon: ezek közül 287 (85%) területet legalább egyszer ivarérett madarak vettek birtokba, míg 51 (15%) esetben erre nem volt példa. A legtöbb fészkelőhelyet többször is felkeresték egy költési időszakban a foglaltság, majd később a termékenység felmérése érdekében. Ugyanakkor a felkeresett területek aránya változatos volt az évek során. Szeretnénk kiemelni a Bayes-i módszerekkel ötvözött területfoglaltsági modellek (MacKenzie *et al.* 2002, 2003) erejét a ragadozó madarak populációdinamikai adatainak elemzésében: a populáció méretének javított becslésére vonatkozóan azokra az esetekre, amikor az adott területet nem vizsgáltuk egy adott évben, valamint annak kiküszöbölésére, hogy a jobbnak tartott fészkelőhelyeket gyakrabban kerestük fel, ezért nagyobb arányban szerepeltek az adatsorban a kevésbé jó területekhez képest. Ezek a modellek lehetőséget adnak a fészkelőhelyek fennmaradásának és benépesülésének becslésére és modellezésére is, ami anélkül adhat képet a populációdinamikáról, hogy a madarakat egyedileg jelölték volna. A dinamikai viszonyok megváltozásai előre jelezhetik a populáció méretének későbbi csökkenését is.

1964 óta a megfigyelt költőpárok száma 17 (1972) és 196 (2008) között változott, ugyanakkor a felkeresett fészkelőhelyek aránya az 1964-es 43%-ról csaknem 80–90%-ra nőtt 2002 után. Ezért is lehetséges az, hogy a populáció teljes mérete alulbecsült. Erős bizonyítékot találtunk arra vonatkozóan, hogy vizsgálataink során egyes területek felkeresése előnyt élvezett másokkal szemben. Ezt figyelembe véve az 1964-es populációt 56 párra becsültünk, ami 1972-re 18 párra csökkent, majd 1995 óta gyors növekedésnek indult, és 2000–2012 között már elérte a 200–210 ivarérett párt. Ezután ismét visszaesett 170–190 párra. A meg nem látogatott költőhelyek miatt a populáció valós méretéhez képest minden egyes évben 5–39%-kal (átlagosan 11%) kevesebb adódott. A használatban lévő költőterületek aránya 78%-ról kevesebb, mint 60%-ra csökkent 1967 és 1972 között, majd gyors növekedésnek indulva a ’80-as évekre meghaladta a 90%-ot. Ez a fellendülés feltételezhetően annak köszönhető, hogy a rovarirtószerek hatásának megszűnése után az egyedek túlélőképessége is gyorsan emelkedett, és ennek következtében a költőhelyek száma ismét növekedésnek indult. Azonban a ’90-es évektől ismét csökkent a fészkelő helyek száma, ami az ivarérett egyedek túlélőképességének ismételt csökkenését jelezheti. Ezzel ellentétben a kolonizációs ráta 3%-ról 46–49%-ra emelkedett 1994 és 2001 között, majd lecsökkent a jelenlegi 33%-ra. A magasabb szirtek stabilabb költőhelynek bizonyultak a közepes vagy alacsony szirtekhez képest.

Az utóbbi 15 év csökkenő tendenciái tükrözhetik az uhu *(Bubo bubo)* növekvő elterjedése következtében fellépő fokozott ragadozó-nyomást, az emberi zavarást vagy más, eddig felderítetlen tényezőket. Fontos megjegyezni, hogy ez a csökkenő mintázat a jelen állapotok előtt is jelen volt. Ezért az itt bemutatott populációdinamikai modellek fontos előrejelzéseket adhatnak a majdani populációs változásokról. Tanulmányunk a modern analitikai módszerek előnyeinek bemutatására is szolgál, melyek javíthatják azokat a hiányosságokat, amelyek csaknem minden hasonló vizsgálatban megjelenhetnek: a költőhelyek hiányos lefedettsége és felismerése (itt csak az előbbit érintettük). A foglaltsági modellek – esetlegesen figyelembe véve a nem véletlenszerű mintavételezést – úgy tűnik, egy értelemszerű analitikai keretet adnak a ragadozó madarak populációs vizsgálatainak kivitelezéséhez.

Kulcsszavak: BUGS, dinamikus foglaltsági modell, kolonizáció, megtalálási valószínűség, kihalás, JAGS, vándorsólyom, fennmaradás, territórium

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Introduction

Long-term studies have a huge value in ecology, but they are extremely expensive to conduct and maintain. Hence, typical long-term studies in population ecology last perhaps 1–2 decades, with population studies of more than 30 years being very rare. The high costs of keeping a study alive over several decades can only be paid in a very powerful scientific study such that funding agencies will keep supporting a study over such long periods, but this is extremely rare. Most of the time, such long-term studies are "paid" by another currency: passion. It is the passion for a species, for an area, for keeping the data record unbroken, for collaborating in a group of like-minded individuals, which pushes some people to continue their population studies for the better part of a human life-time. Birds of prey (raptors and owls) have often cast an especially powerful spell on human observers, and hence, they have received perhaps a more than proportional shares of long-term population studies compared to almost any other bird groups. The Peregrine must be one of the most studied raptors in the globe, with long-term population studies being conducted in many parts of the world. Many examples of this can be gleaned in the series of books on Peregrine world conferences by Hickey (1969), Cade *et al.* (1988), Sielizki and Mizera (2009) as well as in Rau *et al.* (2015).

Here, we briefly describe what must be one of the longest-running Peregrine surveys worldwide: the population study in the French Jura mountains (Monneret 2006, 2009, 2017). The surveys started in 1964 and have been a collaborative team effort led by the first author ever since. At the time of writing this field study is in its 55th year. Here we summarize the first 53 years of this survey until 2016. We document some spatial and temporal patterns of occurrence (presence or absence of an adult pair at a site) and population size trajectories.

In particular, we highlight the power and flexibility of multi-season occupancy models (MacKenzie *et al.* 2003, 2017, Royle & Kéry 2007) as a natural analytical framework for abundance in typical raptor population studies such as ours, where a set of sites is visited over multiple breeding seasons. These models, and in particular their Bayesian implementation using Markov chain simulation (MCMC) methods, for instance in the generic statistical modeling software BUGS (Lunn *et al.* 2013), offer tremendous advantages for the analysis of abundance data in raptor population studies. Depending on the kind of data recorded, they allow one to estimate population size corrected for two kinds of observation errors which are due to (1) the lack of visits to some sites in some of the years (coverage bias) and (2) to imperfect detection, i.e. when an occupied site is visited but no pair is detected (detection bias). Unless corrected for, these errors will both lead to underestimation of population size. In this study, we show how to correct for coverage bias in raptor population studies.

In addition, the dynamic version of such multi-season occupancy models allows one to estimate and model the two processes that underlie any population change at the level of an occupied site: the site-level persistence rate and the site-level colonization rate. Persistence is the probability that a site occupied now will still be occupied in the next season, while colonization is the probability with which a site that is unoccupied now will become occupied by the next season. These two rate parameters together describe the population dynamics of a raptor population at the level of a site and can provide interesting hints at the reasons for an observed population change at the level of the population size alone. For instance, declines in persistence or colonization can be used as an early-warning signal for future population declines.

One objective of this paper is to make occupancy models more widely known among analysts of data from bird population studies, because they offer so much power to estimate population size correcting for non-visited sites (and potentially also imperfect detection) and to investigate temporal trends in the site-level dynamic rate parameters that govern the annual changes in population size. Thus, we chose a somewhat verbose or "how to" style of a manual for such analyses in the hope of making them more easily understood and more widely used.

Methods

Study area

Our study area comprised the entire French part of the wild and wonderful Jura mountains, which are a middle-elevation mountain range in France and Switzerland. The Jura is a geologically young range rich in limestone cliffs, which bends in a banana shape more than 300 km long almost from Lyon in France up to the Swiss town of Schaffhausen. At its widest, it measures about 60 km in Northwest-Southeast direction. Elevation varies from under 200 m to 1,718 m at the highest peak, the Crêt de la Neige. The highest chains are in the inner (Eastern) part, and successive chains ebb away in lesser elevations as one goes West. About half of the Jura is wooded, with the rest being mostly pasture and only little arable land, since the climate is often too cold, windy or wet for much arable agriculture. Human population density is low at 89 per km^2 on average. The French Jura is shared by the three departments Ain (5,762 km^2), Jura (4,999 km^2) and Doubs (5,234 km^2) and totals 15,995 km^2. The overall study area covered only that part of these departments that contains some cliffs or some of the rare Peregrines nesting on buildings in our study area. Applying the method of Ratcliffe (1962) to delimit the area inhabited by a Peregrine population by adding a buffer strip of half the mean nearest neighbor distance to the convex hull defined by the locations of the pairs yields areas of 3,118, 4,618 and 4,978 km^2, respectively, for the Ain, Jura and Doubs, for a total 'occupied area' of 12,714 km^2.

We distinguish 'cliff objects', one or several of which form a potential Peregrine territory or a 'site'. The former are cliffs and, in a very few cases in our study area, tall buildings, that have been or could in principle be occupied by a Peregrine pair. Territories are formed by one or a cluster of cliffs and can only be occupied by a single Peregrine pair at any given time. Nesters on buildings are extremely rare in our study area, but have started to show up in very small numbers since about 2010. We have included them in our survey and this study alongside the cliff haunts. Here, we use the terms 'site' and 'territory' interchangeably. As is well-known, the definition of what represents a territory in a raptor study can be somewhat arbitrary. In particular, the territory definition by single-pair-occupancy can change over time, especially when a population is increasing or declining. During increases, double or even triple "splits" may be observed (Ratcliffe 1993), i.e. a territory formerly occupied by only one pair becomes a haunt for two or three pairs. When assigning cliff objects to territories, we naturally based our decision on the majority of years. That is, when a set of cliffs were occupied by a single pair in most years but by two pairs in just a few years, we designated these cliffs to be a single territory.

Field methods

Starting in 1964 and conducted and organized ever since by the first author, in every year members of the *Groupe Pèlerin Jura* sought to visit as many of the previously known Peregrine sites and cover as many hitherto unknown sites as possible. Either deliberately or unconsciously, most observers will first have targeted “good” sites, previously known to be occupied or to have a good history of nesting, rather than “bad” sites, known to be occupied only irregularly or to have poor breeding success.

During the first decades, field work was conducted by a small group of 5–10 dedicated people in each department, who communicated via (paper) mail and over the phone. Since the late 1990s, communication by email has become the main mode of information exchange among the members of the group. All information was centralized and housed on paper documents by the first author in the beginning and, starting in the 1990s, was migrated into an Excel data base. Each site was accurately localized on a map (IGN), to avoid misidentification of sites between observers.

Field work was conducted by individuals or small groups of observers, using binoculars and telescopes, between 1 February and early July, with most effort spent during the courtship period (15 February – 15 March) to find and confirm occupancy by single birds or pairs, in late March and early April for incubating pairs and in May to count well-grown and nearly fledged young to obtain a measure of fecundity. Most sites were visited multiple times during a breeding season, thus we expected overall detection probability to be rather high, i.e. we expected only few pairs to be overlooked at those sites that did receive visits in a given year.

Occupancy models to estimate population size and site-level colonization and persistence

The site-year format of survey data from raptor population studies

In our study, the basic survey data can be summarized in a site-by-year table of dimensions 287 (corresponding to the number of territories) by 53 (corresponding to the 53 years). A subsection of this table, with four sites and 17 years (2000–2016), and therefore a total of 68 site-year combinations, is shown as *Table 1*, and also shows the site names in the first column.

One main goal in this study is to show how to deal with one of the two types of uncertainty in such data, surrounding the interpretation of the zeroes and the missing values (= missing visits = the asterisks) in *Table 1*. For instance, perhaps we think that it is possible that an adult pair did in fact occur at Bolozon in some years after 2009 but was missed. Can we say something about the likelihood of this possibility for the 18 cases where there are zeroes in this table and if possible, factor this in to obtain an improved estimation of the population

Table 1. A small part of the data analyzed in this study, showing results of surveys of four sites in 17 years (2000–2016). A 1 and a 0 mean that a site was visited at least once in a given year and an adult pair was or was not detected. The asterisk (*) is our missing value symbol and says that no visit took place (or is recorded) for a site-year combination. In this table, out of a total of 68 site-year combinations, there is uncertainty for 44 (65%) of them: 26 are missing visits and 18 represent zero observations. For the former, obviously we have no information whether a pair was present (resulting in coverage bias), while for the latter, a pair may have been present but overlooked (resulting in detection bias)

1. táblázat Az elemzett adatok kis szelete, mely 4 terület 17 évet átölelő felmérését mutatja (2000–2016). Az 1 és 0 értékek azt mutatják, hogy adott költőhelyet legalább egyszer felkerestek az adott évben, és ott jelen volt-e ivarérett pár vagy sem. A csillag (*) a hiányzó adatokat jelöli, ami azt jelenti, hogy az adott területet nem keresték fel az adott évben, vagy nincs feljegyzés róla. Ebben a táblázatban a 68 terület-év párosításból 44 esetben (65%) figyelhető meg bizonytalanság: 26 hiányzó látogatás és 18 nulla megfigyelés. Az előbbi esetben nincs arról adat, hogy a költőpár jelen volt-e (lefedettségi eltolódás), míg az utóbbiban jelen lehetett, de nem sikerült ténylegesen megfigyelni (észlelési eltolódás)

Site	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**
Bolozon	1	*	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Chézery	*	*	1	*	0	*	*	*	0	1	*	1	0	*	0	*	*
La Fauconnière de Belleydoux	0	*	0	0	0	*	*	1	1	0	1	1	1	*	1	1	1
Fort l'Ecluse	*	1	1	1	*	0	*	*	1	*	*	*	1	*	*	*	*

size (= number of adult pairs)? And what about the 26 years in which these four sites were not visited at all? Is it not highly likely that pairs did occur at least in some of these years but had no chance of being recorded in our data simply because a site was not visited in a given year? For instance, an adult pair was recorded at Bolozon in every year between 2000 and 2008 except for 2001: would it not be natural then to assume that a pair was probably present in 2001, when no visit took place, too? But how likely is this and how would we deal with this in a formal estimate of population size? And similarly for the Fauconnière in 2001 and 2013, two years when no visit to this site was recorded. The year 2001 at that site is surrounded by years when no pair was recorded, while 2013 is surrounded by years when a pair was in fact recorded. How would this affect the likelihood that a pair was or was not present in these years with missing values and how would we deal with this in an estimate of total population size in those years? And what about the year 2009 at the Fauconnière, when the absence of an adult pair was recorded, while several years before and afterwards all had records of adult pairs? Could it not perhaps be possible that a pair was present also in 2009 but was simply missed? Can we somehow factor in this possibility when estimating population size?

And what about the processes that underlie the dynamics of the presence or absence of an adult pair at a site: can they somehow be described? And can we perhaps investigate factors that may influence Peregrine population dynamics at the level of a site occupied by an adult pair or any other descriptor of site occupancy?

It turns out that we can do all of the above by application of multi-season occupancy models to appropriate population survey data. We next describe the dynamic variant of these models in some detail, because they are so incredibly powerful for the analysis of raptor population surveys including our own, but in our opinion the power of dynamic occupancy has not yet been sufficiently recognized in the community of raptor biologists.

Dynamic (multi-season) occupancy models

Dynamic site-occupancy models (MacKenzie *et al.* 2002, 2017) are a variant of so-called multi-season occupancy models that describe change in binary systems, such as whether a set of Peregrine sites is found to be occupied or not over a series of multiple years. (Another variant are static multi-season site-occupancy models (MacKenzie *et al.* 2017), which are a simpler version that we briefly describe in the following section.). In these statistical models, the dynamics are estimated by first describing the initial state of the system, i.e. whether each site is occupied or not, as a probabilistic function of a parameter ψ (pronounced 'psi'), which is the probability that a site is occupied in the first of a series of years, which is the year 1964 in our data set. In algebra, we write this for the occupancy status $z_{i,t}$ at site i in year $t = 1$, e.g. presence $z_i = 1$ or absence ($z_i = 0$) of a pair at site i as follows:

$$z_{i,1} \sim Bernoulli(\psi_i)$$

We can read this as *'z is a draw from a Bernoulli distribution with parameter psi'*. The Bernoulli is the statisticians' equivalent for chance processes that work like the flip of a coin and produce two complementary outcomes with probability θ and $1 - \theta$, respectively. Thus, for Peregrine pair survey data, a site is either occupied or it is not, and this is governed by the occupancy probability ψ_i. This parameter is indexed by site i, indicating that it could be different for each site and thus could be modeled by site-specific covariates when the model is fit to a data set.

For all later years, the presence or absence of a pair in year $t = 2 \ldots T$ (where $T = 53$, corresponding to the year 2016, in our data set) is described as a recursion in terms of two random processes. These two processes describe the two transitions that are possible for a site that is initially occupied and another that is initially unoccupied. A site i that is occupied by a pair in year t can either remain occupied in the next year $t + 1$ with probability $\varphi_{i,t}$ (pronounced 'phi') or it can become abandoned in year $t + 1$ with probability $1 - \varphi_{i,t}$. Similarly, a site i that is unoccupied in year t can either be colonized in year $t + 1$ with probability $\gamma_{i,t}$ (pronounced 'gamma') or it can remain empty in year $t + 1$ with probability $1 - \gamma_{i,t}$. These two parameters are called the persistence probability φ and the colonization probability γ (Note that the former two transitions can also be described in terms of extinction probability ε, which is simply $1 - \varphi$). Both persistence and colonization parameters are here indexed by site i and time interval t. This indicates that they may differ by both site and time interval and may be modeled by covariates that vary by site or time either alone or in combination.

In algebra, we get the following for a site initially occupied by a pair (and where $z_{i,t} = 1$):

$$z_{i,t+1} \mid z_{i,t} = 1 \sim Bernoulli(\varphi_{i,t})$$

In contrast, for a site that is unoccupied at time t (and where $z_{i,t} = 0$), we get:

$$z_{i,t+1} \mid z_{i,t} = 0 \sim Bernoulli(\gamma_{i,t})$$

Thus, remarkably, by combining just three Bernoulli random processes (or, three coin-flip-like chance processes), we can describe the entire dynamics of our data on the presence or absence of a pair at each of the 287 sites for each of the 53 years in our study. We call this the description of the *true ecological process* underlying our survey data. But is this description a complete representation of our data?

Of course, any person who has ever watched Peregrines or indeed any animal or plant study species knows that a species, even when it is present in reality, is often missed when it is looked for. Hence, a datum of 0 in Table 1 (e.g. at the Fauconnière in 2009) may well refer to such an instance where a site was occupied by a pair and we did visit the site, but failed to detect the Peregrine pair. How can we make our model more realistic to account for this possibility in our data? The answer is that we simply add another Bernoulli distribution to our model. This fourth chance process describes how our "measurements", or observations, of the presence/absence of a pair at a site in a given year, $y_{i,t}$, are linked to the true state $z_{i,t}$ at that site:

$$y_{i,t} \sim Bernoulli(z_{i,t} * p_{i,t})$$

Thus, in our case, whether we detect a pair ($y_{i,t} = 1$) or not ($y_{i,t} = 0$) is the outcome of a random process and depends on two things: whether the site is occupied or unoccupied (i.e. whether we have $z_{i,t} = 1$ or $z_{i,t} = 0$) and on a second quantity, detection probability $p_{i,t}$. For an unoccupied site, we detect a pair with probability $z_{i,t} * p_{i,t} = 0 * p_{i,t} = 0$ (we assume here that we cannot erroneously detect a pair at a site that is not occupied by a pair in a given year). Otherwise, at an occupied site, we detect a pair with probability $z_{i,t} * p_{i,t} = 1 * p_{i,t} = p_{i,t}$.

Now, having added this fourth coin-flip-like random process to our statistical model for the data in *Table 1*, we have an adequate statistical model for inference about the number of pairs with which we can correct for both missing visits and imperfect detection and which moreover enables inference about the dynamic rates that underlie any change in the number of pairs. All four parameter types can be modeled, i.e. we can introduce in the model covariates or unobserved grouping factors (i.e. random-effects) to accommodate additional structure or to test whether a covariate such as elevation of a site can have an effect on occupancy or, say, whether colonization rates differ by year, department or even site. In our study, we tested for an effect of cliff height (small, medium, and big) on both persistence and colonization probability.

This is the dynamic occupancy model, which can be fitted using maximum likelihood or Bayesian techniques (Royle & Kéry 2007, MacKenzie *et al.* 2017). Bayesian model fitting is particularly appealing in our case because of the ease with which missing values are dealt with when a statistical model is fit using Markov chain Monte Carlo (MCMC) methods: missing values such as the asterisks in Table 1 are then simply estimated as a side-product of the model fitting procedure itself (Kéry & Royle 2016).

To be able to separately estimate all four types of parameters in the model, i.e. the probabilities of occupancy (ψ_i), persistence ($\varphi_{i,t}$) and colonization ($\gamma_{i,t}$) and of detection ($p_{i,t}$), we need replicate observations for at least some of the sites in at least some of the years (MacKenzie *et al.* 2003, 2017, Royle & Kéry 2007, Kéry & Schaub 2012). That is, we need individual records of the results of multiple visits to some Peregrine sites in some years (and ideally repeat visits to all sites in all years). Assuming closure, i.e. that site occupancy status z does not change within a breeding season, we can then separately estimate the parameters that describe the true ecological process (i.e. ψ_i, $\varphi_{i,t}$ and $\gamma_{i,t}$) from the parameter which describes the observation process (i.e. $p_{i,t}$).

Unfortunately, in our study (see *Table 1*), although there usually are multiple visits, we only record a summary, as if we had conducted a single visit per site and year only. Thus, in our analyses we are not able to separately estimate the parameter describing one of the two types of uncertainty described above for *Table 1*; we cannot estimate detection probability $p_{i,t}$. This means that we will underestimate occupancy and persistence probability and population size and overestimate colonization probability (Kéry & Royle, in prep.). We can assume, however, that this bias is only slight, since detection probability of Peregrine pairs can be high (Kéry & Royle 2016) and this is compounded for multiple visits. We expect combined detection probability per site and year to be greater than 90% and thus in this study will ignore the slight negative bias in population size estimates induced in our analyses by our inability to estimate detection probability.

Static (multi-season) occupancy models

A simpler variant of a multi-season occupancy model is the static model (also termed "implicit dynamics model" by MacKenzie *et al.* 2017), which can be fit to exactly the same data as a dynamic occupancy model. It lacks the parameters for the yearly dynamics and instead simply has separate occupancy and detection parameters for every year ($\psi_{i,t}$ and $p_{i,t}$). If interest focuses on population size or trends rather than dynamics, this simpler model may be preferable to the model with explicit dynamics, e.g. because the annual occupancy parameters may be constrained by a linear model with 'Year', which allows a population trend to be estimated directly. In our study, when trying to account for preferential sampling (see next section) with a more complex dynamic occupancy model, we failed to achieve numerical convergence of the algorithm and therefore had to resort to the simpler static (multi-season) occupancy model.

Preferential sampling in population studies

In many population studies such as ours, not all sites are surveyed in every year and the sites surveyed are not chosen at random. Rather, sites previously known to be occupied or to be 'good' are usually surveyed first and 'bad sites' only later, if at all. Thus, when not all sites are surveyed, the sampled sites do not form a random sample from all sites known in a study area but rather form a biased sample of higher-than-average quality. We refer to *preferential sampling* (PS) when better sites have a higher probability of being surveyed than less good sites (Conn *et al.* 2017). When PS is not accounted for in a model that estimates population size by extrapolating results from the surveyed to the unsurveyed sites, population size estimates will become too high.

The solution is to fit a joint model for the survey results, with one submodel for the survey results (i.e. whether a site is found to be occupied or not, i.e. the data in *Table 1*) and another submodel for a derived variant of such a table, which simply distinguishes sites that are visited from sites that are not visited in a year. This second submodel for site visits is parameterized in terms of site visitation probability. Importantly, in such a joint model, a link between the two submodels is added, such that the *quality* of a site is used as a covariate in the submodel for visitation. In the usual case of positive preferential sampling we expect a positive effect of the site-quality-covariate on visitation probability.

We expressed site quality in two ways: first as a Gaussian random site effect on the logit transform of annual occupancy probability. This PS model variant 1 assumes that there is some average quality of a site that does not change over time and that affects the likelihood with which a site is visited. In PS model variant 2, we simply used the presence or absence of a pair at a site in year t-1 as a predictor in the model for visitation probability in year t. These PS variants of a multi-season occupancy model allow us to correct for the biasing effects of preferential sampling when extrapolating the survey results to unsurveyed sites in our attempt to estimate the true annual population size (i.e. correcting for unsurveyed sites).

Fitting the models in our study

We fit a total of five multi-season occupancy models to our full data set on 287 sites and 53 years, of which *Table 1* shows a small section. First, to estimate the trajectories of population size over the years, and to correct for sites not visited in a year, we fit four *static* multi-season occupancy models (see *Table 2* for an overview):

- Model 1 was the base model that assumed that all sites were identical in terms of their occupancy probability (i.e. no differences in site quality) and that did not account for preferential sampling (PS).
- Model 2 did not account for PS either, but assumed that each site was of different quality by adding, on the logit scale of occupancy probability, a site-specific, Gaussian random effect.
- Model 3 was an extension of model 2 that accommodates PS and where the link between occupancy probability and the visitation probability of a site was the random site effect in occupancy. We also call this PS model 1.

Table 2. Overview of four occupancy models fit to the Peregrine data to obtain estimates of population size that correct for incomplete and time-varying visitation of the 287 sites during 1964–2016

2. táblázat Négy foglaltsági modell áttekintése, melyek a vándorsólymok populáció méretének becslésére szolgálnak, figyelembe véve a 287 költőhely hiányos vagy időben változó felkeresését 1964 és 2016 között

	Site quality allowed to vary	**Site visitation random or preferential**
Model 1	No	Random
Model 2	Yes	Random
Model 3	Yes	Preferential sampling (PS variant 1)
Model 4	Yes	Preferential sampling (PS variant 2)

- Model 4 also had the random site effect in the submodel for occupancy, but used the binary indicator for presence or absence of a pair at site i during year t-1 as a predictor for visitation probability in year t. We also call this PS model 2.

Second, to infer the population dynamics, we fit a dynamic occupancy model (but without accounting for PS) with random site and random year effects and smoothed the year effects by a random walk (Link & Barker 2010) to better distinguish temporal patterns in the parameters underlying the site-level population dynamics and to gauge the variability in the quality of sites in terms of persistence and colonization probability. We also fitted an effect of cliff height (small, medium, big) on both persistence and colonization.

We fit all models with Bayesian methods in program JAGS (Plummer 2003), run from program R using package jagsUI (Kellner 2016), specifying vague priors and running the chains for sufficiently long that convergence was reached based on the Brooks-Gelman-Rubin statistic (Kéry & Royle 2016). We present posterior means as our point estimates and posterior standard deviations and 2.5 and 97.5 percentiles as Bayesian versions of a standard error and for a 95% Bayesian confidence interval (CRI).

Results

A brief overview of Peregrine distribution and density in the French Jura mountains

In the 53 years between 1964 and 2016, we recorded survey results from a site and a year in 11,697 cases (=site-year combinations). In 6,737 cases, a site was found to be occupied, in 6,156 cases by pairs and in 5,879 cases by adult pairs. We distinguished a total of 449 cliff sites in 338 potential Peregrine territories: 287 (85%) of these territories were found to be occupied by a pair at least once during the 53-year period, while in 51 (15%)

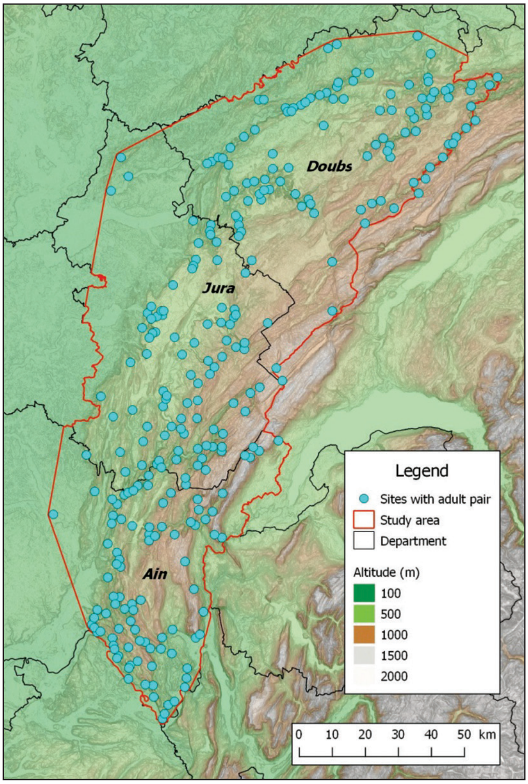

Figure 1. Distribution of 287 Peregrine sites in the French Jura mountains, stratified by three political departments (study area 12,715 km^2). A Peregrine site was defined by the observation of a Peregrine pair at least once during 1964–2016.

1. ábra A 287 vándorsólyom fészkelőhely eloszlása a francia Jura-hegységben három osztályba sorolva (vizsgálati terület mérete 12 715 km^2). Egy területet akkor tekintettünk vándorsólyom költőterületnek, ha a költőpárt legalább egyszer megfigyelték 1964 és 2016 között we never detected adult Peregrine pairs. In our analysis, we define a Peregrine site to be one such territory where a Peregrine pair was observed at least once between 1964–2016. In the Département Ain, there were 94 Peregrine territories, 91 in the Jura, and 102 in the Doubs; see *Figure 1*. The area occupied by the study population was 12,715 km^2, hence, the overall average territory density was 2.26 Peregrine sites/100 km^2. Large-scale density varied a little by department: Ain: 3.01, Jura: 1.97, Doubs 2.04. Clearly, these are maximal values, since not all territories were occupied in all years, see below.

Within a department, there was substantial local-scale variation in territory density, which we expressed by the nearest-neighbor distance (NND), i.e. the distance from one territory to the nearest neighbor. In the entire study area, NND ranged from 0.71–15.00 km, with a mean of 3.1 and a median of 2.64 km. These distances are based on the mean territory coordinates, which is often an average of multiple cliffs in a territory. The absolute minimum distance between two pairs in one year was 190 m (R. Ruffinoni unpublished, also see Kéry *et al.* 2005).

Estimation of population size using occupancy models

The observed Peregrine population (i.e. number of adult pairs) declined from 34 in 1964 to a minimum of 17 in 1972, thereafter it increased to a maximum of 191 pairs in 2012, and declined again to 169 pairs in 2016 *(Figure 2)*. However, the total of 287 sites were never all surveyed in any given year; rather, on average only about 200 sites (i.e. 70%) were visited. Hence, we would naturally assume that the observed number of pairs would underestimate the true population size. In addition, the proportion of sites visited increased from 43% per year in 1964 to over 80% during most of the 2000s *(Figure 2)*. Therefore, we would expect the degree of the underestimation of population size to vary over the years.

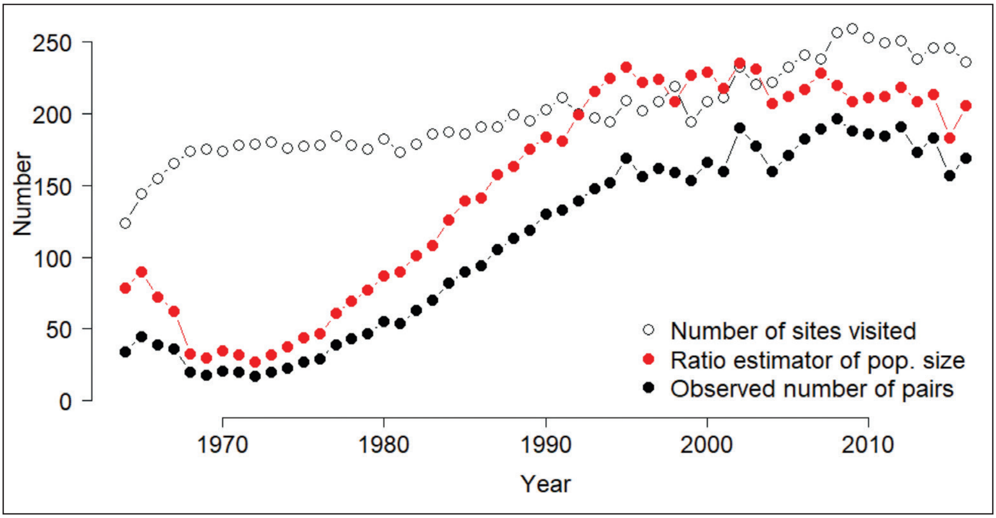

Figure 2. Number of visited sites, observed number of pairs and ratio estimator of population size for a total of 287 identified Peregrine territories in the French Jura mountains during 1964–2016

2. ábra A felkeresett költőhelyek száma, a megfigyelt költőpárok száma és a becsült populáció-méret a 287 különböző vándorsólyom territóriumon, a francia Jura-hegységben, 1964 és 2016 között

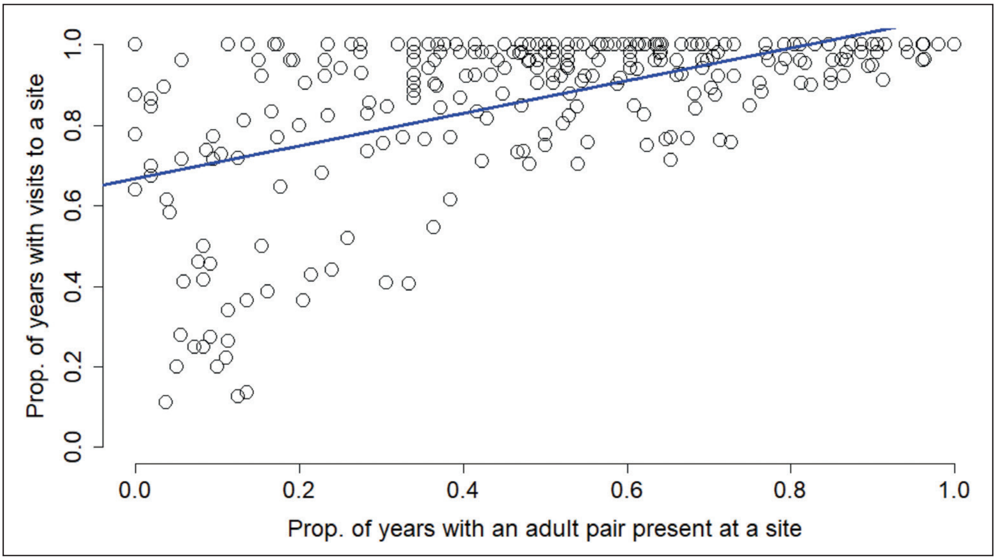

Figure 3. Relationship between the proportion of years with visits to a site (site visitation frequency) and the proportion of years in which a site was occupied (site quality). The blue line is the line of best fit of a linear regression, which explains 31% of the variance

3. ábra A meglátogatott költőhelyek években mért arányának (látogatottsági gyakoriság) és az elfoglalt helyek években mért arányának (költőhely minősége) kapcsolata. A kék egyenes egy lineáris regresszió illesztését mutatja, mely a változatosság 31%-át magyarázza

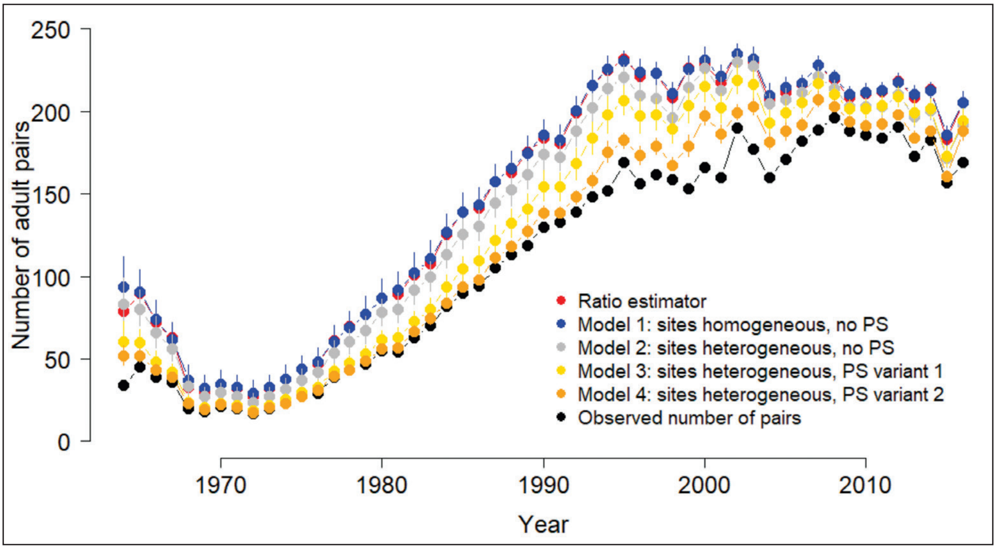

Figure 4. Observed number of pairs, ratio estimator and estimates for Peregrine population size under four occupancy models in the French Jura mountains 1964–2016, as described in the Methods and in *Table 2*.

4. ábra A költőpárok vizsgált száma, valamint a négy foglaltsági modell eredménye a francia Jura-hegység vándorsólyom populációjának becslésére 1964 és 2016 között. Bővebb leírás a Methods részben, valamint a *2. táblázat*ban található

As a first, and simplest, estimator of population size that corrects for the incomplete coverage of our surveys, we computed a ratio estimator as the observed number of pairs divided by the proportion of sites visited. This suggested that population size was severely underestimated in every year and that the magnitude of this bias varied substantially, being greatest in the initial years and during the years of the steepest recovery 1985–2005.

However, the ratio estimator is based on two assumptions that may invalidate it in practice for many raptor studies: first, it assumes that there is no difference in the quality of the sites, i.e. in the likelihood that a site is occupied, and second, it assumes that sites are visited at random. In reality, however, it is well known that there is substantial variability in the quality of raptor territories (Newton 1979, Ratcliffe 1993), such that some sites are virtually always occupied, while others only occasionally so. In addition, in many studies and especially also in ours, "good" sites are visited in preference to "bad" sites. This is illustrated in *Figure 3*, which also shows the relationship between site quality and the frequency of site visitation. Clearly, there is substantial variation in site quality, with some sites being occupied by an adult pair in every year and some only rarely if ever. Furthermore, better sites (which are more frequently occupied) were more likely to be visited than lesser sites. Thus, there was (positive) preferential sampling rather than a random visitation scheme of the sites, as required by use of the ratio estimator.

Accounting for heterogeneous site quality and preferential sampling produced substantially different population size estimates compared with the ratio estimator, which assumes the absence of both of these patterns *(Figure 4)*. The simplest occupancy model (model 1, blue symbols) essentially reproduced the estimates from the ratio estimator, because in this model, too, we make the assumptions of homogeneous site quality and random, rather than preferential, sampling. Accounting for heterogeneous site quality (model 2, grey symbols) reduced the population size estimates somewhat. Finally, accounting also for preferential sampling reduced the population size estimates even more; less so for PS variant 1 (model 3, golden symbols) than for PS variant 2 (model 4, orange symbols).

Given the strong evidence for preferential sampling in our study, we consider the population size estimates under models 3 and 4 the most reliable. However, we lacked any criterion by which to gauge which of the two was better, hence, as our best estimate at the Peregrine population size we model-averaged the estimates under these two models. In *Figure 5*, we summarize the observed number of adult pairs, the ratio estimator and the model-averaged estimates from models 3 and 4.

The model-averaged estimates (brown in *Figure 5*) indicated that the final phase of the population crash up to 1972 was steeper than observed and that the ensuing recovery was steeper, too, than what the observed number of pairs suggested. Our best correction for incomplete coverage of the 287 sites, i.e. the model-averaged estimates, indicated that population size declined from 56 pairs in 1964 to a minimum of 18 in 1972. Thereafter, the population recovered up to a maximum of 212 in 2007; since then there has been a slow decline down to an estimated 191 pairs in 2016.

The observed data underestimated the true population size by 40% in 1964 and between 10 and 20% during 1965–1969 and 1981–2007. During the "darkest years" (1970–1980) and now during the last 10 years since 2008, the underestimation was on the order of 5–10%. We

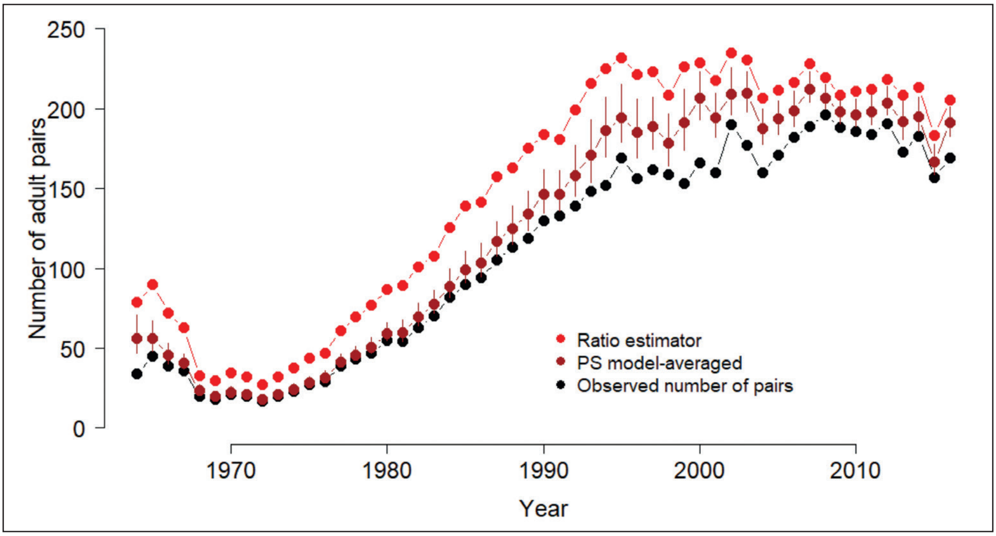

Figure 5. Observed number of pairs, ratio estimator and average between the two occupancy models with preferential sampling (models 3 and 4) for Peregrines in the French Jura mountains 1964–2016

5. ábra A költőpárok vizsgált száma, valamint azon két modell átlagolt értékei (modell 3 és modell 4), amelyekben figyelembe vettük a mintavételezés eltolódását (előnyben részesített helyek), vándorsólyom-populáció a francia Jura-hegységben 1964 és 2016 között

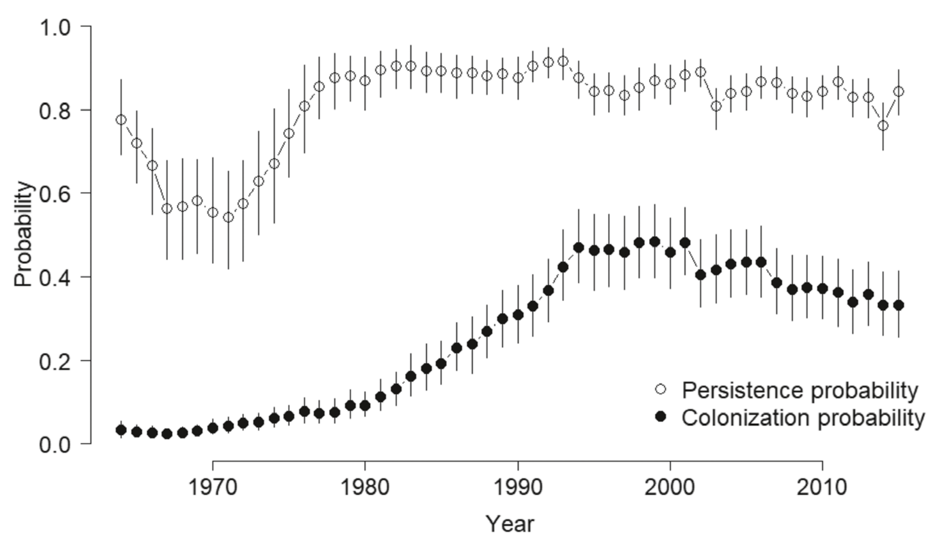

Figure 6. Estimated trajectories of the probability of site persistence (open symbols) and site colonization (solid symbols) for Peregrines in the French Jura mountains 1964–2016 based on a dynamic occupancy model

6. ábra A költőhely-foglaltság (üres körök), valamint a költőhelyek kolonizációja (sötét körök) arányainak becsült görbéi a francia Jura-hegység vándorsólyom populációjában 1964 és 2016 között, a dinamikus foglaltsági modell alapján

Table 3. Effects of cliff height (a factor with three levels: small, medium, big) on persistence and colonization probability (in %) in a dynamic occupancy model. These estimates are scaled to the beginning of the study (1964), but could equally well be estimated for any other study year. Point estimates (posterior means) and uncertainty (95% CRI) is shown for each level of the cliff height factor

3. táblázat A szirtek magasságának hatása (alacsony, közepes, magas) a foglaltsági és kolonizációs arányokra (%-ban) dinamikus foglaltsági modell alapján. Ezek a becslések a vizsgálatsorozat első évére (1964) vonatkoznak, de bármelyik másik évre alkalmazhatóak. Az átlagos értékeket és a 95%-os intervallumot minden egyes szirtmagassági kategória esetén feltüntettük

Parameter	**Small cliff**	**Medium cliff**	**Big cliff**
Persistence probability	73.8 (61.0–78.7)	74.0 (62.2–78.7)	81.1 (77.7– 89.2)
Colonization probability	1.5 (0.6–1.8)	2.0 (0.9–2.5)	5.1 (2.3– 6.0)

note, though, that in this analysis we could not correct for imperfect detection; hence, our population size estimates will be slight underestimates.

Inference into population dynamics using dynamic occupancy models

A second important benefit of occupancy modeling in raptor population studies is that the dynamic variants of these models provide insights into the two processes that underlie all changes in population size: namely, the probabilities of site persistence and site colonization. A dynamic occupancy model revealed annual site persistence rates that declined from 78% to less than 60% during 1967–1972, and then increased rapidly to over 90% during 1980–1990 *(Figure 6)*. This may suggest that once pesticide effects had vanished, individual survival probability increased rapidly and, as a consequence, also site persistence probability. Since the 1990s, there has been a slow but ongoing decline in persistence, which may indicate decreasing survival of adult Peregrines. In sharp contrast, colonization rates increased steadily from about 3% in the early years to maxima of almost 50% during 1994–2001 *(Figure 6)*. Since then, colonization has also declined steadily and currently reaches only about 33%. The colonization curve seems to reflect the trajectory of population size, with a greater population size producing more recruits to colonize empty territories.

Importantly, we note that both persistence and colonization rates began to decline many years before the recent population decline became apparent after about 2007: persistence started to decline more than 10 years earlier and colonization about 5 years earlier. Hence, analysis of population studies using dynamic occupancy models may provide early-warning signals for future population declines.

Big cliffs had both a greater persistence probability and colonization probability than did small or medium-sized cliffs *(Table 3)*.

Regional and site-stratified population trends

One fundamental quantity that is estimated in occupancy models is the matrix of the presence or absence of an adult pair at each site and year. We can inspect these estimates if we

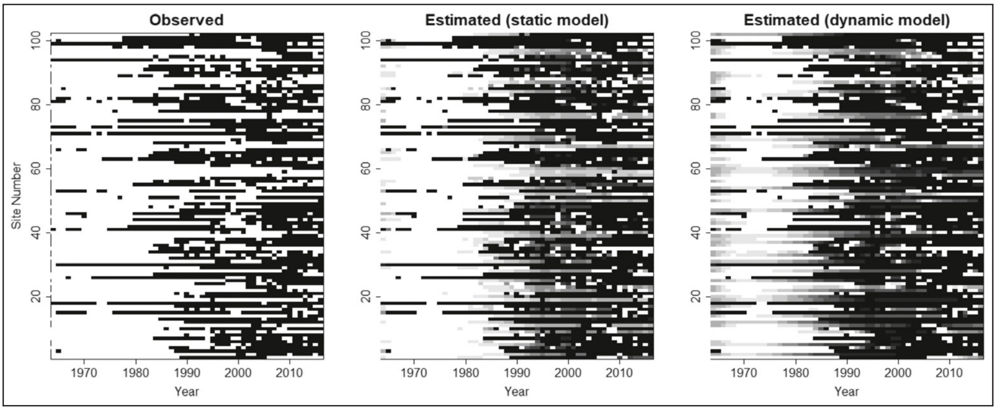

Figure 7. Illustration of the estimation of site-stratified population trends: observed presence/absence matrix of adult pairs at the 102 sites in the Département du Doubs (left) and estimates of the same matrix (corrected for missing visits) under a static (middle) and a dynamic occupancy model (right). The estimates of the presence/absence states are probabilities of presence, hence, we have shades of grey instead of only black and white. Darker shades correspond to a higher likelihood that a site is occupied

7. ábra A költőhelyek szerinti populáció méretek becslésének bemutatása: megfigyelt értékek Département du Doubs régió 102 költőhelyén (balra), ugyanannak a mátrixnak az újrabecslése (hiányzó felkeresésekre korrigálva) egy statikus (középen) és egy dinamikus modellben (jobbra). A becsült előfordulás arányban van megadva, ezért az ábra szürkeskálás, és nem csupán fekete-fehér színeket jelenít meg; a sötétebb árnyalatok egy terület foglaltságának magasabb valószínűségét jelentik

Table 4. Conditional estimates of the probability of presence of an adult pair under the dynamic occupancy model for the same sites and years as in *Table 1*. These are conditional estimates because they include the information from the observed data. Hence, whenever a pair was detected, the conditional probability of presence becomes 1

4. táblázat A dinamikus foglaltsági modell alapján kapott jelenléti arányok feltételezett becslései ivarérett költőpárok esetén, ugyanazokra a területekre és években, mint az *1. táblázatban*. A becsült értékek azért feltételesek, mert tartalmazzák a megfigyelési adatokat is. Ezért, ha egy költőpár valóban megfigyelhető volt, akkor kizárólag 1-es értéket kaphatott itt

Site	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Bolozon	1.00	0.96	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chézery	0.85	0.85	1.00	0.66	0.00	0.16	0.19	0.16	0.00	1.00	0.87	1.00	0.00	0.08	0.00	0.15	0.21
La Fauconnière de Belleydoux	0.00	0.18	0.00	0.00	0.00	0.48	0.72	1.00	1.00	0.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00
Fort l'Ecluse	0.81	1.00	1.00	1.00	0.55	0.00	0.58	0.77	1.00	0.75	0.70	0.79	1.00	0.75	0.66	0.56	0.62

want to obtain the best guess as to whether any given site was or was not occupied in any given year. In our analysis, these estimates only account for missing site visits, but in more typical applications of occupancy models, the estimates would in addition correct for imperfect detection. For illustration, in *Figure 7* we compare the observed presence/absence matrix of adult pairs for the 102 sites in the Département du Doubs with the estimates of this matrix under a static and a dynamic occupancy model.

While the total population size estimates (i.e. the aggregation of these matrices across the rows) are similar for a static and a dynamic model, the site-specific estimates can be quite different. In the dynamic model, the observed data in earlier and later years influence the estimate in any given year. Thus, if there is an interest in the best possible guess of whether a site did or did not have a pair in any year when there was no visit, the dynamic model is most appropriate. For years when an adult pair was observed, this estimate will be equal to 1. For years when no visit took place, the estimate will in general be unequal to 0 or 1 and will be based on earlier or later observations of presence or absence *and* on the estimates of the probability of persistence or colonization linking that year with such observations on either side. We illustrate this in *Table 4* for the four sites that we used for illustration in *Table 1*.

As a final illustration of the use of the estimates of the site-level trends of presence or absence, we give the population size estimates for each of the three departments separately (under the average of the two occupancy models with preferential sampling; as above in *Figure 5*) and compare them to the observed number of pairs in these departments *(Figure 8)*. We see that the observation error due to incomplete coverage of the sites is different in the three departments. The observed data in the Jura are the most precise, reflecting the superior observation effort over many years in that department by the two first authors.

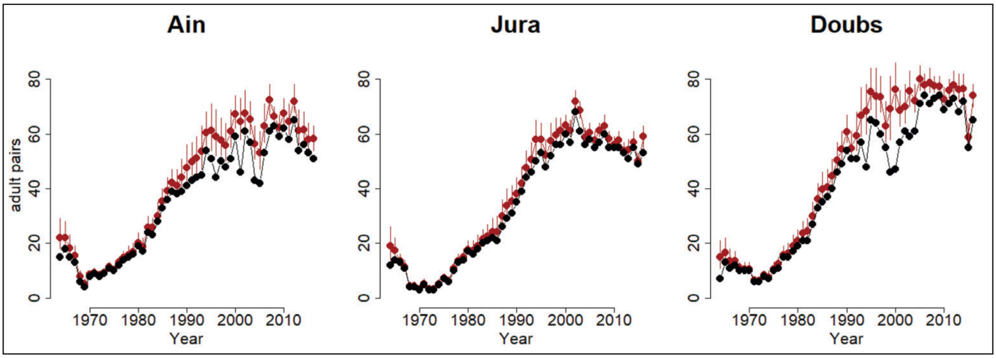

Figure 8. Regional population size estimates of Peregrine falcons for each of the three Départements in the Jura mountains 1964–2016. The brown symbols show the model-averaged estimates under the static occupancy models with preferential sampling (with 95% CRIs), while the black symbols show the observed number of pairs

8. ábra A becsült vándorsólyom populációk területenkénti bontásban a három különböző területre 1964 és 2016 között. A barna jelek a statikus foglaltsági modellek átlagértékei, ahol az eltolódott mintavételezést figyelembe vettük (95%-os intervallumokkal). A fekete jelek a ténylegesen megfigyelt párok számát mutatják

Discussion

We have briefly described what must be one of the longest-running Peregrine population studies in the entire world: that in the French Jura mountains, which was launched in 1964 and is now in its 55th year (Monneret 2006, 2009, 2017). We found the typical population size trajectory of a Peregrine population that was heavily affected by the use of pesticides: the first years of the study marked the final years of the pesticide crash. The nadir of our population was reached in 1972, with an estimated 18 adult pairs, with recovery to the maximum population size of 212 in 2007, followed by a marked decline in recent years that has taken the population size down to 191 pairs in 2016. The French Jura hosts a high density of breeding Peregrines, which was about 1.7 adult pairs per 100 km^2 at its highest, 10 years ago.

The reasons for the recent population decline are not entirely clear, but are likely to be due in the first place to predation by one of the major natural predators of the Peregrine in Europe: the Eagle Owl *(Bubo bubo)*. Itself recovering from century-long persecution, the Eagle Owl has greatly expanded its range in France in recent decades, from the original refuges mainly in the South of France where it never became extinct. A large number of Peregrine sites in the French Jura have since become occupied by Eagle Owls. Establishment of a new pair of Eagle Owls at a Peregrine site usually causes failure to produce any young, intermittent occupancy of a site by Peregrines or altogether site abandonment by the Peregrines (Monneret 2010). Thus, in one former high density patch near Baumes-les-Messieurs in the Départment du Jura, there were 7 Peregrine pairs before the arrival of the Eagle Owl, but now there are several pairs of Eagle Owls and only 3 pairs of Peregrines. Other reasons for the decline may include illegal persecution such as poisoning by pigeon fanciers or shooting by hunters, disturbance by rock climbers, delta and paragliders, bird photographers and generally people in the outdoors that may inadvertently come too close to Peregrine nesting sites.

The situation of the Peregrine in the French Jura mountains is not yet downright threatening, but the recent declines are definitely reason for concern and have changed the way in which many of us think about the Peregrine, e.g. as being entirely out of the danger zone. Rather, the recent declines have created a new awareness that all is not well and that a population that may seem very healthy in one decade may suddenly face new threats only a few years later. Hence, continuous surveillance monitoring is needed in the future, as well as efforts to curb illegal persecution, to avoid the effects of human disturbance and mitigation efforts such as creation and maintenance of artificial or improved nesting site. The first two authors have over decades expended a huge effort in Peregrine nest site creation and nest site improvement, and this has been shown to greatly boost the fecundity of a Peregrine site (Monneret *et al.* 2015). This important work should be continued over the coming decades.

A major focus of this study lies on the methodological aspects of a raptor population study such as ours, where incomplete survey coverage (not all sites can be visited in every year and the proportion visited is variable) and preferential, rather than random sampling ("good" sites are visited in preference to "bad" sites) pose severe challenges to the estimation of annual population size. We have highlighted the power of occupancy models (MacKenzie *et al.* 2002, 2003, 2017) to mitigate these problems. We have shown how the latent occupancy status of a site not visited can easily be estimated and how preferential sampling can be accommodated in a joint model for the bird population and for site visitation, where site quality is estimated in the former submodel and used as a covariate in the latter submodel (Conn *et al.* 2017). These benefits of occupancy models for the crucial objective of any population study, to assess population size, are huge and appear to make occupancy modeling a method of choice for the data analysis in many bird population studies.

But in addition, dynamic occupancy models (MacKenzie *et al.* 2003, Royle & Kéry 2007) enable one to estimate the parameters that govern the dynamics of a population, i.e. the change in population size over the years, even without individually marking the animals. These parameters are the probabilities of persistence and colonization, and we have emphasized how changes in the population size may often be preceded by earlier changes in these parameters, by many years or even decades (see also van Strien *et al.* 2011). This is what we found in our study population, where declines in persistence and colonization probabilities started in the 1990s and around 2001, respectively, although the resulting population decline only became apparent after about 2007. Hence, dynamic occupancy models can serve the important goal of providing early warning signals when something in a bird population takes a turn for the worse.

We are certainly not the first to use occupancy modeling for the analysis of raptor or owl population studies; indeed, the very first application in the paper that developed the dynamic occupancy model (MacKenzie *et al.* 2003) was for a population of cavity-nesting owls (Northern Spotted Owls *(Strix occidentalis)* (see also MacKenzie *et al.* 2009)). Some other important examples of occupancy modeling for raptor and owl population studies include Martin *et al.* (2009a, 2009b) for Golden Eagles *(Aquila chrysaetos)* and Bruggeman *et al.* (2016) for Alaskan Peregrine Falcons. The latter study provides some neat examples of how the dynamic rates governing the change in population size (i.e. persistence and colonization) can be modeled with covariates, such as cliff height, percentage of water within the territory or the distance to the nearest occupied Peregrine territory.

However, we have perhaps emphasized more than any other study before us how very powerful and suitable occupancy models are precisely for the analysis of typical population studies of raptors and owls. We believe that occupancy modeling should become a method of choice in the analysis of many population studies with unmarked individuals, where there is a clear notion of "sites", or territories that are more or less stable over the years. Of course, this is a very typical situation in raptors and owls, and hence, we believe that occupancy modeling is particularly useful for raptor and owl population studies.

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We owe a special debt of gratitude to all the friends and colleagues in the Groupe Pèlerin Jura, who have monitored Peregrines in the wonderful French Jura. Without them, this study could not have been conducted. One of the authors (René Ruffinoni) died before this study could go to press; Ruffi is sadly missed! Olivier Gimenez, Aurélien Besnard and Frédéric Jiguet provided a very welcome review of an earlier draft of this paper which made us realize the importance of preferential sampling and thus, we believe, led to greatly improved results.

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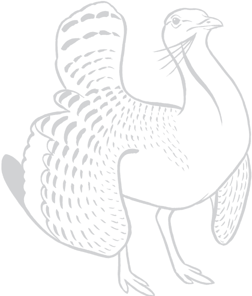

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Population trends of the Peregrine Falcon in Switzerland with special reference to the period 2005–2016

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Summary We study population trends of the Peregrine Falcon *(Falco peregrinus)* in Switzerland with special reference to the development since 2005 and three study areas, South West Switzerland (4,993 km^2, 1960–2015), the Northern Jura mountains (3,270 km^2, 2005–2015) and the Canton of Zurich (1,748 km^2, 2002–2015). We used dynamic occupancy models, which allow the territory-specific extinction and colonization parameters – the demographic rates (at the territory level) underlying a population trend – to be estimated. The Swiss peregrine population has developed in line with trends observed in many other countries and regions in North America and Europe: after the pesticide-induced collapse between the 1950s and 1970s, the population largely recovered up to the turn of the millennium. However, in recent years, we detected significant declines again: in SW Switzerland, the population decreased from 51 to 33 pairs during 2008–2015 (-35%), in the N Jura from 70 to 40 pairs during 2009–2015 (-43%) and in Zurich from 6–7 to 2–4 pairs during 2010–2015 (-50%). In the same time, the local extinction rate in the three study areas (more than) doubled from (0.05) 0.1 to 0.2, while the colonization rate dropped from 0.3 to 0.1 in one of the areas, while no change was detectable in the other two. We discuss two factors responsible for these strong, recent declines of Swiss peregrines: (1) predation by Eagle Owls *(Bubo bubo)* and (2) direct and illegal persecution by humans. In addition to these two factors, growing human disturbance (e.g. through climbers, bird photographers, paragliders, hikers, geocachers, etc.) and fatalities due to collisions with man-made structures (power lines, glass, wind turbines, etc.) are also suspected to contribute to the population decline.

Keywords: dynamic occupancy model, Jura mountains, Peregrine Falcon, persecution, predation, raptor

Összefoglalás A vándorsólyom *(Falco peregrinus)* populációs irányait tanulmányoztuk Svájcban – különös tekintettel annak 2005 utáni változására – három vizsgálati területen: Svájc délnyugati része (4993 km^2, 1960–2015), északi Jura-hegység (3270 km^2, 2005–2015) és Zürich kanton (1748 km^2, 2002–2015). Dinamikus foglaltsági modelleket alkalmaztunk, melyek egy területre jellemző kihalási és kolonizációs paraméterek – a populációs irányzatok mögött megbújó demográfiai arányok (területi szinten) – becslésére is alkalmasak. A svájci vándorsólyom populáció hasonló mintázatot mutat más országokban (Észak-Amerika és Európa) megfigyelt tendenciákkal: az 1950-es és 1970-es évek közötti fokozott rovarirtó használat után a populációk többé-kevésbé rendeződtek az ezredfordulóra. Az utóbbi időszakban azonban újabb hanyatlást figyelhetünk meg: Svájc délnyugati részén a populáció 51 párról 33 párra esett vissza 2008 és 2015 között (-35%), a Jura-hegység északi részén 2009 és 2015 között 70-ről 40 párra (-43%), és Zürich térségében 2010 és 2015 között 6–7 párról 2–4 párra (-50%). Ezzel egyidejűleg a kihalási ráta mindhárom területen közel megkétszereződött: (0,05) 0,1-ről 0,2-re, viszont a kolonizációs ráta az egyik régióban 0,3-ről visszaesett 0,1-re (a másik két régióban nem azonosítható változás). Két fő tényezőt szeretnénk kiemelni, melyek felelősek lehetnek a svájci vándorsólyom populáció ilyen mértékű csökkenéséért: (1) az uhu *(Bubo bubo)* fokozódó elterjedése, valamint (2) a közvetlen és törvénytelen emberi zavarások. Az említett tényezők mellett a fokozódó emberi jelenlét (hegymászók, madárfotósok, siklóernyősök, túrázók stb.), valamint mesterséges tárgyak (elektromos vezetékek, üveg, szélturbinák stb.) okozta pusztulások is hozzájárulhatnak a populáció méretének csökkenéséhez.

Kulcsszavak: dinamikus foglaltsági modell, Jura-hegység, vándorsólyom, zavarás, predáció, ragadozó madarak

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Introduction

This study was undertaken following signs that Peregrine Falcon populations *(Falco peregrinus)* in Switzerland have recently been decreasing and in light of a growing number of reports of illegal persecution by pigeon fanciers. We focus primarily on the most recent population trends of the Peregrine in Switzerland and examine what impact the recent increase in instances of proven or suspected poisoning could have on the population.

Methods

In order to evaluate the recent population status of the Peregrine in Switzerland, we used high-quality data from nesting territories in the three best-monitored study area in the country. Data from population surveys in Switzerland in sufficiently detailed temporal resolution are available from three areas, all situated in the North or West of Switzerland *(Figure 1)*: South West Switzerland, the Northern half of the Jura mountains ("Northern Jura mountains") and the Canton of Zurich. Peregrine falcons utilize the same cliffs or ranges of cliffs for breeding purposes (Ratcliffe 1993, White *et al.* 2013), some of which have been occupied for centuries. To designate this basic „unit“ for the presence of Peregrines in an area, we use the terms site, territory or eyrie interchangeably.

Data

In South West Switzerland, Gabriel Banderet and his group of volunteers have been monitoring most of the known Peregrine sites in an area of 4,993 km^2 since 1960 on an annual basis, making multiple visits during the breeding season and recording occupancy and breeding success for each pair. This Peregrine survey is the longest-running population study of any avian species in Switzerland. Our analysis spans the 56 years between 1960 und 2015. For the purposes of our study, we included only the presence or absence of a breeding pair, i.e. a territorial pair which lays eggs, because the data for territorial pairs in this study was not available for the whole of the timespan.

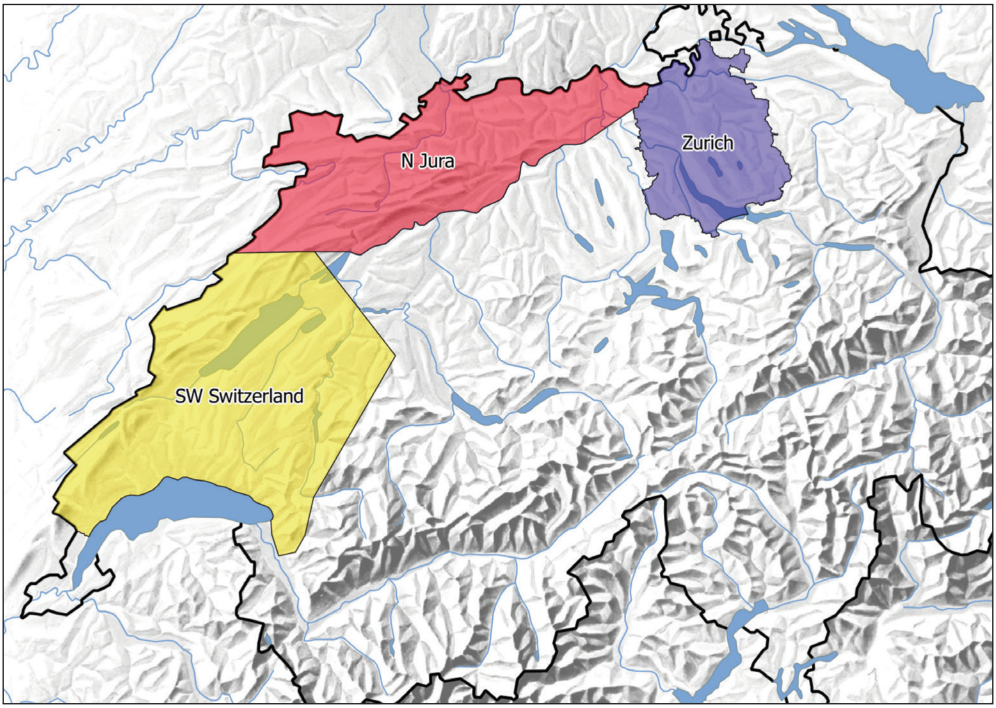

Figure 1. Map showing the three study areas for the Peregrine Falcon: South West Switzerland (yellow; Cantons of Fribourg, Neuchâtel, Vaud, Berne and Valais; monitoring group led by G. Banderet from 1960; 4,993 km^2), Northern Jura mountains (red; Cantons of Berne, Jura, Solothurn, Basel-Land, Basel-Stadt, Argau; monitoring group led by M. Kéry from 2005; 3,270 km^2) and the Canton of Zurich (violet; data from Orniplan AG/Martin Weggler, from 2002; 1,748 km^2). Base map © Institut of Cartography ETH Zürich

1. ábra A három vándorsólyom vizsgálati terület térképe: Délnyugat-Svájc (sárga; Fribourg kanton, Neuchâtel, Vaud, Berne and Valais; a kutatócsoportot 1960 óta G. Banderet vezeti; 4993 km^2), északi Jura-hegység (piros; Bern kanton, Jura, Solothurn, Basel-Land, Basel-Stadt, Argau; a kutatócsoportot 2005 óta M. Kéry vezeti; 3270 km^2) és Zürich kanton (ibolya; az adatokat Orniplan AG/Martin Weggler szolgáltatták 2002 óta; 1748 km^2). © Institute of Cartography ETH Zürich

In the Northern Jura mountains (the Jura mountains north of a line from La Chaux-de-Fonds to Biel/Bienne, an area of 3,270 km^2) Marc Kéry, Martin Neuhaus and colleagues have been monitoring as many known territories as possible since 2005, also recording occupancy and breeding success. In our report we analysed the presence/absence of territorial pairs, i.e. independently of whether the pairs bred or not.

In the Canton of Zurich (an area of 1,748 km^2), Orniplan AG (Martin Weggler, Martin Neuhaus and colleagues) have been collating all records of Peregrine Falcons at known nesting sites since 2002 and inputting them into a database from which all Peregrine breeding data were extracted on 25 April 2016. In our report we also analysed the presence/absence of territorial pairs, independently of whether the pairs bred or not.

We note therefore that we apply slightly different measures in the three study areas for assessing the population status of the Peregrine, i.e. breeding pairs in South West Switzerland

and territorial pairs in the two other study areas. As not all territorial pairs produce eggs, the number of breeding pairs will typically be lower than the number of territorial pairs. For assessing the trend – our primary objective – it is immaterial whether we analyse breeding or territorial pairs. When we refer to pairs in the following, it will be clear from the context whether we mean territorial or breeding pairs.

Statistical analyses

The data from each of the three study areas were summarized in a matrix where the rows corresponded to the known nesting sites and the columns to the years (see *Figure 2* for an example). The elements of the matrix (the content of a cell defined by a specific site and a specific year) contain the presence (coded as a one) or the absence (coded as a zero) of a territorial pair (pairs in a territory) or of a breeding pair (pairs with proven clutches).

To analyse the population trend and the probabilities of local extinction and colonization at a site from one year to the next, we used a variant of multi-season occupancy model (MacKenzie *et al.* 2003, Kéry & Schaub 2012), also known as dynamic occupancy model (Kéry *et al.* 2013). With this variant, we omitted the customary model components which correct for false-negative observation error. Thus, no correction was made for the possibility that a site which was in fact occupied in a given year was recorded as “unoccupied” in the survey because no birds were detected although they were present. We had to make this assumption because we lacked the repeat measurements needed to correct for this type of observation error or because the “observation results” for a specific visit, although almost always noted in the field, were not recorded in the databases. We fit these models to the data from each study area, using Bayesian estimation techniques (Kéry 2010, Kéry & Schaub 2012) implemented with the program JAGS (Plummer 2003). We used so-called “vague priors” which produce estimates which, for customary sample sizes, correspond numerically to those of the also commonly used maximum likelihood estimation methods (Kéry 2010, Kéry & Royle 2016).

Although the datasets available for the three study areas contain high-quality observation data, interpreting the population trend (i.e. change in the number of pairs over the years) was complicated by gaps in the data due to the fact that in most years the sites were not entirely monitored. Thus, in order to arrive at an estimate of the total population in an area in a given year, the occupancy status for these missing years/sites had to be estimated. A great advantage of a Bayesian analysis is the ease with which such missing values can be estimated, combined with appropriate error propagation (Kéry 2010). The confidence intervals of our population estimates fully allow for the estimation uncertainty resulting from these “missing values”.

In order to estimate the development over time of the colonization and extinction parameters underlying the population changes as accurately as possible and to correct for the autocorrelation over time in these parameters, we built into our models a random-walk smoothing over time (Johnson & Hoeting 2003). Using this method, it can happen that the smoothed data lie below the values actually observed because they indicate a multi-year tendency and average out annual fluctuations.

In the case of the data matrix from the South West Switzerland study area, for many years in the first half of the study period (1960 until approx. 1980) it was not always clear if a site had been surveyed and found to be unoccupied (which we denoted by a zero) or if it had not been monitored at all (which corresponds to missing data). In this dataset, we were thus unable to distinguish clearly between zeros and missing data. As we can however assume that the number of pairs observed nevertheless provides a satisfactory enough picture of the population trend of the Peregrine within this area, even in the initial years of the study period, we elected not to use a dynamic occupancy model for the site/year matrix for investigating the long-term population trend in this area but instead a simpler Poisson regression with an additive (i.e. smoothed) term over time. We conducted this analysis with the software package mgcv in program R (Wood 2006).

Results

South-West Switzerland

The 1960–2015 period coincides with the final phase of the worldwide pesticide-induced population crash of the Peregrine Falcon (Ratcliffe 1993), which in the year 1973 led to the complete extinction of the Peregrine in South West Switzerland. Thereafter, from the second half of the 1970s onwards the population recovered, accelerating particularly in the 1980s

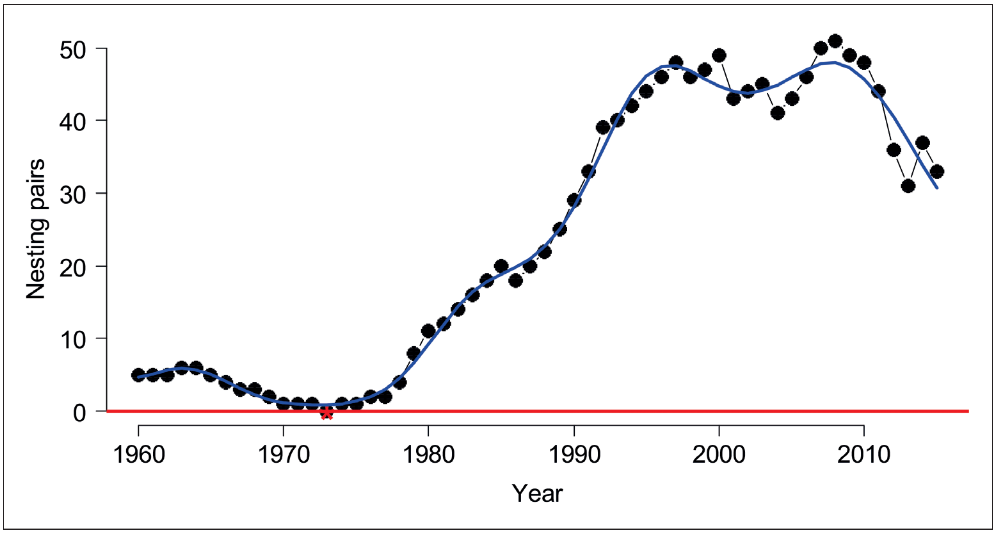

Figure 2. Population trend of the Peregrine Falcon in the South West Switzerland study area. The black dots show the number of breeding pairs detected (pairs which laid eggs). The red star highlights the year 1973 in which the Peregrine Falcon totally disappeared as a breeding species in the study area. The blue line depicts the smoothed population trend

2. ábra A vándorsólyom populációs mintázata Délnyugat-Svájcban. A fekete pontok a megfigyelt költőpárok számát jelölik (tojást is raktak). A piros csillag 1973-at jelöli, amikor a vándorsólyom nem költött a térségben. A kék vonal a populációs trend változását szemlélteti

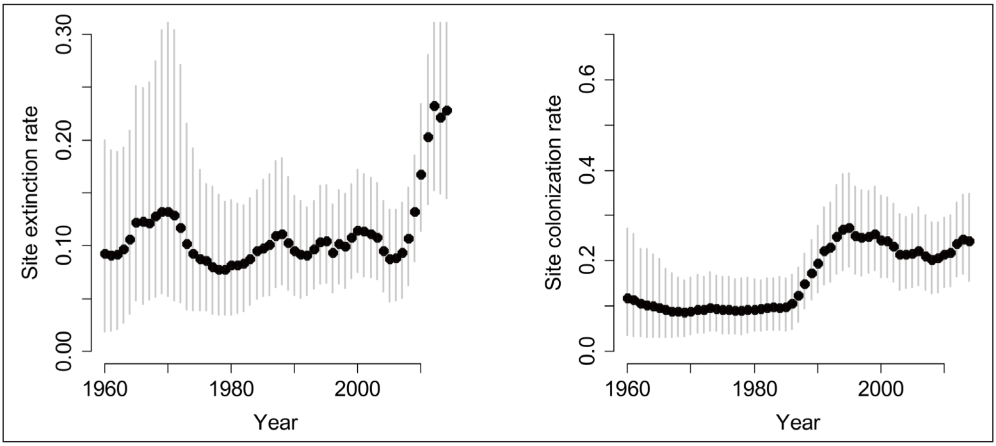

Figure 3. Time series of the demographic site extinction and site colonization rates underlying the population dynamics of the Peregrine Falcon in South West Switzerland (with 95% Bayesian credible intervals)

3. ábra A vándorsólyom populációdinamikája mögött rejlő kihalási és kolonizációs ráták időbeli megoszlása Délnyugat-Svájc költőhelyein (95%-os Bayesian intervallumokkal)

and 1990s and stabilizing at approximately 50 pairs since 1996. More recent years have seen a renewed decline *(Figure 2)*. This figure may arguably exaggerate the original decline and subsequent recovery somewhat as the study area in the1960s and 1970s was somewhat smaller than in subsequent years and the relatively small population in the 1960s is also influenced as a result.

Since 2000 it can be seen that the Peregrine suffered a population decline from 51 (2008) to only 33 pairs (2015). Thus, during this seven-year period the number of breeding pairs in South West Switzerland decreased by 35%.

More detailed analysis of the population dynamics by estimating the demographic rates (probability of site extinction or local colonization) in the dynamic occupancy model showed that the extinction rate shot up towards the end of the study period (from approx. 2008) to reach values well in excess of those at the end of the pesticide crash in the 1960s (*Figure 3* left). By contrast, the colonization rate in South West Switzerland increased after the pesticide crash and, in the last ten years, remained roughly in line with the values of the preceding years (*Figure 3* right).

Northern Jura mountains 2005–2015

The Peregrine population in the North Jura study area declined from approx.70 pairs (in the years 2005–2009) to only around 40 pairs in the final year of the study period (2015) *(Figure 4)*. This represents a decrease of 43% in the space of only 6 years (2009–2015).

Analysis of the demographic rates in the North Jura study area shows that, over the same time span, the likelihood of extinction at an occupied site doubled from 10 to 20% (*Figure 5* left) while the likelihood of colonization of an unoccupied site dropped from approx. 30% to not much more than 10%.

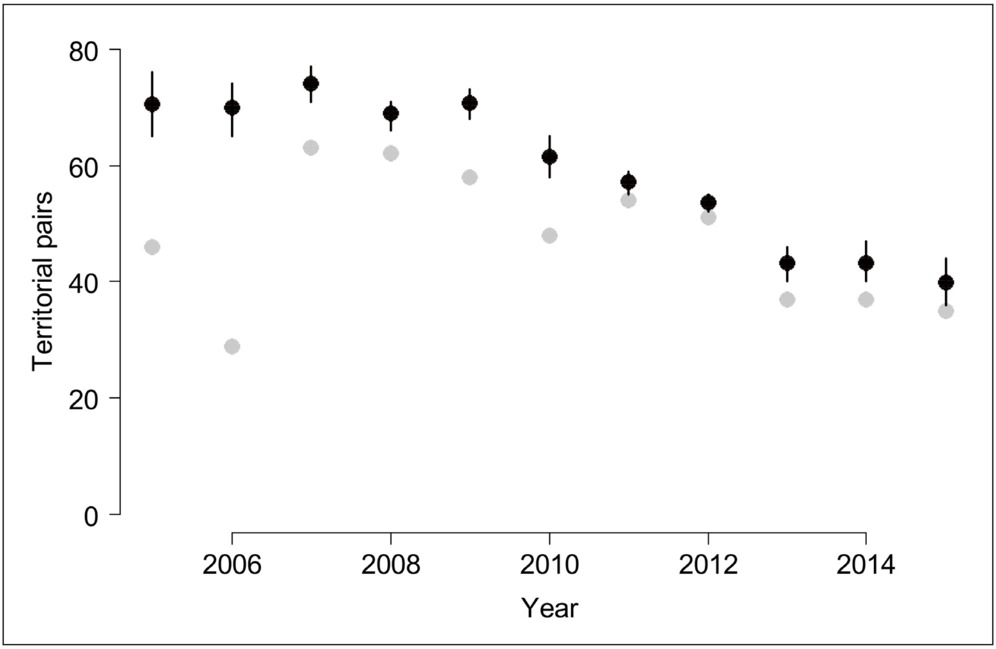

Figure 4. Population trend of the Peregrine Falcon in the Northern Jura mountain study area during the 2005–2015 period. The grey dots correspond to the number of pairs observed, which is however distorted due to annual fluctuations in the number of sites monitored. The black dots depict the corrected number of territorial pairs, accounting for the likely occupancy status of sites not visited in a given year (with 95% Bayesian credible intervals)

4. ábra A vándorsólyom populációs mintázata az északi Jura-hegységben 2005 és 2015 között. A szürke pontok a megfigyelt költőpárok számát jelölik, azonban a felkeresett költőhelyek éves változásával torzítottak. A fekete pontok az adott évben kihagyott költőhelyek lehetséges foglaltságával javított értékeket szemléltetik (95%-os Bayesian intervallumokkal)

Canton of Zurich 2002–2015

Occupancy, i.e. the presence or absence of a territorial pair, for the eight Peregrine sites known since 2000 is shown in detail in *Table 1*. Using the Bayesian implementation of the dynamic occupancy model allowed us to correct for annual fluctuations in the number of nesting sites monitored *(Figure 6)* and suggested that the population numbered six to seven pairs up until 2010, thereafter declining successively to only 2–4 pairs (2014/2015). This represents a drop of at least 50% within the space of only 4–5 years.

Analysis of the demographic rates shows that in the same period the likelihood of extinction of an occupied site has multiplied from approx. 5 to over 20% (*Figure 7* left). The likelihood of colonization of an unoccupied site can only be estimated imprecisely owing to the very small numbers involved but here too the estimates point to a decline at the end of the study period (*Figure 7* right).

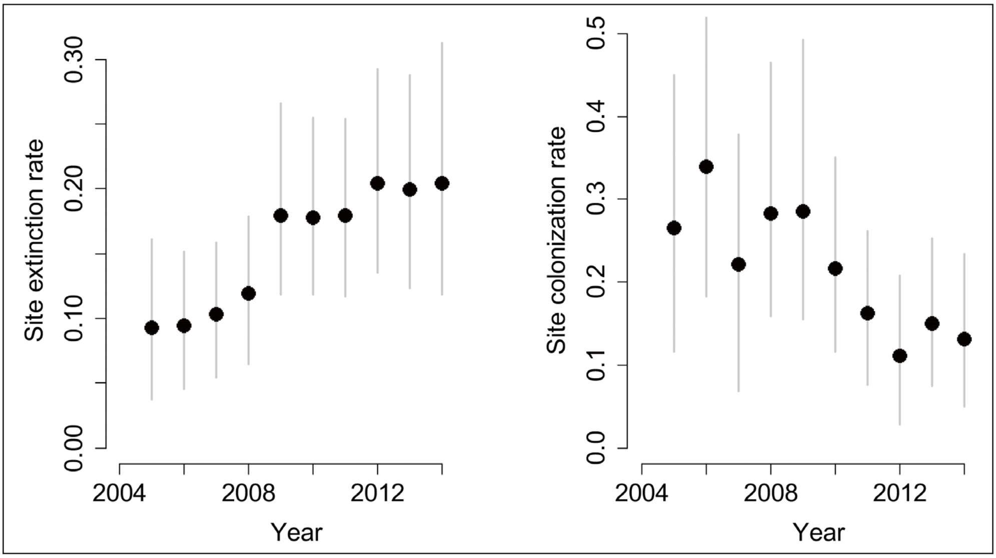

Figure 5. Time series of the demographic rates (extinction and colonization rates) underlying the population dynamics of the Peregrine Falcon in the Northern Jura mountains study area (with 95% Bayesian credible intervals in grey)

5. ábra A vándorsólyom populációdinamikája mögött rejlő kihalási és kolonizációs ráták időbeli megoszlása az északi Jura-hegység költőhelyein (95%-os Bayesian intervallumokkal)

Table 1. Occupancy of the eight Peregrine Falcon sites known in the Canton of Zurich since 2000 according to data provided by Orniplan AG (M. Weggler) and M. Neuhaus. A 1 signifies that a Peregrine pair was detected at a site in a given year and a 0 that the site was monitored but no Peregrine pair was detected. 'NA' signifies a missing value, i.e. that a site was not monitored in a given year

1. táblázat Az ismert vándorsólyom költőhelyek foglaltságai Zürich kantonban 2000 óta Orniplan AG (M. Weggler) és M. Neuhaus által szolgáltatott adatok alapján. 1 jelöli, ha az adott területen ténylegesen megfigyeltek költő vándorsólyom párt az adott évben, és 0 mutatja, ha a területet felkeresték, de nem sikerült költőpárt megfigyelni. NA a hiányzó adatokat jelenti, vagyis azokat az eseteket, amikor a területet egyáltalán nem monitorozták egy adott évben

Site	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**
A	1	1	NA	1	1	1	1	1	1	1	1	1	1	1
B	NA	NA	NA	NA	1	1	1	1	1	NA	1	0	0	0
C	1	1	1	1	1	1	1	NA	1	0	0	0	0	0
D	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0	1
E	1	1	1	1	1	1	NA	NA	1	1	1	1	1	NA
F	NA	1	1	1	1	1	1	1	1	0	1	0	0	1
G	1	NA	NA	NA	1	1	1	1	1	1	0	1	0	0
H	1	1	1	1	1	1	NA	1	1	1	0	0	0	0

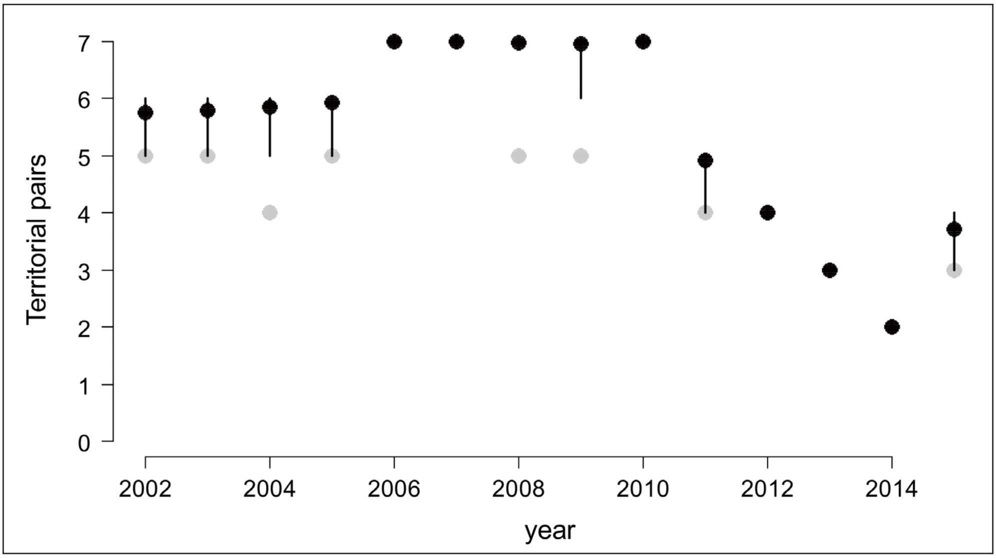

Figure 6. Population trend of the Peregrine Falcon in the Canton of Zurich during the 2002–2015 period. The grey dots correspond to the number of pairs observed which is however distorted due to annual fluctuations in the number of sites monitored. The black dots depict the corrected number of territorial pairs (with 95% Bayesian credible intervals)

6. ábra A vándorsólyom populációs mintázata Zürich kantonban 2002 és 2015 között. A szürke pontok a megfigyelt költőpárok számát jelölik, azonban a felkeresett költőhelyek éves változásával torzítottak. A fekete pontok az adott évben kihagyott költőhelyek lehetséges foglaltságával javított értékeket szemléltetik (95%-os Bayesian intervallumokkal)

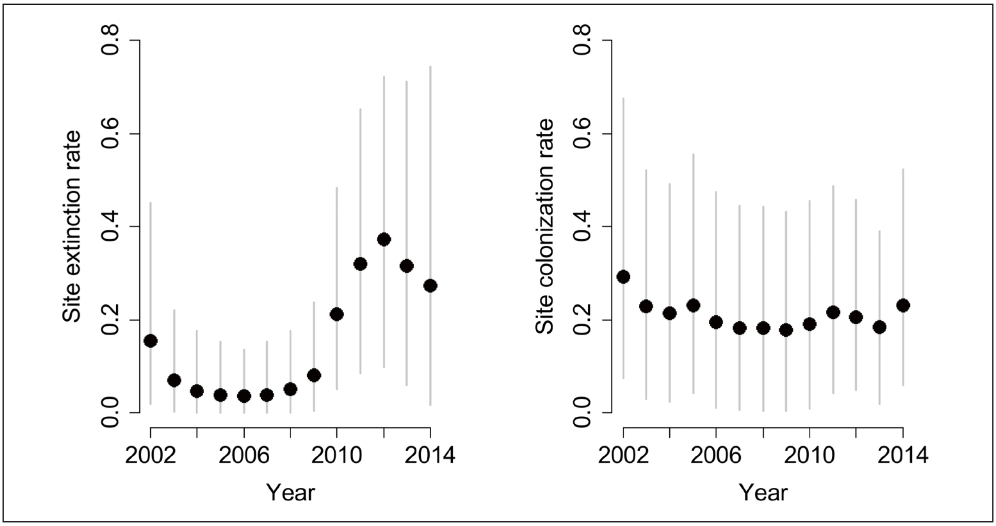

Figure 7. Time series of the demographic rates (site extinction and colonization rates) underlying the population dynamics of the Peregrine Falcon in the Canton of Zurich (with 95% Bayesian credible intervals in grey)

7. ábra A vándorsólyom populációdinamikája mögött rejlő kihalási és kolonizációs ráták időbeli megoszlása Zürich kanton költőhelyein (95%-os Bayesian intervallumokkal)

Discussion

Population trends and their demographic drivers

The population trend of the Peregrine Falcon in Switzerland largely mirrored that observed in many other countries in Europe and North America (Ratcliffe 1993, White *et al.* 2013): following a population crash caused by environmental toxins like the pesticides DDT and Dieldrin between the 1950s and the 1970s, numbers largely recovered again up until 2000. The Peregrine thus embodies one of the great success stories in nature conservation, in Switzerland and globally.

In more recent years, however, the trend has no longer been so positive, a fact that is still little known and hardly published. Our investigation shows that in three of the best monitored sub-populations of the Peregrine Falcon in Switzerland (South West Switzerland, Northern Jura mountains, Canton of Zurich), numbers in the past 10 years dropped by between 35 and at least 50%: in the South West Switzerland study area from 2008–2014 from 51 to 33 breeding pairs (-35%), in the Northern Jura mountains study area from 2009–2015 from 70 to 40 territorial pairs (-43%) and in the Canton of Zurich from 2010–2014/2015 from 6–7 to only 2–4 territorial pairs (corresponding to a decline of 50% or more). These unexpectedly sharp declines in all three populations are astonishing, and their synchronicity (they all began to show between 2008 and 2010) appears to point to common causes operating on a wide geographic scale.

The demographic drivers behind this population trend were investigated by analysing the local, or site, extinction rates (i.e. the likelihood of an occupied nesting site being abandoned the following year) and the local, or site, colonization rates (i.e. the likelihood of an abandoned site being reoccupied the following year) within the framework of a dynamic occupancy model (MacKenzie *et al.* 2003). The analysis showed that over the same period (beginning around 2008–2010) the extinction rate rose sharply in all three study areas (South West Switzerland and North Jura from 0.1 to 0.2, Canton of Zurich from around 0.05 to 0.2) while the colonization rate in one study area (North Jura) dropped sharply (from 0.3 to 0.1) but in the other two study areas, South West Switzerland and the Canton of Zurich, showed no clear change throughout the period of the recent population declines.

Additionally, in the past 5 years, more and more immature (one-year-old) Peregrines have been found paired in the territories (G. Banderet, M. Kéry, M. Neuhaus pers. obs.). In a long-lived species like the Peregrine this suggests that the "reserve" of adult "floaters", i.e. birds not yet holding a territory but able to take over if a territorial bird is lost, is exhausted. One-year-old Peregrines breed far more rarely and less successfully than adults so that a significant proportion of paired one-year-olds will automatically mean a drop in reproduction within a Peregrine population.

What factors influence the demographic rates underlying the population trends?

Based on the data and information available within Switzerland and from neighbouring countries (France and Germany), two factors in particular would appear to be to blame for the recent declines in Swiss Peregrine numbers: the recovery in the Eagle Owl *(Bubo bubo)* population and renewed human persecution, probably predominantly through poisoning by pigeon-fanciers. Two further factors, i.e. human disturbance (climbers, bird photographers, paragliders, hikers, geocaching etc.) and additional mortality due to collisions with man-made infrastructure (power lines, fences, windows, wind turbines, vehicles) probably also played a role, especially since the incidence of both sets of causes has greatly increased in recent years.

The Eagle Owl is the primary predator of the Peregrine falcon and to a large extent shares the same breeding habitat: mainly high cliffs. Up until the 1980s, the Eagle Owl in Switzerland had been largely exterminated for many decades outside of the Alps. Subsequently, isolated pairs began to establish themselves following local reintroduction efforts, especially within the Canton of Basel-Land within the Northern Jura mountains study area. The past 10–20 years, however, have seen a widespread and almost explosive recolonization of much of Switzerland probably fuelled primarily by immigration from naturally expanding populations both in Germany and France (Rau *et al.* 2015). As a result, numerous pairs of Eagle Owls have established themselves in cliffs previously occupied by Peregrine falcons within all three study areas. As a rule, this means these sites are abandoned by the falcons (or that would-be breeders run a serious risk of being predated by the neighbouring Eagle Owls). The population recovery of the Eagle Owl in Switzerland is in full swing. In the North Jura study area, for example, Eagle Owl density is probably now comparable to that of the Peregrine (unpublished data from the Northern Jura mountains monitoring group).

A second important factor to be envisaged as partly responsible for the declining Peregrine population is direct persecution, primarily through poisoning by pigeon-fanciers. There are indications of such illegal practices mainly in the Zurich and Basel areas but locally also from East Switzerland and Aargau. Although only an indicator and not hard and fast proof, the synchronicity between the incidence of suspicious Peregrine deaths (instances of poisoning) and the population decline from 2008–2010 is nonetheless striking.

Can the poisoning of just a few Peregrines significantly impact population levels?

For the small to medium-sized Peregrine populations in the three study areas the answer is definitely affirmative. Peregrines are relatively long-lived raptors with a comparatively low rate of reproduction. In animals with a similar life history, the survival rate for reproducing adults is especially critical for maintaining population levels (Saether & Bakke 2000). For instance, Schaub *et al.* (2009) have shown that in a small but growing population of Bearded Vultures in the Alps numbering 50 adult individuals, 2–3 additional deaths (e.g. as a result of persecution) would in all likelihood lead to the population's long-term extinction.

We owe a particularly relevant and highly topical study to Altwegg *et al.* (2014), who examined an urban population of Peregrine falcons breeding on buildings in Cape Town, South Africa from 1997–2010. During the study period this population expanded sharply from 3 to 18 breeding pairs. Altwegg and his colleagues were, however, able to show that this urban population was strongly dependent on immigration from the surrounding countryside (e.g. from the cliffs of Table Mountain) and that without this immigration the urban population would not have increased so strongly but instead would have declined or at best stagnated. In their "integrated population model" (IPM) they were even able to calculate how many adult Peregrines immigrated into the urban environment annually and began to breed there; it was no more than 1 or 2 birds per year.

This study by Altwegg *et al.* (2014) shows emphatically that in small populations each individual bird matters. To obtain comparable figures for the three Swiss populations, we can simply extrapolate proportional to the population size. If in a population of 18 pairs (at the end of the study period of Altwegg *et al.* 2014), a maximum of two individuals can make the difference between an increasing and a decreasing population, this would similarly hold true for the Peregrine in Switzerland. In a population like the size of South West Switzerland's, which at 50 pairs is 2.78 times bigger than Cape Town's (18 pairs), $2.78 * 2 \approx 6$ Peregrine fatalities could therefore make the difference between a stable and declining population. By analogy, in the Northern Jura mountains with its original count of approx. 70 pairs, the loss of $(70/18) * 2 \approx 8$ individuals per year would then lead to a steep decline instead of a stable population (as could still be observed in 2005). And transposing Altwegg *et al.* (2014)'s findings to the very small Zurich sub-population strongly suggests that even a single poisoned Peregrine per year could lead to a critical decline in the population level.

Of course, these extrapolations presuppose that productivity in the populations of Cape Town and Switzerland is comparable. However, the population studied by Altwegg *et al.* (2014) had a higher productivity in this urban population breeding largely in nestboxes than in "natural populations" like those in Switzerland, where eyries are frequently more exposed to the elements and natural terrestrial predators like martens and foxes. Where productivity is lower, however, immigration becomes even more important. Thus, it can be assumed that the above extrapolations we made for Switzerland are more on the conservative side, and that the loss of even fewer individuals than those cited above could already have a critical impact on the population level.

Acknowledgements

We owe a special debt of gratitude to all the friends and colleagues who monitor sites in the three study areas and transmit their findings to the coordinators. Sämi Wechsler kindly produced the map in *Figure 1*.

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Long-term monitoring of a successful recovery program of Peregrine Falcons in Virginia

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Abstract The Peregrine Falcon *(Falco peregrinus anatum)* was believed to be extirpated as a breeding species in Virginia by the early 1960s. An aggressive restoration program was initiated in 1978 that involved the release of captive-reared birds totaling 115 on the Coastal Plain (1978–1985) and 127 in the Mountain physiographic region (1985–1993). The first occupied territory was established and the first breeding attempt was documented in 1979 and 1982, respectively. We have monitored the size, distribution, reproductive rate, and substrate use of the resulting breeding population (1979–2016). The population proceeded through an establishment phase (1979–1993) driven by releases with an average doubling time of 3.8 yrs to a consolidation phase (1994–2016) with an average doubling time of 23.1 yrs. The state supported 31 breeding pairs by 2016. Per capita reproductive rates have increased significantly over the study period from 0.89 (1979–1993) to 1.86 (1994–2016). Average nesting success increased from 67.1% to 82.7% over the same period. Nesting attempts (n = 469) have been documented on dedicated peregrine towers (52.1%), bridges (26.1%), buildings (4.1%), and various man-made structures (13.0%) with only 4.7% documented on natural cliffs. The population appears to be self-sustaining with reproductive rates exceeding 1.5 young/pair every year since 1999. An ongoing management concern is that only 8.9% of known territories (n = 45) identified since introductions and 4.7% of documented breeding attempts (n = 469) have occurred within the historic mountain breeding range.

Keywords: *Falco peregrinus anatum,* restoration program, breeding population, reproductive rate

Összefoglalás Az 1960-as évek elejére úgy tűnt, hogy a vándorsólyom *(Falco peregrinus anatum)* Virginia államból kipusztult, mint költő faj. 1978-ban elindult egy energikus visszatelepítési program, ami magában foglalta 115 fogságban felnevelt madár parti síkságon (1975–1985), és 127 madár hegyvidéki régióban (1985–1993) történő szabadon engedését. Az első territórium foglalást 1979-ben, az első költési kísérletet pedig 1982-ben írták le. Nyomon követtük a létrejött költőállomány méretét, elterjedését, költési sikerét és a fészekalapok típusát 1979–2016 között. Az állomány először egy alapítási fázison ment keresztül (1979–1993), amikor az állomány mérete 3,8 évenként duplázódott meg, majd a konszolidációs fázis következett (1994–2016), amikor az állomány duplázódási ideje 23,1 évre nőtt. 2016-ra az államban 31 költő pár volt. Az egy egyedre vetített szaporodási ráta jelentősen növekedett a vizsgált időszak alatt 0,89-ről (1979–1993) 1,86-ra (1994–2016). Az átlagos költési siker ugyanezen időszak alatt 67,1%-ról 82,7%-ra emelkedett. Költési kísérletek (n = 469) tornyokon (52,1%), hidakon (26,1%), épületeken (4,1%) és egyéb ember alkotta építményeken (13%) voltak és csak 4,7% volt természetes sziklákon. A populáció önfenntartónak bizonyult, 1999 óta minden évben 1,5 fióka/pár reprodukciós rátával. Továbbra is némi aggodalomra ad okot természetvédelmi kezelés szempontjából, hogy a visszatelepítés óta csupán a territóriumok 8,9%-a és a költési kísérletek 4,7%-a fordult elő az eredeti hegyvidéki költőterületeken.

Kulcsszavak: *Falco peregrinus anatum,* visszatelepítés, költőpopuláció, szaporodási siker

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Introduction

The historical population of Peregrine Falcons *(Falco peregrinus anatum)* in the eastern United States was estimated to contain approximately 350 breeding pairs, relied on open cliff faces and cut-banks for nesting, and was mostly confined to the Appalachian Mountains (Hickey 1942). The population experienced a precipitous decline throughout the 1950s (Hickey 1969) due to contaminant-induced reproductive suppression (Anderson & Hickey 1972) and was believed to have been extirpated by the early 1960s (Berger *et al.* 1969). A retrospective assessment of the historic peregrine falcon population in Virginia identified 24 historical eyries in the Appalachian Mountains (Gabler 1983). Two additional nesting sites were documented on old osprey nests along the Virginia portion of the Delmarva Peninsula (Jones 1946).

The Peregrine Falcon was listed as endangered on the U.S. Federal List of Endangered and Threatened Wildlife (50 CFR 17.11-17.12) in June 1970. In 1975, the U.S. Fish and Wildlife Service appointed an Eastern Peregrine Falcon Recovery Team to develop and implement a recovery plan (Bollengier *et al.* 1979). In the absence of any residual breeding stock, one of the key components of the recovery strategy for the eastern population was the production and release of captive-reared falcons (Cade & Fyfe 1978, Cade 2003). The breeding stock used for the captive program was of mixed heritage and contained individuals from non-indigenous subspecies *(F. p. cassini*, *F. p. brookei*, *F. p. pealei*, *F. p. peregrinus*, *F. p. tundrius*, *F. p. macropus)*, as well as native *F. p. anatum* (Barclay & Cade 1983). Within a relatively short period, a captive breeding program was established with enough capacity to sustain an aggressive release program (Barclay & Cade 1983, Barclay 1988).

Between 1978 and 1993, 242 captive-reared falcons were released in Virginia including releases on the Coastal Plain (1978–1985) and in the Mountain physiographic region (1985–1993). Beginning in 2000, a translocation program was initiated in Virginia that has moved wild-reared birds from coastal territories to be hacked from mountain release sites. A large portion of the young used in this program have been produced on coastal bridges. Translocating birds from bridges to the mountains serves to release bridge workers from access restrictions imposed during the breeding season and helps to restore birds to their historic mountain breeding range. More than 250 birds have been moved since the inception of the program (Watts & Watts 2016).

The successful establishment of a breeding population of peregrine falcons within Virginia has clearly contributed to the recovery of the broader eastern population (Enderson *et al.* 1995, Millsap *et al.* 1998) and to the eventual removal of the species from the U.S. Federal List of Endangered and Threatened Wildlife (Mesta 1999). The breeding population is well established and expanding. Here we describe the establishment, growth, breeding performance and nesting substrate use for this emerging population.

Study area

We have monitored and managed peregrine falcons throughout the state of Virginia. Virginia extends from the Atlantic Ocean to the Appalachian Mountains and contains three physiographic regions including the Coastal Plain, Piedmont, and Mountains and Valleys. The Coastal Plain is bounded by the Atlantic Ocean to the east and the fall line to the west. The fall line is an erosional scarp where the metamorphic rocks of the Piedmont meet the sedimentary rocks of the Coastal Plain. Between these two boundaries the land slopes gently toward the fall line where it generally reaches an elevation of less than 80 m. The Piedmont is bounded to the east by the fall line and to the west by the escarpment of the Blue Ridge Mountains. In the northern parts of the state the Piedmont is only 75 km wide but broadens to the south reaching nearly 300 km wide at the state line. The land slopes up to the west reaching 300 m in elevation at the escarpment. The Mountains and Valleys Region is bounded by the east slope of the Blue Ridge Mountains and the state line. The region supports many areas above 1,000 m.

Methods

We determined the number of territorial pairs, clutch size, brood size, nesting success and productivity by regular monitoring. Between 1977 and 2009, we established more than 60 structures specifically for breeding peregrine falcons within the Coastal Plain of Virginia. An effort was made annually to check all existing structures on the Coastal Plain for evidence of resident falcons. An initial survey of breeding structures was conducted between 1 March and 30 April by foot, boat or plane. The number of adults attending sites and/or activity within nesting structures was recorded. Remaining sites on bridges or within urban areas were surveyed on the ground for occupation and breeding activity. In addition to specific peregrine structures, the area supports many man-made structures that may be suitable for nesting. Although some prominent man-made structures have been monitored by biologists over the years for peregrine activity many of these nesting sites were initially reported by the public. The mountains of Virginia support a considerable number of historic eyries (Gabler 1983) and cliffs suitable for nesting (Watts 2006). Many of these sites are remote and have been surveyed only periodically since reintroduction efforts were initiated in the mountains during the mid-1980s (Reynolds 2004, Watts 2006, Harding 2015).

We monitored sites known to be occupied during a given year 2–5 times from March through July to document breeding activity. We considered a breeding territory to be occupied if a pair of adult peregrines was resident during the breeding season. We considered nests to be active if eggs or young were detected and successful if >1 chick survived to banding age (>20 d). We did not assess fledging rates in all years and believe that banding age is a good proxy for fledging since more than 95% of young banded survive to fledging age (~45 d). Furthermore, satellite tracking within this population has demonstrated that mortality occurs primarily in the first month post-fledging (Watts *et al.* 2011). We documented clutch size when possible and determined hatching rates for those eggs where fates could be determined. We report brood sizes for young that reached banding age.

Colonization rates were expressed using the average time (in years) required for the nesting population (number of territorial pairs) to double in size (t_{double}). Doubling time was calculated using the growth equation $N_t = N_0e^{rt}$ where N_t is the population size in 2016, N_0 is the population size in 1979, e is the base of the natural logarithm, r is the intrinsic rate of increase, and t is the time interval between population estimates. With this configuration, $t_{double} = \ln(2)/r$. Success rate was calculated for nesting attempts with known outcome (successful nests/nesting attempts with known outcome X 100). We used goodness-of-fit tests (G-test with Yates correction) to compare frequencies of categorical data. We used two-sample t-tests to compare means of continuous variables between categories. We tested distributions for possible deviation from normality using the Kolmogorov-Smirnov test and found no significant differences from expected normal distributions.

Results

From a single pair in 1979, the Virginia peregrine falcon population has grown to 31 pairs by 2016 with an average doubling time of 7.5 years *(Figure 1)*. The establishment phase through 1993 (year when captive-reared releases were discontinued in the state) was particularly dramatic with an average doubling time of 3.8 years. The release of 242 birds

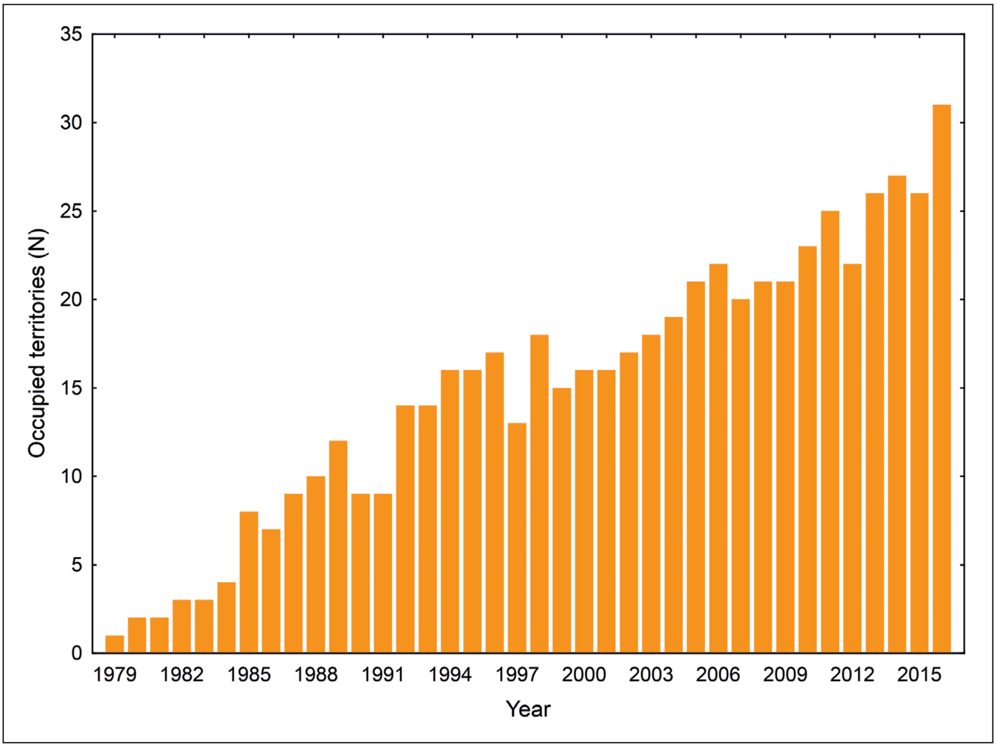

Figure 1. Size of the Peregrine Falcon breeding population in Virginia (1979–2016)
1. ábra A vándorsólyom költőpopulációjának mérete Virginia államban (1979–2016)

resulted in the establishment of 16 territories in 15 years. Since 1993, the average doubling time has increased to 23.1 years as the population has become self-sustaining. Reproductive rates have exceeded 1.5 young/pair every year since 1999.

During the study period, 469 breeding attempts were documented that produced 965 young. Average, annualized rates were 80.2 ± 2.65% (mean ± standard error) and 1.45 ± 0.109 for breeding success and reproductive rate, respectively. Mean clutch and brood sizes were 3.6 ± 0.04 and 2.8 ± 0.05, respectively. Of 360 clutches where size was documented, 25 (7.0%) contained 2 eggs, 93 (25.8%) contained 3 eggs, 226 (62.8%) contained 4 eggs and 16 (4.4%) contained 5 eggs. For those eggs with known fate (N = 1,256), hatching rate was 70.8%. Of 346 clutches monitored, 55 (15.9%) hatched no eggs, 132 (38.1%) had partial hatch and 159 (46.0%) hatched all eggs. Hatching rate varied annually from a low of 19% and a high of 100% with a mean of 72.0 ± 3.26%.

Per capita reproductive rates increased significantly over the study period ($R^2 = 0.66$, F [1,36] = 68.4, $p < 0.001$). Reproductive rates averaged 0.89 ± 0.088 for the establishment period compared to 1.86 ± 0.071 for the consolidation period *(Figure 2)*. The overall increase in per capita reproductive rate appears to have resulted from a significant increase in

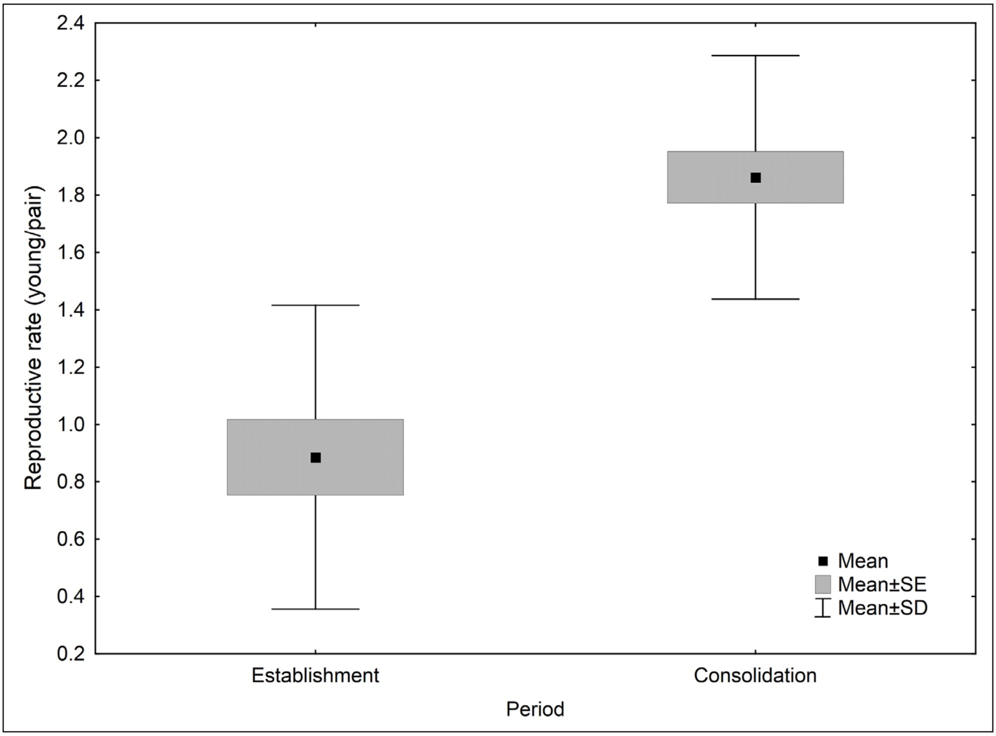

Figure 2. Comparison of Peregrine Falcon reproductive rates in Virginia between the establishment period (1979–1993) and the consolidation period (1994–2016). Rates were found to be significantly higher during the consolidation period

2. ábra A vándorsólyom reprodukciós rátáinak összehasonlítása Virginia államban a telepítési időszak (1979–1993) és a konszolidációs időszak (1994–2016) között. A konszolidációs időszakban a ráták szignifikánsan magasabbak voltak success rate (G-statistic with Yates Correction = 16.3, df = 1, $p < 0.001$) rather than average brood size (t-statistic = 0.72, $p > 0.05$). Success rate increased from 67.1% (47/70) for the establishment period (1979-1993) to 82.7% (330/399) for the consolidation period (1994-2016). Brood size did not show the same pattern with 2.9 ± 0.19 young per successful nest during establishment and a similar value (2.7 ± 0.17) during consolidation.

We have identified 52 structures used for nesting within the study area. The most common structures were peregrine towers (n = 18), bridges (n = 12) and buildings (n = 5) that collectively represent 67.3% of the total. Less common structures have included 5 natural cliff faces, 3 abandoned shacks, 2 military ships, 2 active smoke stacks within coal-fired power plants, and 1 ground nest in a dune. One of the most unusual structures has been a pair that laid within the smoke box of a derelict brick chimney isolated in a marsh. The smoke box was only 3 feet above the marsh surface. Another pair was resident on a duck blind for two years but nesting was never confirmed. A pair nested on the ground within a dune and was successful 1 of 2 years (Boettcher & Mojica 2016). Substrates used for nesting have diversified through time. Birds released from towers returned to establish breeding territories on towers during the early establishment period. The first bridge and building were not used until 1993 and 2003, respectively. In 1990, 83% of known pairs were still nesting on towers. By 2016, towers accounted for less than 35% of substrates.

Discussion

The captive breeding and release program executed in Virginia as part of the federal recovery plan (Bollengier *et al.* 1979) has been successful in establishing a breeding population of peregrine falcons in the state. The growth rate of this population is comparable to those in other regions of North America that have included intensive reintroduction efforts (Enderson *et al.* 1995, Mesta 1999, Kauffman *et al.* 2003, Watts *et al.* 2015) with a clear establishment phase driven by releases and a more gradual consolidation phase driven by internal productivity. All the early breeding pairs resulted from released birds returning to hack towers. However, colonization of the historic mountain range has not been as rapid or as extensive as that observed on the outer Coastal Plain. A total of 115 birds were released on the coast between 1978 and 1985 and by 2016 the known breeding population had grown to 28 pairs. A total of 127 captive-reared birds were released in the mountains between 1985 and 1993 and the first occupied territory was documented in 1994. By 2016, relatively little additional establishment has been observed with the known population only including 2 pairs. This despite the fact that between 2000 and 2016 more than 260 wild-reared falcons have been translocated from the Coastal Plain and released in the mountains (Watts & Watts 2016).

It remains unclear why breeding falcons have been slow to recolonize the historic mountain range in Virginia. The mountain region is large with a number of potential eyries that are remote and have been surveyed infrequently suggesting that there may exist pairs that are currently unknown. However, many historic eyries are accessible and have been monitored routinely. It seems highly unlikely that the number of unknown pairs in the mountains is significant or large enough to reach the historic population estimate of 25 breeding pairs. Many of the eyries on natural cliff sites that were documented in the early 1900s have been revegetated since that time and now appear to be of low site quality (Gabler 1983). Reproductive rates appear to support this claim. Of the breeding attempts in the mountains where outcomes are known, pairs produced 1.2 young per year.

Although we have not performed a population viability analysis (Wootton & Bell 1992), both reproductive performance and the population trajectory suggest that the state-wide population is self-sustaining. Reproductive rates have become more stable over the past decade and have been maintained well above 1.25–1.50 young per occupied territory, generally believed to support positive population growth rates (Grier & Barclay 1988, Wootton & Bell 1992). Releases of captive-reared birds during the establishment phase averaged just over 15 birds/yr. The population has exceeded this production every year since the last year of releases and in 2016 produced more than three times this number. Elevation in reproductive rates over the study period has resulted from increases in breeding success rather than in brood size. The underlying cause of this improvement is unclear but may be an artifact of a shifting age structure as the population has become established. Clum (1995) has shown that nestling survival increased throughout the lifespan of peregrines breeding in captivity. Mearns and Newton (1988) document an increase in both clutch and brood size with female age in Scotland.

It is possible that ongoing management activities may partially explain the increase in reproductive rates observed over time. We have used a range of management techniques for nesting peregrine falcons on artificial management structures to improve nesting success and to help stabilize nesting sites. Techniques have included adding gravel to structures used for nesting, installing nest trays, installing nest boxes and installing predator guards. The use of management structures has had a positive influence on breeding performance (Watts & Watts 2017). Breeding success has increased significantly following the installation of management structures compared to before installation. In addition to an increase in breeding success, pairs nesting on management structures produced significantly more young birds compared to pairs nesting without such structures. Pairs nesting within boxes or on trays produced more than twice as many young compared to those that did not.

Even though the ancestry of the introduced population reflects a very large portion of the global range, the breeding population has successfully adapted to Virginia. Migratory status is mixed. Of 61 hatch-year birds tracked with satellite transmitters from Virginia (Watts *et al.* 2011), half migrated south to establish winter territories ranging from North Carolina to Colombia, South America. Remaining birds established winter territories within the mid-Atlantic region of the United States from Virginia through New York. Diet during the breeding season generally reflects the availability of bird species. Pairs nesting within inland locations feed primarily on Rock Pigeons *(Columba livia)* and migratory passerines (Long 2009). In contrast, migratory shorebirds are the dominant prey used by pairs nesting on the outer coast, representing 52% of the prey (Long 2009). Willets *(Tringa semipalmata)* and Short-billed Dowitchers *(Limnodromus griseus)* were taken in the highest numbers.

The population continues to be vulnerable to several mortality risks. Approximately half of the breeding pairs nest on bridges and buildings and are vulnerable to the array of factors associated with living in an urban landscape (Cade & Bird 1990, Cade *et al.* 1996).

Collisions with urban structures such as buildings, tower guy-wires, and transmission lines represented 40% of mortality identified during a tracking study in the state (Watts *et al.* 2011). Young from bridge nests frequently drown around fledging time when they are unable to fly back up to eyries due to the lack of updrafts. Exposure to some classes of contaminants such as flame retardants are believed to be higher within urban settings compared to the coastal areas, as indicated by higher concentrations within addled eggs (Morse 1993, Chen *et al.* 2008, 2010, Potter *et al.* 2009). By contrast, pairs along the outer coast appear to have higher exposure to legacy contaminants such as DDT and its metabolites, possibly due to their higher consumption of migratory shorebirds that winter in the tropics (Potter *et al.* 2009). However, eggshell-thinning rates relative to pre-DDT estimates have varied through time and space, making the general connection between contaminant exposure levels and spatial variation in reproductive rates difficult to assess within the population (Burns *et al.* 1994, Potter *et al.* 2009, Chen *et al.* 2010).

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Breeding population of Peregrine Falcon *(Falco peregrinus)* in Lazio, Central Italy: 1983–2017

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Abstract In 1983–1984 the nesting population of Peregrine Falcon *(Falco peregrinus)* in Lazio was estimated to 25–30 pairs located mainly in the limestone massifs of the Southern Anti-Apennines and the Ponziane Islands. The monitoring carried out in the following years showed a steady increase in population size and range. In 2014–2017, the breeding population was 166–193 pairs distributed over most of the regional territory. In four regional macro-geographic areas characterized by different morphologies, lithological and landscape typologies, the density was calculated by NND method, which varied from a minimum of 0.90 to a maximum of 1.77 pairs/100 km^2; average distance between sites from 3848.18 m to 6526.87 m. The urban population of Rome increased from the first nest found in 2001 to 15 currently breeding pairs; the first artificial nest was discovered in 2001 on the building, currently 14 are known. At present in Lazio 16 nests are located in quarries. In the years 2008, 2014, 2015 and 2016, the fledging rate registered was 2.26 (SD = 0.94; bp = 153).

Keywords: monitoring, estimate size, habitat selection, density, fledging rate

Összefoglalás A vándorsólyom *(Falco peregrinus)* költő populációjának méretét csak 25–30 párra becsülték 1983–1984-ben, melyek főleg az Anti-Appenninek Ponziane-szigeteinek (Dél-Lazio) mészkő masszívumain költöttek. Az ezt követő időszak rendszeres felmérései mind a populáció méretében, mind elterjedésében növekedést mutattak. A 2014–2017-es években már 166–193 párra becsülték az állományt, mely a teljes régióban elterjedté vált. Geomorfológiai, kőzettani és tipológiai szempontból elkülöníthető makro-geográfiai területeken a legközelebbi szomszéd távolság (NND) becslésével 0,9 és 1,77 pár/100 km^2 nagyságúra tehető a költő populáció sűrűsége. Az átlagos territóriumok közötti távolság 3848,18 és 6526,87 méter között változott. A Rómában fészkelő városi populáció mérete az első, 2001-ben megfigyelt fészek óta jelenleg 15 párból áll. Az átlagos kirepülési siker a 2008, 2014, 2015 és 2016 év adatait felhasználva 2,26 (SD = 0,94; bp = 153) fiókának adódott.

Kulcsszavak: monitoring, habitat szelekció, denzitás, kirepülési ráta

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Introduction

In the last thirty years in Italy, the Peregrine Falcon *(Falco peregrinus)* had increasing population size and a substantial expansion of its distribution range (Nardelli *et al*. 2015) as well as in Europe (BirdLife International 2015, 2017). In the early '90s the population was estimated to 470–524 pairs, of which about half were distributed in Sicily and Sardinia, and the rest in the Italian Peninsula (Fasce & Fasce 1992). A decade later, 826-1048 pairs were recorded, doubling the population size and highlighting a strong expansion on the Apennines, the Alps and the Prealps (Allavena & Brunelli 2003). The most recent estimates, from non-systematic surveys throughout the country, point out a growing population of 1100–1400 pairs with a favourable conservation status (Nardelli *et al*. 2015, Gustin *et al*. 2016).

In Lazio, the breeding population of Peregrine Falcon has been constantly monitored since the early '80s (SROPU 1987), hence it has been possible to accurately follow the evolution of distribution and population size to date.

In 2014, based on the proposal of the Regional Directorate of Lazio, a monitoring network was set up to survey the nesting populations of Peregrine Falcon together with other cliff-nesting raptors such as Golden Eagle *(Aquila chrysaetos)* and Lanner Falcon *(Falco biarmicus)* (Borlenghi *et al*. 2014).

In this study we summarize and compare the available data on widespread process recorded on Peregrine Falcon in Lazio in the period of 1983–2017. Furthermore, values were related to reproductive success and density are also presented.

Study area and methods

The surveys covered all areas suitable for the Peregrine Falcon in Lazio, a region extended 17,200 km^2 located in Central Italy, bounded by Tyrrhenian Sea in the west and by Apennine Mountains in east.

In this study we summarized and compared data available on the breeding population of Peregrine Falcon collected from five different surveys, 1982–83, 1993–95, 2003, 2008 and 2014–17 (SROPU 1987, Bassi & Brunelli 1995, Brunelli 2004, Aradis *et al*. 2012, Borlenghi *et al*. 2017). The observations have been registered from February to May, in the most favorable period for the detection of the species at the nesting sites. All the identified locations were geo-referenced and stored in a database containing 214 breeding sites. It included all the sites in which the species has nested at least once until 2008 or assumed to alternative site. We considered a territory being occupied if nest or pair in typical behaviour, courtship, brood or young were identified (Newton 1979, Ratcliffe 1993).

We calculated the species densities in four geographic macro-areas (northern and central high hilly landscape, Preapennines and central Apennines, southern Anti-Apennines and southern Apennines) and in seven units (Vicani, Reatini, Simbruini and Lepini Mountains, Rome urban area, hills of Lazio Volcano and Mount of Cairo) included in the last four *(Figure 1)*, using the Nearest Neighbour Distance (NND) method, counting only the active nests in 2014–2017 (n = 158). These macro-areas and units were well separated from each other by different morphology or by sectors where the species has not been found; the coastal sites and those for which the nearest site was not known were excluded (Ratcliffe 1993).

We tested the correlation between the percentage of area of 17 landscapes identified in Lazio (APAT, 2003) and the percentage of breeding sites of Peregrine Falcon falling in the 17 landscapes by Spearman's coefficient (Rs); similarly we tested the percentage of nesting sites falling in six altitude classes (0–250, 251–500, 501–750, 751–1000, 1001–1250 and >1251 m asl.) and the percentage of regional altitude values subdivided. The latter was extract from a 40×40 m DEM (Digital Elevation Model) layer.

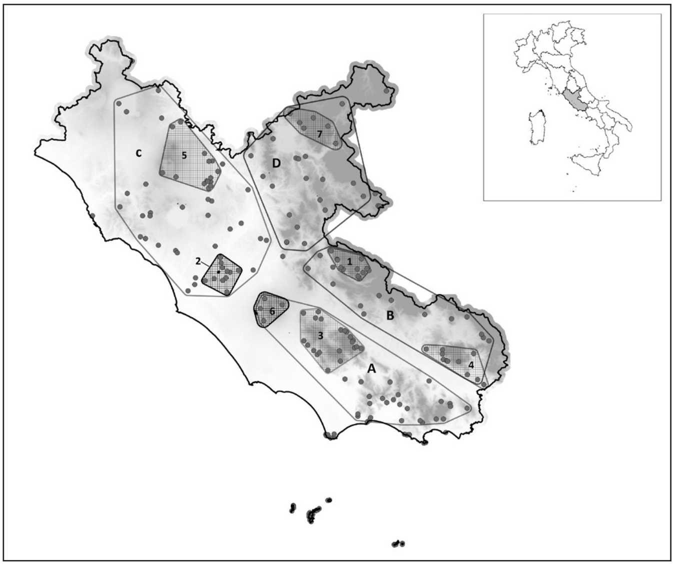

Figure 1. Study area in Lazio, with all the known Peregrine Falcon breeding sites, the four "Macro-geographic areas" and the seven "Landscape units" shown. The orography of region is depicted in shades of grey. See *Table1* for letters and numbers correspondence

1. ábra A vizsgált terület Lazioban, az összes ismert vándorsólyom költőhely, a négy „makro-földrajzi terület" és a hét „tájkép egység" között. A régió tagoltságát szürke árnyalatokkal ábrázoltuk. A betűk és számok jelentését lásd: *Table 1*

In the years 2008, 2014, 2015 and 2016 data on fledging rate were collected (fledged young/pairs) (Cheylan 1981, Ratcliffe 1993).

Results and Discussion

The first detailed data on size and distribution of Peregrine Falcon's breeding population in Lazio can be traced back to the years 1982–1983 when a population of 25–30 breeding pairs was estimated, mainly concentrated in the limestone chains of the southern and central Apennines and the Ponziane Islands (SROPU 1987). After that, the population grew up to 38–45 pairs in the years 1993–95 (Bassi & Brunelli 1995), 58–72 in 2003, with a new colonization of species in the central high hill landscape and north part of Region, with some pairs breeding in urban areas (Brunelli 2004). The estimated trend is shown in *Figure 2*, where the breeding population reaches 92–106 pairs in 2008 (Aradis *et al*. 2012) and 166–193 pairs in 2014–2017 (Borlenghi *et al*. 2017), almost uniformly distributed in all the study area except the north-west sector. In the whole period 1983–2017 the breeding population grew up of 575%, although an underestimate in the first survey (1983) could be possible. Comparing all the breeding sites in the whole period (n = 214) with 17 regionally recognized landscape types it was detected that more of the half (63.5%) of the breeding population is concentrated in the "carbonatic mountains" (Apennine and Anti-Apennine chains, 46.7%) and "volcanic hilly landscape with planks" (Northern and central high hilly, 16.8%) landscape types; however this distribution does not related to greater extension of the last two types. In fact, there is no statistically significant correlation between the distribution of sites and landscape areas (Rs = 0.022; p = 0.570). Additionally, the species seems to select certain types of landscape beyond their representativeness on the Lazio territory, probably due to their morphology, lithological characteristics and trophic availability (Pezzarossa 2014–15).

The altimetric distribution of the reproductive sites emphasize a strong predominance of the areas up to 500 m a.s.l., where 62.6% of these areas were found. Also in this case, the distribution of the breeding sites in six classes of altitudes and the distribution of altitudes extracted from DEM grids are not statistically correlated (Rs = 0.020; p = 0.803): Peregrine Falcons in Lazio choose certain classes of altitude, mostly coastal and hilly.

In parallel with the increasing number of the breeding pairs, the discovery of nests placed on artificial substrates has become more frequent. In fact, no sites on these substrates were detected before 2001, while currently 30 sites are known (14% of total sites known), of which 14 on buildings (6.5%) and 16 in quarries (7.5%), the latter are mostly inactive. The increase recorded in the city of Rome and its surrounding areas was particularly significant. The first nesting pair was detected in 2002 and 15 pairs were found in 2017, of which 10 in continuous urban fabric, probably due to the huge abundance of wintering and breeding

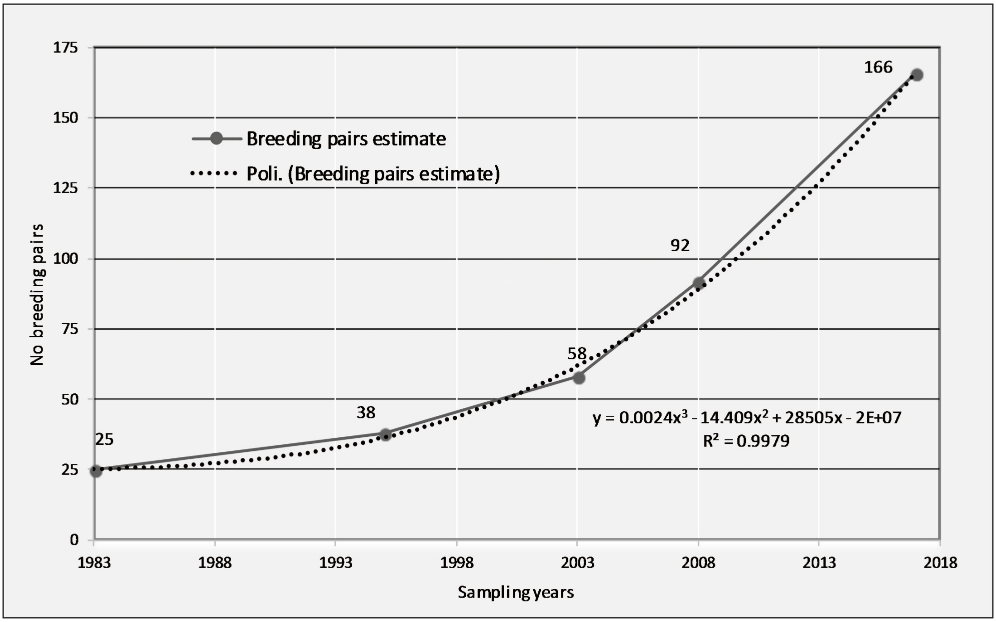

Figure 2. Trends of breeding population of Peregrine Falcon in Lazio in five surveys between 1983–2017 (min number of pairs)

2. ábra A vándorsólyom költőpopulációjának trendjei Lazioban, 5 felmérés során 1983 és 2017 között (párok min. száma)

Table 1. Peregrine Falcon densities in Lazio, subdivided in macro-geographic areas and in seven landscapes units. The table also pointed out the number of pairs, the unit area, the observed mean distance of breeding sites (Nearest Neighbour Distance) and the density value

1. táblázat A vándorsólyom denzitása Lazioban, makrogeográfiai területenként, illetve 7 tájegységben. A táblázat mutatja a párok számát az egységterületet, a költőterületek átlagos távolságát (NND) és a denzitás értékét

Geographical areas	No. pairs	Area km^2	NND in m	Density pairs/100 km^2
Macro-geographical areas				
A – Sourthern Anti-Apennines	46	2600.33	3848.18	1.77
B – Southern Apennines	33	2208.00	4202.97	1.49
C – Northern and Central high hilly landscape	55	4383.79	4243.26	1.25
D – Preapennines and Central Apennines	24	2680.73	6526.87	0.90
Total density in four macro-areas	158	11872.85	4705.32	1.35
Landscape units				
1 – Simbruini Mountains (Southern Apennines)	9	166.37	3025.20	5.41
2 – Rome urban area (hilly landscape)	10	200.57	3129.19	4.99
3 – Lepini Mountains (Southern Anti-Apennines)	18	520.58	2900.31	3.46
4 – Mount of Cairo (Southern Apennines)	10	299.25	4001.08	3.34
5 – Vicani Mountains (hilly landscape)	16	544.82	2875.57	2.94
6 – Hills of Lazio Volcano (Southern Anti-Apennines)	4	167.48	5982.00	2.39
7 – Reatini Mountains (Central Apennines)	6	267.58	5727.74	2.24

population of Starlings *(Sturnus vulgaris)* and Feral Pigeons *(Columba livia domestica)* (Cignini & Zapparoli 1996, Cignini 1998, Cecere *et al.* 2005).

Furthermore, *Table 1* shows the Peregrine Falcon densities in Lazio in four macro-geographic areas and in seven sub-geographic units. The densities of macro-geographic areas are similar to other Italian study areas, with values between 1.76 to 1.16 pairs/100 km^2 (Magrini *et al*. 2001, Pandolfi *et al*. 2004, Rizzoli *et al*. 2005, Brambilla *et al*. 2006, Mascara 2012), although lower values have been recorded as well as for example in the Western Alps between 0.55–0.56 pairs/100 km^2 (Bionda & Bordignon 2006, Beraudo & Toffoli 2009). Overall the macro-area densities show greater values from north-west to south-east and lower from coast toward the Apennines. A similar trend of densities at the level of the sub-units can also be detected *(Table 1)*, but all the values in these cases are higher due essentially to NND calculation method. In particular the density values of two areas it is necessary to underline: Simbruini Mountains and the city of Rome, both with the highest densities 5.41 and 4.99 pairs/100 km^2, respectively, probably due to the high availability of suitable sites for nesting and, in the case of Rome, also to the huge availability of trophic resources. It is known that particular favorable conditions for the species can increase more density values, such as comparison with Lake District (NW England) with 8.5 pairs/ 100 km^2 (Ratcliffe 1993).

Between 2008–2016, we have also collected data on reproductive success. We found 2.26 (SD = 0.94) young reared successfully by pair (bp = 153), consistent with other data available in Italy (cf. Brunelli 2007). In 2008 we registered the highest value of young/pair, 2.82 (SD = 0.94, bp = 22), with two pairs composed by five fledged young, a rather occasional event for this species (Ratcliffe 1993).

The considerable increase in the size and distribution of Peregrine Falcon in Lazio, as well as the values found in densities and reproductive success, would seem to depict the species in a favorable status of conservation.

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Population trends and diversification of breeding habitats of Peregrine Falcon *(Falco peregrinus)* in the Czech Republic since 1990

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Abstract The population of the Peregrine Falcon *(Falco peregrinus)* in the Czech Republic recovered from a nearly total extinction during the 1960s and 1980s (0-3 breeding pairs) and the first successful breeding after this interval was confirmed in 1995. The increase of the population size accelerated after 2000 and it is still growing despite the limited amount of suitable natural breeding opportunities. There were 89 known pairs in 2016, 70 of them were proven to breed with altogether at least 121 reared young. Several breeding attempts on historical buildings in city-centres were recorded up to 2002 (in Prague and Pilsen), but this breeding habitat was abandoned later. More and more pairs are nowadays breeding on industrial buildings. The first breeding on a power plant chimney, 300m above the ground was discovered in 2010. Moreover, 16 breeding pairs were found on industrial buildings in 2016 (mainly tall chimneys or cooling towers and power-plant buildings), all of them breeding in nest boxes. The colonization of industrial buildings started in western part of the Czech Republic and continues eastwards every year. Currently, the easternmost colonized building is in Mladá Boleslav. We have no recent tree-breeding pairs and all eight published historical cases are at least doubtful. Most of the observed Peregrines ringed abroad came from Germany, indicating a strong influence of German population on restoration of the population in the Czech Republic. Within these recoveries, some of Peregrines were released in the tree-breeding population restoration project in Germany and Poland, but all these birds bred on rocks.

Keywords: Peregrine Falcon, Czech Republic, population, nest boxes, natural breeding sites

Összefoglalás A Cseh Köztársaság területén élő vándorsólyom *(Falco peregrinus)* populáció az 1960–1980-as évek alatt csaknem teljesen kipusztult (0–3 költőpár). Ezen időszak után az első sikeres költést 1995-ben regisztrálták. A populációméret növekedése a 2000-es év után felgyorsult, és az alkalmas fészkelési lehetőségek korlátozott száma ellenére továbbra is tart. 2016-ban a 89 ismert költőpárból 70 nevelt fel összesen legalább 121 fiatal egyedet. 2002-ig számos költési kísérletet jegyeztek fel a városközpontok műemlék épületein (Prágában és Pilsenben), de a madarak ezeket a helyeket később elhagyták. Napjainkban egyre több pár fészkel ipari épületeken. 2010-ben írták le az első olyan költést, amely egy erőmű kéményén történt 300 méteres magasságban, 2016-ban már 16 költőpárt találtak ipari épületeken (főként magas kéményeken, hűtőtornyokon, illetve erőműveken), melyek közül mindegyik költőládában fészkelt. A vándorsólymok először a Cseh Köztársaság területének nyugati részén kezdték kolonizálni az ipari épületeket, majd ez a terjeszkedés minden évben a keleti területek felé folytatódott. A legkeletebbi kolonizált ipari épület jelenleg Mladá Boleslav területén van. Egyetlen olyan költőpárról sem tudni, amely fán fészkel, a nyolc korábbi publikált eset is kétséges. A megfigyelt, külföldi gyűrűs sólymok többsége Németországból származik, ami jelzi a német populáció szerepét a Cseh Köztársaság területén élő állomány helyreállításában. Néhány visszafogott egyedet a fán fészkelő populáció megerősítését célzó projekt keretein belül engedtek el Németországban és Lengyelországban, de ezek a madarak később mind sziklákon költöttek.

Kulcsszavak: vándorsólyom, Cseh Köztársaság, populáció, fészekodú, természetes fészkelőhelyek

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Introduction

The Peregrine Falcon *(Falco peregrinus)* has probably never been a common raptor species in the Czech Republic. There is scarce historical data from the 19th century, but it is hard to establish the real population size for those days (Šír 1890). Dramatic fluctuations of the population led up to a total extinction during the 1960s. Reoccupation of our country in the early 1990s correlates with the DDT ban and with the increase of the European population in general. First breeding was confirmed in 1995 and since then, the Czech population continues to increase despite the limited amount of suitable breeding places on the rock cliffs. Consequently, Peregrines started to breed on industrial buildings as well in 2010. Also, less suitable rock cliffs (suboptimum breeding habitats) were occupied. Up to 2001, Peregrines bred only in the mountain border zone (with the exception of two pairs breeding in the towns of Prague and Pilsen), but they started to breed in more populated areas. Breeding on historical buildings (churches) was recorded only in Prague (Peške 1995, 1997) and Pilsen (Hruška *et al*. 2000, Mlíkovský & Hruška 2000) for several consecutive years and was probably related to release of captive-bred individuals in these towns. Recently, breeding on industrial buildings is more common (Hlaváč & Beran 2011). The most interesting case was observed in the region of South Moravia between 1997–2003, where a pair of Peregrines occupied a large hollow in a large poplar-tree in the artificial "Nové Mlýny" lake (and later a wooden nestbox installed on the same tree), but this pair has never bred successfully, most probably they never laid clutch (Horal 2013).

The Czech Republic is a medium-sized country (78,866 km^2) in Central Europe. The population is cca. 10.5 million people living in an average density of 134/km^2, which means that not much space is left for wildlife. The most remoted places are concentrated especially in the mountainous border areas. In general, there are not so many natural breeding areas – rock cliffs. Those few are scattered in the border mountain ranges, few sand-stone, limestone and karst areas and deep canyons of larger rivers. The majority of the rocky areas are situated in protected areas (especially in 4 national parks – 1.5% and in 26 protected landscape areas – 13.6% of the total country area). Unfortunately, most of the rock cliffs are under a heavy pressure by tourism. Special precautions (mainly no entrance and disturbance) have to be undertaken during the breeding season on most of the natural breeding sites. There are 41 special protected areas – SPAs as a part of Natura 2000 network (ca 9% of the country area) but only 2 of them are designated for Peregrine Falcons (Labské Pískovce – 12 pairs, Broumovsko – 7 pairs in 2017). In SPA Jeseníky (originally not designated for Peregrine Falcon), population reached 16 breeding pairs in 2017 (Šaj 2018). On the contrary, industrial buildings are distributed mainly in the lowlands and therefore supplement the

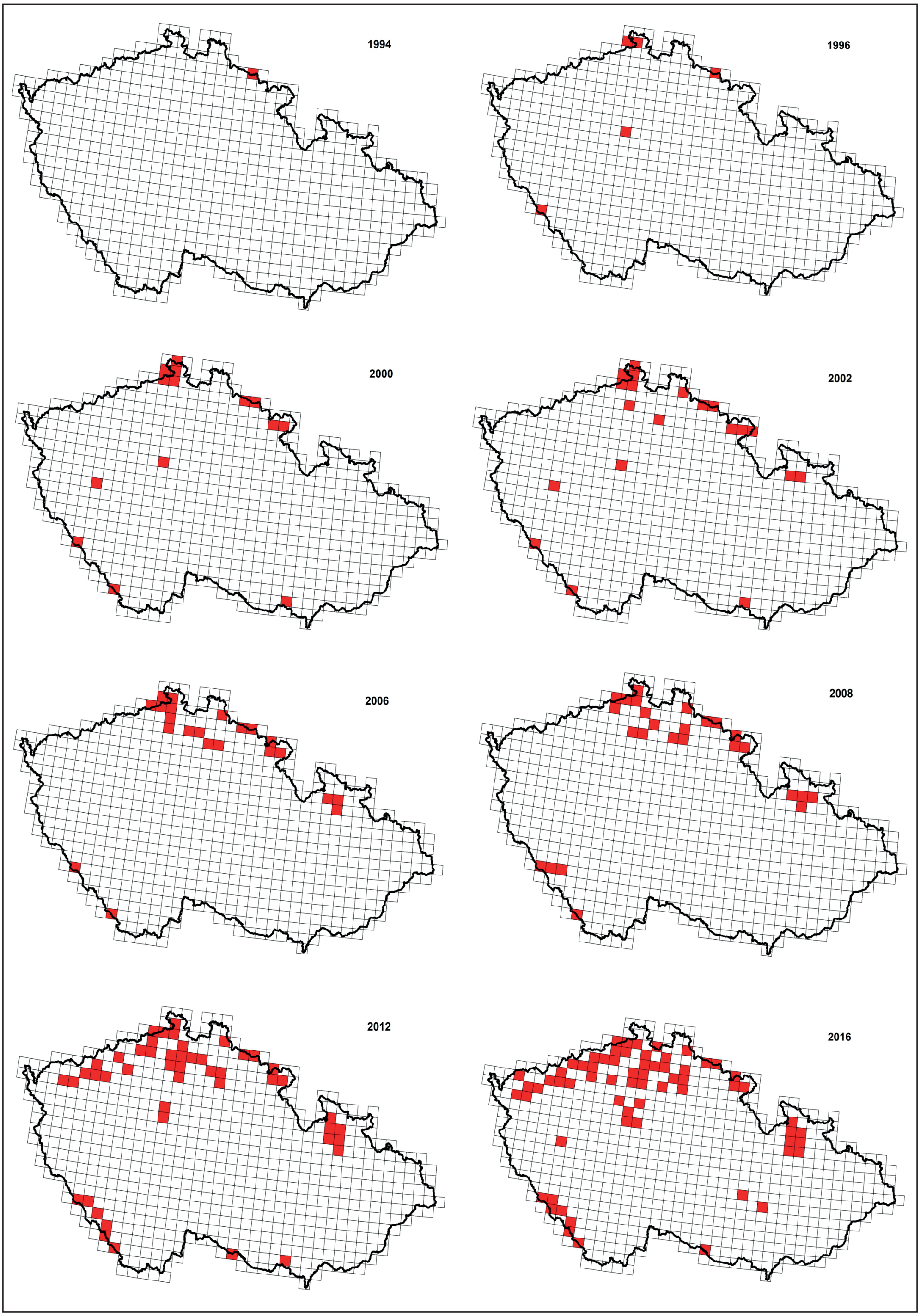

Figure 1. Distribution map of the Peregrine Falcon from 1994 to 2016 in the Czech Republic
1. ábra A vándorsólyom elterjedési térképe a Cseh Köztársaság területén 1994 és 2016 között

mainly mountainous natural breeding sites. Artificial breeding opportunities (mainly nest boxes) are installed at industrial buildings to provide safe breeding. The only source of disturbance (occasional technical controls) can be eliminated through appropriate communication with owners.

Results and Discussion

Maps on *Figure 1* show the recolonization of the Czech Republic since 1994. Continuous population growth (see graph on *Figure 2*) is well visible on the distribution maps as well. Border mountain areas (less populated) were reoccupied first and Peregrines were restricted to them up to 2001 (excluding two pairs breeding in Prague and Pilsen). Sandstone areas in northern Bohemia were occupied since 2002. Along with the continuous increase in numbers, further range expansion happened in 2010, when further areas of northern Bohemia were occupied and first pairs on industrial buildings settled down in north-west Bohemia. Expansion continues in the next years, more and more grid squares in north-west Bohemia are occupied every year. Finally, two breeding pairs took over historical breeding grounds in southern Moravia in 2016. Slow expansion to other parts of the Czech Republic is expected in the future.

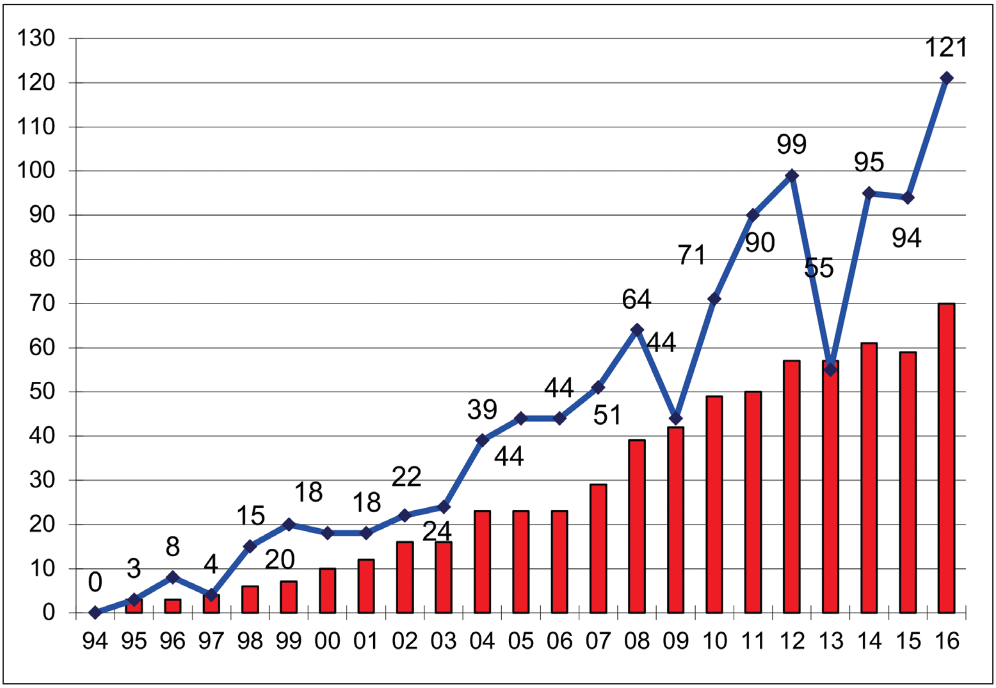

Figure 2. Continual increase of the Peregrine Falcon breeding population (red column) in the Czech Republic since 1994 and the total number of fledged young (blue line)

2. ábra A vándorsólyom költőpopulációjának folytonos növekedése a Cseh Köztársaság területén 1994 óta, valamint az összes kirepült fiatal egyed száma

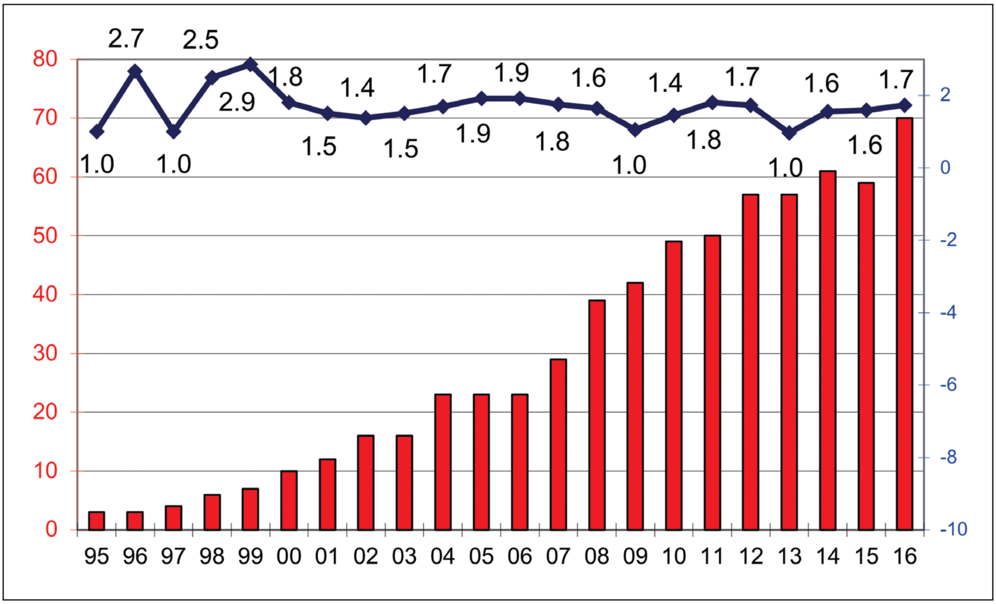

Figure 3. Continual increase of the Peregrine Falcon breeding population in the Czech Republic since 1994 (red column) and the average number of fledged young per nest (blue line)

3. ábra A vándorsólyom költőpopulációjának folytonos növekedése a Cseh Köztársaság területén 1994 óta, valamint az összes kirepült fiatal egyed átlagos száma/fészek

Mainly Common Raven *(Corvus corax)* nests are occupied in the rocky areas, but sandstone cavities and grassy ledges are also used for breeding.

The increase of Czech population is shown on *Figure 2*. Number of fledged chicks is increasing related to the increase of breeding pairs, but the average number of chicks fledged per successful nest is fluctuating (see *Figure 3*). Breeding data for the year 2016 are summarized in *Table 1*.

Table 1. Data about breeding population of Peregrine Falcon in the Czech Republic in 2016

1. táblázat A Cseh Köztársaságban 2016-ban költő vándorsólymok költési adatai

	2016
Found pairs (total estimate)	**89 (91)**
Confirmed breeding pairs	**70**
Found nests with known breeding result	**68**
Successful nests	**45 (66.2%)**
Successful nests on rocks	32 (61.5%)
Successful nests on buildings	13 (81.3%)
Minimal number of fledged juveniles	**121**
Average of juveniles / successful pairs	2.80
Average of juveniles / all nests	1.78

According to the ringing recoveries, there is a strong influx of birds from Germany (mainly females). The question is, if the average number of chicks per successful nest of 1.6 is high enough for continuous increase of the population.

The increasing population and limited amount of natural breeding sites probably created new phenomenon – breeding on industrial buildings. First pairs were observed in northern Bohemia in 2008, but first breeding

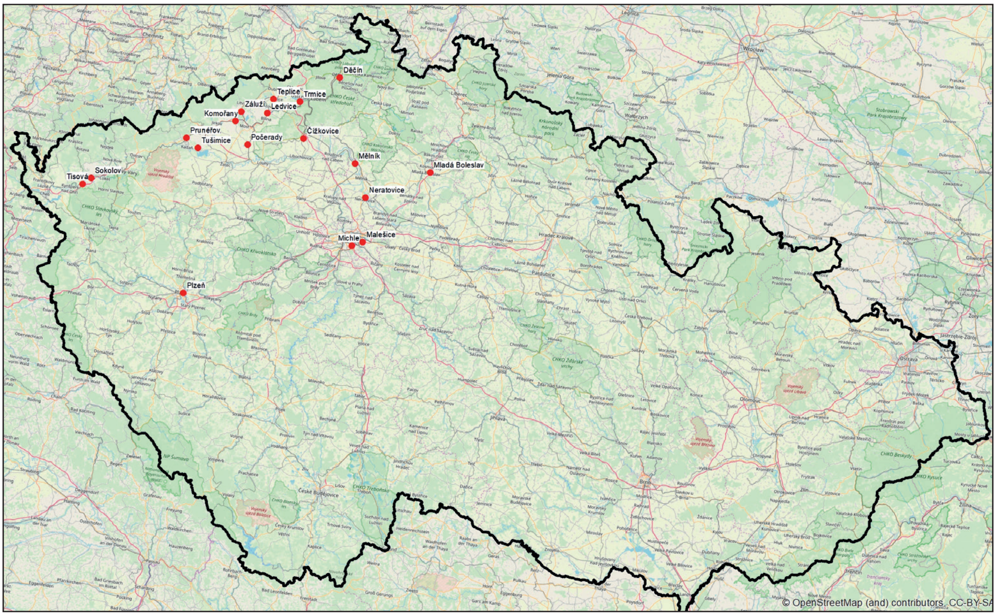

Figure 4. Distribution of Peregrine Falcon pairs breeding in nest boxes on industrial buildings in 2016. 17 out of 44 nest boxes installed on industrial buildings were occupied in 2016

4. ábra Az ipari épületekre kihelyezett költőládákban fészkelő vándorsólyom párok eloszlása 2016-ban. Ebben az évben a 44 költőládából 17-et foglaltak el a madarak

was proved accidentally in 2010 on a chimney of Tušimice power plant. Planned demolition of the chimney had to be postponed by one month, because a Peregrine “nest” with two eggs was found in a roll of cables in the height of 300 meters above ground. Unfortunately the eggs did not hatch, probably because of bad shape of the nest. The chimney was demolished and the pair was breeding successfully in a nest box on a cooling tower next year. Number of pairs breeding on industrial buildings is increasing every year, new nest boxes are installed and successfully occupied. The phenomenon is spreading from the west and most of the pairs on industrial building are still situated in northwest Bohemia. The easternmost pair on an industrial building was breeding in Mladá Boleslav in 2016 despite the fact, that the nest boxes are installed on several buildings more to the east. Many adults breeding on the industrial buildings are of German origin. This probably explains, why breeding on industrial buildings is spreading from the west *(Figures 1, 4).*

The following numbers of pairs breeding in various types of eyries in 2016 are: 52 on natural nests on rock cliffs, 2 on natural nests in quarries, 16 in nest boxes on industrial buildings. No pairs bred on historical buildings or on a tree nests. Tree nesting has never been confirmed in the Czech Republic and all the eight published historical cases are doubtful (Horal & Bělka 2013).

Ringing recoveries

During the modern Peregrine Falcon history (1997–2018), 159 recoveries (66x Czech Republic Prague (CZP), 70x Hiddensee ringing centre (DEH), 8x Radolfzell ringing centre (DER), 2x Budapest ringing centre (HGB) a 13x Polish ringing center Gdansk (PLG) of 44 tagged birds (17 males, 24 females and 3 unsexed birds) have been obtained in the Czech Republic. Identified birds tagged with either ornithological and/or colour rings originated from four European countries – Germany 22 (21 DEH, 1 DER), CZP19, PLG 2 and HGB 1. The origin of birds involved in breeding pairs was systematically searched for only in Broumov hills and and in Jeseniky mountains in last few years. In the other regions, mostly accidental data obtained from e.g. photographs were used. The data are continuously refilled.

During the first years after species recovery, birds originating from NW direction (Germany, border region with Czech Republic – Sächsische Schweiz, Oybin) prevailed at the Czech rock nesting sites. In 2000–2015, total 15 of these birds were recorded at nest sites in Czech Republic. E.g. female 1CY (Oybin, born 2003) reared altogether 22 young (with 4 different males) between 2005–2012 at Teplické skály rocks. Later on, along with successful production of juveniles, the proportion of German birds at the natural nest sites started to decline gradually. E.g. in Broumov hills, German females in local breeding pairs were fully replaced by females from strong Jeseníky (Altvatergebirge) Mts. population. At certain nest sites, very old German-ringed Peregrines might be still present in the breeding pairs: e.g. male 0DP (Oybin 2004) was still in 2018 in the pair in Lužické hory (Lausitzer Gebirge) mts., or female 5FE (Sebnitz, 2005) bred in 2016 in Česká Lípa (Bömisch Leipa) region. These two birds are also the oldest known colour-ringed male and female, respectively, in the Czech Republic.

At present, Peregrines started to occupy nest boxes installed on high chimneys (17 pairs in 2017). Peregrine parents breeding at these nest sites (e.g. Litvínov / Leutensdorf, Most / Brüx, Teplice / Teplitz, Mladá Boleslav / Jung Bunzlau, Prague), are again mainly of German origin (DEH, DER). Most of them were even born in the same type of breeding habitat – in nest boxes on industrial buildings. These data are gathered systematically with the use of photo traps.

Data on four captive bred Peregrines involved in breeding in the area of the Czech Republic are known. Male EA32706 released in Germany (Pirna 1992) bred for six years (1995–2000) in the centre of Prague (alternating two different churches, see http://www.peske.wz.cz/peregrine.htm) and reared altogether nine chicks (plus two captive-bred were added, L. Peške pers. comm.). Female 5AW released in Poland (Milicz 2005) as a part of tree-breeding population restoration has bred in Broumov hills on a rock nest for six years (2009–2014) and reared altogether 11 young. Male 7CT from the similar project in Germany (Lieberose 2010) alternates two pairs / territories in Prague and has bred on a chimney for at least five years: in the first territory, one young was reared in 2013; in the other one, min 15 young were reared between 2014–2017. In 2018, most probably the same male bred here again but unsuccessfully (D. Rak pers. comm.). Male 7KH, released in Germany (Lilienstein, 1995) bred on the Czech side (Dolní Žleb) in 1997 (result of breeding not known) and was found dead in April 1999. Also, another female 7AX, released in Poland (Milicz

2004) during the same project as 5AW (see above), was found dead in Jeseníky Mts (Skalka) in July 2009; it was not known whether this bird bred or not.

One of the most interesting recoveries is the breeding of female B8 born in northern Hungary (Bükk National Park, 2013). This bird formed a pair in the area of Moravian Karst / Mährischer Karst which has been abandoned by Peregrines for nearly 50 years. This female breeds successfully in this area annually since 2016; the distance to her place of origin is 326 km SE.

Recoveries revealed the fact that breeding Peregrine males are philopatric. Codes of 5 breeding males were read in 2016, four of them show that males usually settle not far from their birthplace (11 km, 13 km, 23 km and 33 km). Only the fifth male – 7CT (originating not from the wild but from the German reintroduction programme, see above) moved much further – 213 km. On the contrary, females are less philopatric. Nine females observed in 2016 were breeding 16 km, 50 km, 71 km, 87 km, 95 km, 96 km, 98 km, 130 km and 270 km from their birth place. Another female C200746 born in 2007 in Český ráj hills settled in Poland (Glogów), 147 km apart, where she bred on a chimney of a copper mine along with German male 6JM (Lubmin 2010) until 2015.

In the town centre of České Budějovice (Budweis, South Bohemia), the repeated wintering of Peregrine Falcon female of the tundra / Arctic subspecies *calidus* was observed for minimum 6 consecutive winters (October to May) . This bird was tagged with satellite transmitter at her breeding ground at Kolguyev Island, Barents Sea, North Russia in September 2014. During the winters 2014/2015 to 2017/2018, her movements from her Arctic breeding place to her wintering site in South Bohemia and back could have been followed via www.movebank.org (under LifeTrack Peregrine falcon project, bird ID: 4203Kper03 ad). Unfortunately, this bird died by unknown reasons in the town centre of České Budějovice in the late January 2018.

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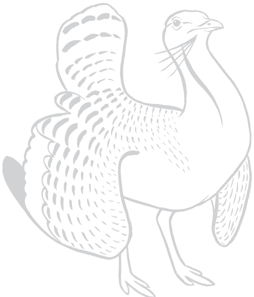

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Results of eighteen years (2000–2017) monitoring study of an extra-alpine Peregrine Falcon *Falco peregrinus* population in North-Western Italy

Pier Luigi Beraudo

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Abstract The Author reports the results of a survey about a breeding extra-alpine Peregrine Falcon population in Cuneo Province, NW Italy. The first reproduction was recorded in 2000, and from that year, the monitoring work localized 16 occupied territories in an area of 1,900 km^2 covering the hills and nearby lowland areas. The average distance between breeding territories was of 7.6 km with a density 0.7 pairs/100 km^2. During the eighteen years, 89 successful breeding attempts were recorded, 81 of them led to fledging of 206 young. Average breeding success was 2.5 juv/reproducing pairs. The nests are located on bridges (motorway viaducts and rail way bridges) and clay/sandstone cliffs. Preliminary prey analyses showed that pigeons and doves represent the 75% of their diet.

Keywords: Cuneo survey**,** density, reproduction, nest site, food

Összefoglalás Jelen tanulmányban egy északnyugat-olaszországi vándorsólyom költési adatait közli a szerző Cuneo tartományból. A faj 2000 óta sikeresen költ a hegyekben és a környező alföldi területeken. A mintegy 1900 km^2 területen azóta 16 territóriumot azonosítottak. Az átlagos távolság két territórium között 7,6 km, a denzitás 0,7 pár/100 km^2. A 18 éves vizsgálat során 89 sikeres költést jegyeztek fel, melyekből 81 esetben összesen 206 fióka repült ki. Az átlagos költési siker 2,54 fióka/költőpárnak adódott. A fészkek főként hidakon, felüljárókon, valamint agyag és homokkőszirteken jellemzőek. Az előzetes eredmények alapján a sólymok táplálékának 75%-át a galambfélék alkotják.

Kulcsszavak: Cuneo tartomány, denzitás, szaporodás, fészkelőhely

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Introduction

In Northern Italy Peregrine Falcon *(Falco peregrinus)* breeds regularly in the alpine area, with few reported cases in lowland and hilly areas. In the Cuneo province (NW Italy, Piedmont Region) this species is reported nesting in the Alps with 17 pairs (Caula & Beraudo 2014) and has bred for the first time outside the alpine area in 2000 (Caula *et al.* 2005, Beraudo & Toffoli 2009), in the Langhe hilly area.

Material and methods

The study area is the lowland and the Langhe and Roero hills, in the Cuneo province *(Figure 1)*. The breeding area (about 1,900 km^2) is the central north-eastern of the Province, between the Stura di Demonte river valley and the eastern boundary of the Langhe hills *(Figure 1)*. From 2000, a research was started, extended on lowland and the hilly areas of Langhe and Roero with the aim to discovering new occupied territories. A territory was considered as occupied if two individuals of different sex were present, of which at least one adult, and observed in territorial defense and courtship activities (Newton 1979). The monitoring of the reproductive biology (Cheylan 1981) was done between February and July of each year. A couple was considered reproductive when he has successfully bred at least one young. The mean territory distance was calculated by the *nearest-neighbour-distance* method (Penteriani & Pinchera 1995). Non-systematic data collection has been allowed to gather some information on prey.

Results

Between 2000 and 2008, 11 occupied territories were found (Beraudo & Toffoli 2009), whereas 5 new territories were identified between 2009 and 2017, amounting a total of 16 occupied sites *(Figure 1)*. Altitudinal range was 200–500 m a.s.l. In 13 sites (81.3%), reproduction was recorded at least once. Mean distance between these sites was 7.6 km (minimum distance = 4.8 km). In the Langhe hills (n = 7 breeding sites), nests were on clay and sandstone cliffs, whereas in the plain the nests (n = 6) were located on bridges (motorway viaduct and railway bridges. On railway bridges, three cases of use of Raven *Corvus corax* and Hooded-Crow *Corvus cornix* nests were observed. One of these breeding sites on

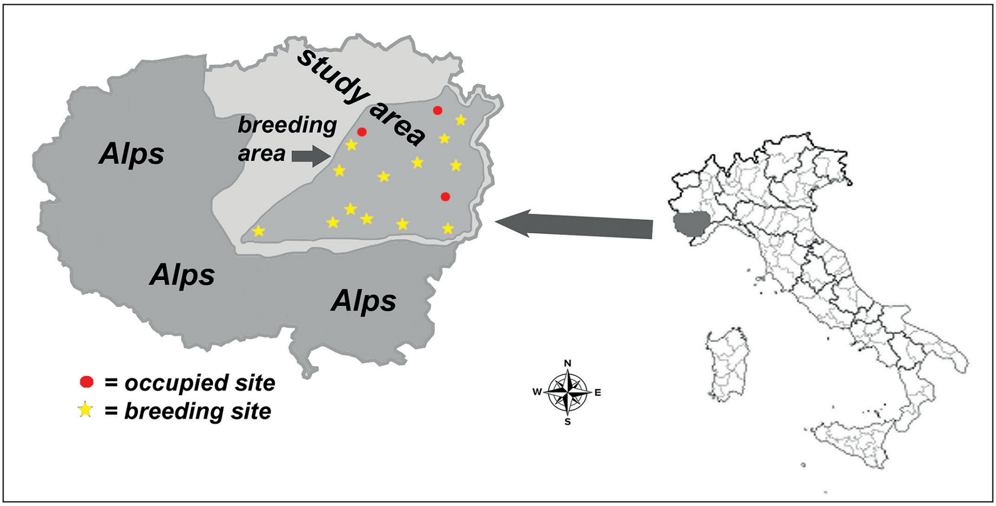

Figure 1. Study and breeding area in Cuneo Province (NW Italy, Piedmont region)
1. ábra A vizsgált terület és a költőhelyek Cueno tartományban (ÉNy-Olaszország, Piemont régió)

Table 1. Reproductive parameters
1. táblázat Költési adatok

monitoring years	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**TOT**
occupied territories (with adults male and female)	1	2	2	3	4	6	7	7	8	10	8	6	10	7	10	11	11	11	–
succesful breeds	1	2	2	3	4	3	6	5	3	5	7	3	9	5	8	6	8	9	**89**
succesful breeds with fledging juv. number known (a)	1	2	2	3	4	3	6	5	3	5	6	3	7	3	5	6	8	9	**81**
fledging juv. (b)	2	4	6	7	8	7	17	13	8	11	14	8	20	9	13	15	21	23	**206**
breeding success (b/a)	2	2	3	2,3	2	2,3	2,8	2,6	2,6	2,2	2,3	2,6	2,8	3	2,6	2,5	2,6	2,5	**2,5**

bridges has been successfully used for nine consecutive years (2006–2014). A nesting site, located on three different cliffs distributed along 1.7 km of a river valley, has been continuously occupied from 2000 to 2017. During this period 16 successful breeding attempts have been recorded. In another breeding site occupied since 2005, after the construction of a touristic trail in close proximity of the nest, breeding attempt has been recorded for nine years (2009–2017) even if during 8 years reproduction failed due to human disturbance. During the eighteen years, 89 successful breeding were recorded, 81 of these have led to fledging of 206 young. Average breeding success was 2.5 *(Table 1)*. The fledging date is known for 58 broods and is between the first decade of May and the third decade of June, with maximum peak in the third decade of May.

Discussion

The studied breeding population, which has probably been originated by the dispersion of individuals from the neighbouring alpine population, is still increasing in this hilly area. In fact, two new breeding pairs have been found between 2015 and 2017. Moreover, two additional breeding sites (one of them occupied since 2012) have been located in the nearby Asti province (Barberis & Gallo Orsi pers. comm.). However, in the lowland, it seems that the expansion of the Peregrine has stopped, probably because all the available nesting sites (mainly motorway viaducts and railway bridges in river valleys) have been filled by breeding pairs. Due to the local high density of some of the potential preys (author's unpublished data), I suggest that the availability of food may be one of the crucial factors behind the high density and reproductive outputs of this breeding population. Preliminary prey analyses (n = 270 items) showed that pigeons and doves (n = 203) represent the 75% of peregrine food, with Feral Pigeon *Columba livia* and Collared Dove *Streptopelia decaocto* representing respectively the 49% and 38% of total of predated Columbiformes.

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Mackenzie River Peregrine Falcon Surveys 1966–2018

Keith Hodson

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Abstract The author with assistants monitored the breeding distribution of Peregrine Falcons *(Falco peregrinus)* along the length of the Mackenzie River, Northwest Territories, Canada from 1966 to 2018. This river traverses a thousand miles (1600 km) of the western Canadian Arctic from Great Slave Lake to the Beaufort Sea and roughly parallels the eastern slope of the Mackenzie Mountain cordillera between latitudes 61 degrees N and 68 degrees N.

All potential nest sites have been checked on each survey and counts of nest sites occupied (at least one bird seen) decreased from the count of 12 sites in 1966 to the lowest count of 7 in 1972. In 1990 the count was 37 and up to 2018 the highest count was 75 in 2010.

A count of nest sites successfully producing young was variable with a low of 5 in 1972 to a high of 58 in 2011.

Production of young averaged 2.43/successful site from 1990 until 2018 (excluding 2012). Production of young averaged 1.4/ occupied site over this period. Recent increases in availability of passerine prey because of widespread fires in the last decades are felt to be the latest phenomena affecting these birds (pers.obs.) Prey utilized by Peregrines was studied over a period of four years and passerines composed 20% of their diet. Two species Lesser Scaup *(Athya affinis)* and Lesser Yellowlegs *(Tringa flavipes)* formed 25% of their diet.

Keywords: Mackenzie River, Peregrine, 50 year surveys, population, pesticides, PIT monitoring, maggots, prey

Összefoglalás A szerző asszisztenseivel monitorozta a vándorsólyom *(Falco peregrinus)* elterjedését a Mackenzie folyó teljes hosszán, Kanada északnyugati területein 1966 és 2018 között. A folyó 1600 km-en keresztül átszeli Kanada arktikus területeinek nyugati részét a Nagy-Rabszolga-tótól a Beaufort-tengerig, és nagyjából párhuzamosan a Mackenzie hegylánc keleti lejtőivel az É 61° és az É 68° szélesség között. Minden felmérés alkalmával az összes potenciális fészkelőhelyet ellenőriztük. Az elfoglalt fészkelőhelyek száma (ahol legalább egy madarat láttunk) az 1966-ban számlált 12-ről az 1972-es évre a legalacsonyabb 7-re csökkent. 1990-ben 37 elfoglalt fészkelőhelyet számláltunk, és 2018-ra is a legmagasabb számlálási érték 75 volt 2010-ben. A sikeresen költő párok száma változó volt, az 1972-es legalacsonyabb 5-től a 2011-ben számlált legmagasabb 58-ig.

Az átlagos fiókaszám 2,43 volt sikeres fészkelésenként 1990 és 2018 között (kivéve 2012). Az átlagos fiókaszám 1,4 volt elfoglalt fészkelőhelyenként ugyanezen időszak alatt. Az énekesmadár zsákmányellátottság recens növekedése – ami az elmúlt évtizedek kiterjedt erdőtüzeinek köszönhető – a legutóbbi jelenség, ami befolyásolja a sólymokat (személyes megfigyelés). A vándorsólymok zsákmányállatait egy négy éves időszakon keresztül vizsgáltuk, amikor a zsákmány 20%-a énekesmadár volt. Két faj, a búbos réce *(Aythya affinis)* és a sárgalábú cankó *(Tringa flavipes)* tette ki a táplálék 25%-át.

Kulcsszavak: Mackenzie folyó, vándorsólyom, 50 év felmérés, állomány ingadozás, növényvédőszerek, PIT monitoring, nyű, zsákmány

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Introduction

"The Peregrine Falcon could be called the world's most successful flying bird, since it occurs in all continents and on many oceanic islands and is everywhere a bird of supreme skill, grace and precision in flight"(quote from Amadon & Brown 1968). It is a highly dynamic aerial hunter feeding almost entirely on other avian species some as large as themselves. Some subspecies are known to feed extensively on bats and on large insects (locusts) and pairs known to be predominately bird feeders sometimes take small mammals. Accurate methods of recording have indicated they may reach in excess of an astonishing 444 km in a dive. Not all prey is taken in a dive though for coastal Peregrines (subspecies Peale's) are reported to sometimes hunt at sea level at high speed. They will spot their prey (murrelets) from afar then drop into a trough between the waves on their approach, whipping over the crest of the waves and into the flock of water skimming birds. Once the murrelet has been "decked" the falcon will engineer a retrieval from the water and return to land (Nelson 1977). Many species are taken by Peregrines including shorebirds, alcids, waterfowl, gulls and passerines.

Occasionally other raptors are also taken. In the 1950's and 1960's the Peregrine drastically declined throughout the world with the most noticeable areas of decline in Europe and North America where they had been studied extensively. Enderson *et al.* (1995) summarize the situation for North America: "Overall this species disappeared by the mid 1970's from temperate regions east of the plains and fell to below one-quarter of former numbers in the west where counts were rudimentary. The Pacific Northwest maritime population was little affected especially in the Aleutians. In interior Alaska and northern Canada, we estimate numbers fell to about a third or less of the pre-decline level."

By the late 1960's sufficient research had been conducted to indict the chlorinated hydrocarbon pesticides as the cause, especially DDT, dieldrin and related compounds. Birds poisoned by these pesticides were eaten by Peregrines who would accumulate residue high enough to affect reproduction. Eggshells became thinner and would crack when being incubated (Ratcliffe 1958). Breeding behavior was also affected.

Materials and Methods

For all survey years from 1969 until the present, the length of the Mackenzie River was travelled by motorboat in July and early August and all known and potential nesting sites were searched intensively for occupancy, looking for telltale presence of "whitewash" (excrement) at perching sites, and for the presence of the birds. Where "whitewash" was abundant the sites were climbed whether the birds were seen or not, and in a few cases nest sites with young were found although the adults were never seen. Occasionally it took the firing of a 22 rifle to rouse the adults at an occupied site.

Over 100 different sites used by Peregrines have been recorded and all were checked each year. In some cases the sites are no longer suitable because of erosion, mass slumping, and the effects of river ice destroying the cliff face. Both sides of the river (up to 2 km apart) were surveyed; and sometimes one side of the river was covered going downriver and the opposite side of the river covered on the return trip. Where it was possible young Peregrines were banded and aged. On the 2000, 2005, 2010 and 2013 surveys the prey utilized by Peregrines was studied. All prey samples in the immediate vicinity of nesting sites were collected including avian primaries, tail feathers, wings, feet and heads and any items from the occasional small mammal. Prey and pellets were collected from 87 eyrie visits.

Feathers were keyed out using reference material collected on site and by the use of reference books (Godfrey 1986, Dunn & Alderfer 2011) and reference keys that use nodes on the feather barbules to identify specimens to Order (Day 1966).

The linear survey along the river is not all inclusive of the Mackenzie River valley because there are sites away from the river that couldn't be checked. In order to include these sites in the five year surveys (1990, 1995, 2000, 2005, 2010, 2015) the ENR (Environment and Natural Resources) of the NWT government has been conducting a helicopter survey in conjunction with our river survey that includes at least 10 additional sites in the Mackenzie Valley.

Results

In 1966 a survey showed a population of 12 active sites and these numbers did not change quickly with the elimination of organochlorine pesticides in the early 1970's. However the shift in numbers had begun and by 1990 there were 37 occupied sites along the river with 26

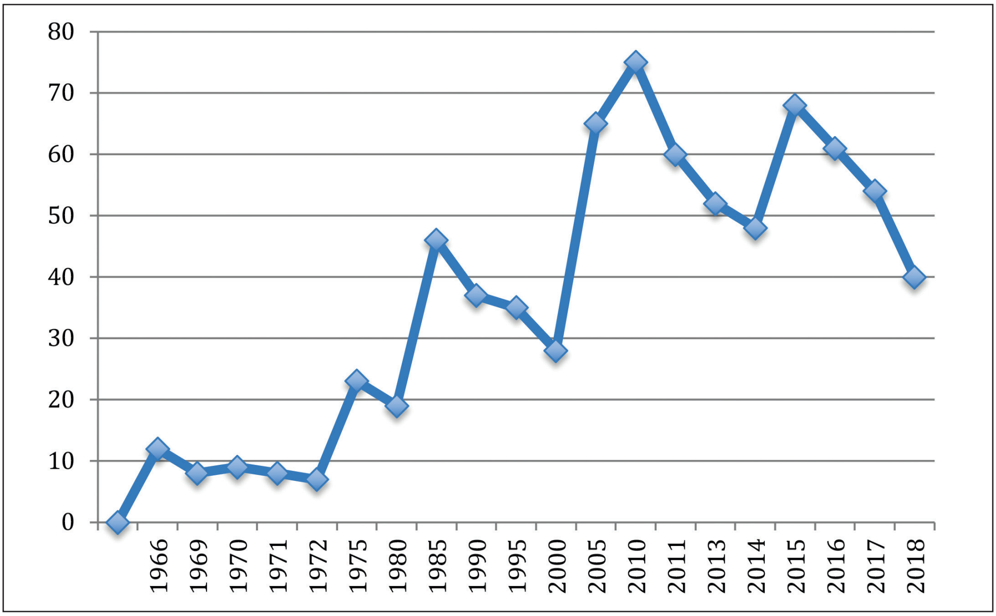

Figure 1. Changes in Peregrine Falcon site occupancy at the Mackenzie River, 1966–2018.
1. ábra A vándorsólyom foglalt fészkelőhelyeinek változása 1966–2018 között a Mackenzie-folyó mentén

sites successfully raising young. By 2015numbers had doubled again with 68 occupied sites and 44 sites successfully raising young. The results of 17 surveys from 1966 to 2018 is presented in *Figure 1* and in *Table 1*.

There were 399 identified prey from 55 species and 108 identified to grouping order *(Table 2)*. In the 507 samples, shorebird (37%) diving ducks (25%) and the passerines (21%) were the most common prey grouping contributing to about 80% of total prey of the identified prey, Lesser Scaup (13.8%) contributed the largest number of individuals and Lesser Yellowlegs (11.5%) the second highest contribution. Overall the Peregrines had a very broad diet eating a wide range of the avian species available along the Mackenzie River. Only birds too big for Peregrines to handle including large waterfowl, corvids, and raptors were absent from the diet. One noted prey included the Yellow Rail *(Coturnicops noveboracensis)* a wing from which was found in a Peregrine eyrie some 500 km north of its previously reported most northerly location. Since 2011, 367 young falcons have been fitted with PIT (Passive integrated Transponder) bands to study mortality, dispersal and turnover of breeding individuals (after Smith & McGrady 2008). We assumed PIT banded individuals would start turning up in the breeding population by 2014–15 but in 2017 we detected a PIT banded bird in the breeding population for the first time (photo only, no data) 482 bands have been put on young Peregrine Falcons since 1969 by the author. From these birds there have been three returns, a bird found in Cuba 1 year 7 months after banding that had travelled 6,262 km, a bird trapped and released in Texas 2 ½ months after banding that had travelled about 4500 km and a bird found in Chile 5 months after banding that had travelled 11,065 km. These distances are exceeded by two others banded by the author about 150 km to the east of the Mackenzie River valley, a bird found in Colombia 3 months after banding

Table 1. Site productivity 1966–2018 (1975, 1980, 1985 ENR Helicopter)
1. táblázat Fészkelési adatok

Year[1]	66	69	70	71	72	75	80	85	90	95	00	05	10	11	13	14	15	16	17	18
Sites Occupied[2]	12	8	9	8	7	23	19	45	37	35	28	65	75	60	52	48	68	61	54	40
Sites Active	12	8	3	5	7				34	28	21	60	65	51	37	33	52	54	46	29
Sites Successful					5				26	26	13	44	48	38	18	28	44	42	18	18
Sites Failed									6	2	7	11	16	3	15	2	3	7	14	12
Success Unknown					2				2		1	5	1	10	4	3	5	5	14	10
Sites Counted & Banded					5				26	22	11	39	45	28	17	20	38	41	17	11
Young Counted & Banded					14				67	51	28	94	115	65	32	51	97	113	40	24
Young counted / Site									2.75	2.3	2.54	2.41	2.55	2.32	1.88	2.55	2.55	2.75	2.35	2.18
Young Banded Conventional					10				58	15	21	35	78	0	32	27	76	93	37	19
Young Banded – PIT													75	33	32	25	77	93	26	19
Sites young not counted									1	12	3	29	13	21	1	18	13	7	3	8

Table 2. Peregrine Falcon diet on the Mackenzie River Northwest Territories ([1] % Diet is for identified prey only)

2. táblázat Vándorsólyom tápláléklista a Mackenzie folyó mentén

Species Group	**% of Diet**	**Species**	**Number**	**% Diet[1]**
Coots & Rails		American Coot *Fulicia americana*	4	1.0
		Yellow Rail *Coturnicops noveboracenis*	1	0.3
Dabbling Duck	8.9	Mallard *Anas platyrhynchos*	8	2.0
		Green-winged Teal *Anas crecca*	16	4
		Blue-winged Teal *Anas discors*	12	3
		Northern Shoveler *Anas clypeata*	6	1.5
		American Widgeon *Anas americana*	2	0.5
		Northern Pintail *Anas acuta*	1	0.3
Diving Duck	25	Lesser Scaup *Aythya affinis*	55	13.8
		Greater Scaup *Aythya marila*	10	2.5
		Surf Scoter *Melanitta perspicillata*	*7*	1.8
		Bufflehead *Bucephala albeola*	*7*	1.8
		Canvasback *Aythya valisineria*	*6*	1.5
		Red-breasted Merganser *Mergus serrator*	*1*	0.3
		Common Merganser *Mergus merganser*	*4*	1.0
		Ring-necked Duck *Aythya collaris*	3	0.8
		Merganser spp. (unidentified)	1	0.3
		Harlequin Duck *Histrionicus histrionicus*	1	0.3
		Duck spp. (unidentified)	32	
Grouse & Ptramigan	0.6	Ruffed Grouse *Bonasa umbellus*	2	0.5
		Rock Ptarmigan *Lagopus mutus*	2	0.5
Gull	6.9	Mew Gull *Larus canus*	23	5.8
		Bonaparte’s Gull *Larus philadelphia*	1	0.3
		Long-tailed Jaeger *Stercuraius longicaudus*	1	0.3
		Gull spp. (unidentified)	1	
Loons & Grebes	2.8	Horned Grebe *Podiceps auritus*	9	2.3
		Red-necked Grebe *Podiceps grisgena*	5	1.3

Species Group	**% of Diet**	**Species**	**Number**	**% Diet[1]**
Passerines	20.7	Say's Phoebe *Sayornis saya*	8	2.0
		Gray Jay *Perisoreus canadensis*	11	2.8
		American Robin *Turdus migratorius*	5	1.3
		Bohemian Waxwing *Bombycilla garrulus*	9	2.3
		Bank Swallow *Riparia riparia*	1	0.3
		Yellow-rumped Warbler *Dendroica coronata*	4	1.0
		Northern Shrike *Lanius excubitor*	1	0.3
		Swainson's Thrush *Catharus ustulatus*	3	0.8
		Water Pipit *Anthus spinoletta*	1	0.3
		Townsend's Solitaire *Myadestes townsendi*	1	0.3
		Fox Sparrow *Passerella iliaca*	1	0.3
		Rusty Blackbird *Euphagus carolinus*	1	0.3
		Grey-cheeked Thrush *Catharus minimus*	1	0.3
		Blackbird spp. (unidentified)	3	0.8
		Small Passerine (unidentified)	24	
		Northern Flicker *Colaptes auratus*	23	5.8
		Three-toed Woodpecker *Picoides tridactylus*	1	0.3
Raptor	1.4	American Kestrel *Falco sparverius*	3	0.8
		Short-eared Owl *Asio flammeus*	2	0.5
		Sharp-shinned Hawk *Accipiter striatus*	2	0.5
Shorebird	32.7	Upland Sandpiper *Bartramia longicauda*	16	4.0
		Lesser Yellowlegs *Tringa flavipes*	46	11.5
		Spotted Sandpiper *Actitis macularia*	17	4.3
		Solitary Sandpiper *Tringa solitaria*	12	3.0
		Common Snipe *Gallinago gallinago*	9	2.3
		Least Sandpiper *Calidris minutilla*	4	1.0
		Golden Plover *Pluvialis dominica*	7	1.8
		Black-bellied Plover *Pluvialis squatarola*	1	0.3
		Short-billed Dowitcher *Limnodromus scolopaceus*	16	4
		Shorebirds spp. (unidentified)	38	
Small Mammal		Small Mammal	1	
		All Prey	**507**	
		Identified Prey	**399**	

Table 3. Peregrine Falcon band returns (from Dunn *et al.* 2009)
3. táblázat Vándorsólyom megkerülési adatok (Dunn *et al.* 2009 alapján)

Band Date	Band	Banding location	Recovery Date	Recovery Location	Km travelled
17/07/69	727-00003	Fort Good Hope 66° N 129° W	14/03/71	Cuba 20°40′ N 77° 00′W	6,262
16/07/73	727-00307	Arctic Red River 6° N 133° W	04/12/73	Chile 20° 10′ S 70° 00′W	11,065
01/07/72	617-21375	Anderson River 69° N 128° W	03/11/72	Colombia 02° 10′ N 78° 30′W	8,351
30/07/73	686-01703	Horton River 69° N 126° W	01/10/74	Argentina 29° 00′ S 66 ° 50′W	11,969
11/07/16	1687-11804	Fort Good Hope 66° W 128° W	09/30/16	Padre Island 26° 28′ S 97° 38′W	4,500

that had travelled 8,351 km and a bird found 1 year 3 months after banding in Argentina that had travelled 11,969 km *(Table 3)*.

Discussion

The graph *(Figure 1)* showing the declining counts of occupied sites until the early 1970's and then the subsequent resurgence until recently shows a remarkable similarity to a number of studies of Eurasian Peregrines over the same period (Sielicki & Mizera 2007). This further substantiates it was the catastrophic effects of organochlorine pesticides in the 1950's and 60's that was pushing numerous top of the food chain species like Peregrines toward extermination. Our figures indicate that the Mackenzie River Peregrine numbers were severely depleted when they were first counted in 1966, about 20% of the high count in 2016 (or decline of 80% by 1966) if we assume carrying capability of the river system had not changed.

A period of rain and severe summer storms when the precipitation is driven into nesting ledges is a factor affecting survival of nestling Peregrines. In 2013 a storm went through the area about Fort Good Hope the third week of June and at 10 nesting sites notes were made that the sites were terribly eroded, slumped or inundated by mud, a result of exceptional periods of rain during the early nesting period. Nestling falcons were buried in mudslides at two sites and two eyasses were found dead below their eyrie after the storm. A more generalized storm period occurred in 2017 and the young at three eyries were found dead in mid-July and nesting ledges were covered by mud at two other sites. 2018 was the poorest year in terms of occupied sites, successful sites and productivity since 2000. This is attributed to a combination of adverse weather again resulting in destroyed sites and one brood killed, and maggot infestation in three eyries. In one of these three the only remaining young was dying and in the second one young was not going to survive. However, in the third all three young had swollen, open ears but the maggots appeared to have had hatched and flown. In 2005 at a few nests young birds were first noted to have maggots coming out of their ears) and in subsequent surveys this seemed to be an increasing problem. It appears that a fly is laying eggs in their ears (because temperatures are rising earlier in the spring than previously and the flies are hatching earlier?). In 2016, 41 nest sites were banded and young checked for maggots; 7 had maggots or 17% of the nests. All young at infected sites were infected. It may not be as bad as it appears though for at sites where I did not think the young would survive because of infestation on a second check of the site to band young about 2 weeks later, the maggots had hatched and flown and the tissue about the falcon's ears was scabbed over and seemed to be healing. On one young similar maggots also were found under the feathers still in blood and causing a terrible mess of the growing feathers Maybe a little squirt of DDT is needed to kill flies and maggots! A veterinarian acquaintance who has worked in the arctic called this maggot problem a condition called myiasis that he has treated in dogs and seen in caribou and wood buffalo caused by the eggs laid by bot flies.

Climate change is having a direct effect on Peregrine nesting along the Mackenzie River. Many nesting sites are on "mud" cliffs sometimes as much as 100 m high presumably held there by frozen permafrost. As the permafrost melts back the cliffs slumps. In a number of cases the falcons have kept on nesting even though their nest site has moved away from its original location.

Despite natural adversity such as occurred during periods of inclement weather or direct mortality by parasites (i.e. the fly maggot) the Mackenzie River Peregrines have increased about threefold since first counted in 1966. The average productivity since 2000 for occupied sites ("active" sites in table 1) is 1.4, which is the average for northern Peregrines (Franke 2016). It would appear that productivity is adequate in this western Canadian population of Peregrine Falcons. Future monitoring will determine if the decreased productivity the past two years is of concern and can be attributed to factors not yet determined.

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There have been seventeen trips on the Mackenzie River from 1966 until 2018 to Monitor Peregrine Falcon nesting numbers. My wife and myself did all trips including two trips by ourselves. Each other trip had one or two volunteers along. They were Randy Semeniuk, Edmonton, Alberta 1969, Kim Hodson, Victoria B. C. 1970, Glen and Thea Ewald, Smithers, B. C. 1990, Bob Little, Smithers, B. C. 1995, John Franken, Smithers, B. C. 2000, Wayne and Betty Sager, Abbotsford, B. C. with John Campbell, Calgary, Alberta 2005, Frank and Kathy Doyle, Smithers B. C. with Jeff Amos, Hazelton B. C. 2010, Craig Hodson, Victoria B. C. 2012, Bob and Evelyn Veitch, Telkwa, B. C. 2013, Arnie Dyson Telkwa, B. C. 2015, Frank Guillon, Smithers B. C. 2016 and Myron Smaha, Wayne Collison and Tom Smith Smithers B. C. 2017.

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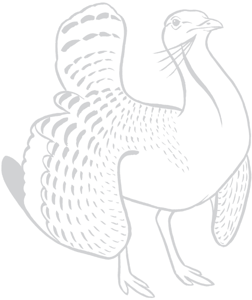

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Monitoring of Peregrine Falcons in the Ariège Pyrenees and Toulouse, Midi-Pyrénées region, France

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Abstract Since the 1980s, the volunteers of the ornithological group of the Nature Midi-Pyrénées association have been monitoring the Peregrine Falcon *(Falco peregrinus)* population in the Ariège Pyrenees and in the Toulouse agglomeration. The data collected over the last 30 years show stability of the Ariège population: little variation has been observed in brood size, occupation rate of the sites or reproductive success. Only the increasing number of known nesting sites is significant, due to better knowledge of the territory by observers over time. In 2017, the breeding population was estimated to be 24 pairs. Urban monitoring proved the presence of individuals in passage, wintering or resident in Toulouse. Since 2002, downtown Toulouse has been visited by several individuals of both sexes and interactions between males and females have been observed since 2005. Despite the multiplicity of possible eyries or nesting sites in Toulouse, and the massive presence of Peregrine Falcons and dedicated bird watchers, no case of breeding has been reported. In addition to monitoring, measures to protect and support the presence of the species have been put in place. In the Pyrenees, in the light of the growth of human activities near nesting sites, some sites are now subject to official protective measures, coupled with constant vigilance and awareness. In Toulouse, to encourage the breeding of the individuals present, two nesting boxes were installed in 2016, on two buildings frequented by a female and a male. In 2017, a first attempt to reproduce in one of these installations confirmed the value of such developments in urban areas.

Keywords: Peregrine Falcon, monitoring, nesting, rupestrian, urban, nest box, Ariège, Pyrenees, Toulouse

Összefoglalás Az 1980-as évek óta a Nature Midi-Pyrénées egyesület végzi a vándorsólyom állomány monitoringját az Ariège Pireneusokban és Toulouse agglomerációjában. Az elmúlt harminc év adatsorának elemzése az ariège-i állomány stabilitását mutatja: kis eltérések figyelhetők csak meg a fészekaljak méretében, a foglalt revírek arányában vagy a költési sikerben. Egyedül az ismert fészkelőhelyek számának emelkedése jelentős, ami a terület egyre részletesebb megismerésének köszönhető. 2017-ben az állományt 24 párra becsültük. A városi monitoring Toulouseban átvonuló, telelő és helyi madarak jelenlétét egyaránt igazolta. 2002-től kezdődően gyakoribbá vált mindkét előfordulása a belvárosban, és 2005-től a hímek és a tojók közötti interakciók is megfigyelhetők voltak. A számos alkalmas revír vagy fészkelőhely, a vándorsólymok jól érzékelhető jelenléte és az elkötelezett madarászok ellenére eddig nem sikerült a faj költését bizonyítani Toulouseban. A monitoring tevékenységgel párhuzamosan védelmi intézkedések is történtek a faj megóvása érdekében. A Pireneusokban, a fészkelőhelyek közelében az erősödő emberi tevékenységek miatt egyes helyek jelenleg a „hivatalos védelmi intézkedések" védelmét élvezik, állandó megfigyeléssel párosítva. Touloseban a jelenlévő egyedek fészkelését elősegítendő két fészekláda került kihelyezésre két épületen, amelyeket egy hím és egy tojó rendszeresen látogatott. 2017-ben az első költési kísérlet megerősítette az ilyen jellegű fejlesztések fontosságát a városi környezetben.

Kulcsszavak: vándorsólyom, monitoring, fészkelés, szikla, város, fészekláda, Ariège, Pireneusok, Toulouse

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Introduction

In 1987 passionate ornithology volunteers formed the "Rapaces" group within the Nature Midi-Pyrénées association. Since its creation, the protection of Peregrine Falcon *(Falco peregrinus)* has been the priority of the group, focusing on the area of the Piedmont Ariège and in Toulouse, capital city of Midi-Pyrénées region. After a census of the sites used by the species, monitoring of this breeding population was quickly established involving local ornithologists and falconers.

From 1988 to 1994 the observations were very intensive with a special regard to possible human disturbances. Some volunteers also invested time in the search for new cliff sites likely to be occupied. This was also encouraged by the introduction of regulatory protection measures (APPB – Biotope Protection measures issued by the Prefecture) covering certain rock nesting sites for raptors.

From 1995 to 2000 the intensity of monitoring of the sites decreased because volunteers focused more on monitoring and safeguarding other sensitive species (Monneret 2017). During that period, emphasis was put on raising awareness among climbers about the APPB regulations, and monitored pairs suffering disturbances.

Activities were reduced from 2000 to 2010, often limited to simply checking the presence of pairs on a sample of known sites. Serious coordination of monitoring started again in 2011 with the objective of updating the data collected in the 1990s. Surveys carried out censuring the breeding population found 31 nesting sites to date in the study area. The very exhaustive censuring of breeding pairs conducted between 2012 and 2014 is now restricted to observations of half of the known sites.

It is now possible to summarize the actions of volunteers over the last thirty years in Pyrenees and Toulouse city. Through the analysis of the collected data, we will attempt to document the status of the Peregrine Falcon breeding population in the study area.

Material and methods

Geography of the study area in Pyrenees

The studied area in Pyrenees *(Figure 1)* is located in the southwest of France in the region of Ariège, on the border with Spain and Andorra. It extends over approximately 1,600 km^2 from the valleys of the Couserans in the west to the valleys of Haute-Ariège and the Pays Cathare in the east (Frémaux & Ramière 2012).

The population density of the region is 31 inhabitants/km^2. The economic activities in the mountainous part of Ariège are mainly composed of extensive agriculture, forestry, tourism and industry (agro-food, paper and textile production, quarrying, and hydroelectricity).

Figure 1. Map of the studied area in Pyrenees Arièegeoises (Ariège department) the studied area is surrounded. Toulouse city is 90 km North of Foix

1. ábra A vizsgált terület térképe Arièegeoises-ben. A vizsgált terület körberajzolva. Toulouse 90 km-re van Foix-től

Environment and habitats in Pyrenees

The nesting sites are between 400 and 1,600 m above sea level, on the hills and mountains of the Pyrenees Ariégeoises. The majority of the areas are oriented to the north, northeast and southwest *(Figure 2)*.

The soil geology is quite heterogeneous with the presence of calcareous, granitic and schistose substrates. The vegetation of the mountains is dominated by mixed beech-fir forests. The valley bottoms and the hills offer more open landscapes with wooded areas, pastures, meadows, hedges, wasteland, copses, sessile and pedunculate oak and hazel forests. Consequently Peregrine Falcon nesting sites in the study area have varied characteristics. In

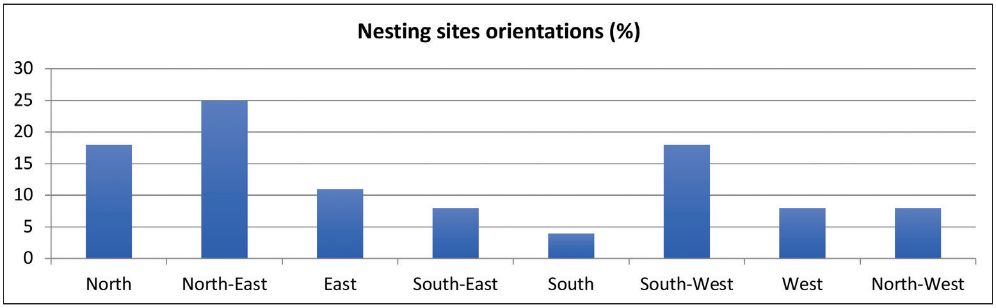


Figure 2. Percentage of nest sites by geographic exposure in the studied Pyrenees area
2. ábra A fészkelőhelyek százalékos megoszlása a vizsgált területen

the east, the areas are mainly on large cliffs sometimes more than 100 m high that dominate an open landscape. We found the highest densities of couples in this section. In the west, the areas are mainly on cliffs some tens of metres high that overhang a more closed landscape and sometimes even entire forests. In general, less than 20% of the nesting sites are on granitic rock cliffs.

Geography of Toulouse area

Toulouse is the capital of the former Midi-Pyrénées region (now Occitanie following the fusion with the Languedoc-Roussillon region). Toulouse is a city of about 480,000 inhabitants, the fourth largest in France. Its urban community involves 37 communes, covers 466 square km and has 800,000 inhabitants. Toulouse is located at the convergence of many territories occupied today by Peregrine Falcons in rocky environments, from the Pyrenees to the Causses in Lot (Boudet 1989) and Aveyron areas (Frémaux & Ramière 2012). However, the great plain of the Garonne river offers very few potential sites and is currently not occupied by the Peregrines: they are only occasionally observed in winter, especially around areas of old gravel pits for potential prey hunting.

The nearest known nesting sites are 54 kilometres away in the rocky areas of the Aveyron gorges and 70 kilometres away in urban areas (Albi city). The agglomeration of Toulouse is at an altitude of only 141 metres but has many attractive buildings for Peregrines (Drewitt 2014, Sale 2016). Religious buildings, as well as apartment buildings or even factories, offer many choices to perch and nest for the Peregrines (Drewitt 2014). This urban jungle also offers them many opportunities to hide from ornithologists!

In Toulouse, Peregrine Falcons are regularly frequent in two sectors: an area covering the historic centre of the city and a sector on the outskirts of the agglomeration, north near the airport zones and south near a former industrial zone. During periods of migration, as elsewhere, one-off data may be obtained for various sectors that are not regularly visited (Ramière 2011).

Climate

The average rainfall is about 1,000 mm/year (Saint-Girons meteorological station – Météo France data) and increases with altitude. The study area is at the eastern edge of the oceanic influence dominated by a north-western airflow. The eastern part (Haute-Ariège, Pays Cathare) is under a Mediterranean influence with a drier climate than in the west (Couserans).

General objectives

In France, since the collapse of the populations between 1945 and 1970, mainly caused by the use of organochlorine pesticides, the capturing of young birds and shooting, the Peregrine Falcon has gradually recolonized its old territories with a net renewal since the 1980s (Thiollay 2004, Monneret 2008, 2017). The Nature Protection Act of July 10, 1976 and the full protection of raptors since 1972 rendered illegal the persecution of these birds (Yeatman-Berhelot 1995, Nidal 2015).

Much of the destruction has been stopped, but some persists and other problems have appeared (Ratcliffe 1993). Thus, from the beginning of the monitoring in the 1990s, there is a suspicion that capture by some unscrupulous falconers seems to be the main factor in the failure of reproduction. Furthermore, mountain sport practices such as climbing, paragliding and gliding are considered to be disturbing factors. It is the same for hunting or animal photography in the immediate proximity of the nesting areas.

Today, the practice of capturing live birds seems to have been abandoned, probably thanks to the progress of the artificial incubation in aviaries. Destruction by illegal shooting also appears to be in decline, but it is difficult to evaluate precisely these factors.

However, the pressure of anthropogenic activities on nesting sites does not diminish. The rise of mountain tourism, new practices of free flight (wingsuit, base jumping), the increasing use of drones, model aircraft, via-ferrata and climbing are causing too many intrusions on rupestrian environments and are disturbing factors during nesting (Monneret 2017). To a lesser extent forestry can also have a negative impact while logging under the cliffs.

The knowledge and monitoring of the breeding population coupled with the surveillance of the effects of human activities on the nesting sites enable the possible threats to be identified and thus to determine the protection measures to be set up (Monneret 2017). This is the main goal of volunteers in this action.

Interspecific competition and predation

The Ariège Pyrenees have a diversity of habitats favourable for many birds that nest in rocky environments. In the study area, two species in particular are in direct competition with the Peregrine Falcon for the eyrie choice: the Northern Raven *(Corvus corax)* and Egyptian Vulture *(Neophron percnopterus)* (Monneret 2017). 25% of the known sites are affected by this competition where the Peregrine Falcons breed in the immediate proximity of one, or even both of the other two species.

Several scenarios have been observed during monitoring. In the case of the Northern Raven, we often see an exchange of eyrie from one season to the next. Sometimes the Ravens drive the Peregrines out at the beginning of the incubation forcing the latter to change eyrie and carry out a replacement egg laying. In the case of the Egyptian Vultures, the Peregrines have the advantage of being installed before the arrival of the migratory Vultures. As a result, the Falcons often take the upper hand, but depending on the individuals and the degree of aggressiveness of their territorial behaviour, the situation can be reversed.

Reproduction losses associated with these interactions between species seem marginal and are rarely observed. The predation of eggs or chicks by ravens is also difficult to measure without the permanent presence of observers (Cugnasse 2012). However, we know that in the event of human disturbance during nesting, Peregrine Falcon broods are more vulnerable to corvid predation. The latter are less fearful of humans and return more quickly to the cliffs.

The predation by Eurasian Eagle Owls *(Bubo bubo)* has not been studied much during monitoring. Since 2010, on one site in particular, we have twice observed a Peregrine couple trying to set up a few dozen metres from the eyrie of an Eagle Owl. Falcons were observed in February-March and disappeared in April and we then found this couple confined a few kilometres away for the rest of the season, without nesting.

According to the monitoring data of the Eurasian Eagle Owl in Ariège (Thomas Buzzi, Nature Midi-Pyrenées), the presence of this nocturnal raptor was noticed at least once between 2002 and 2017, near 20% of the known nesting sites of Peregrine Falcons (within a radius of max. 2 km). No specific listening campaign has yet been undertaken to check the presence of these owls at all the peregrine sites.

Since the resumption of regular monitoring in 2012, the disappearance of adults during breeding is very rarely observed. We cannot pronounce on the possible disappearance of individuals by predation by the Eagle Owls. It would really be necessary to observe the capture by the nocturnal raptor or to analyse their pellets.

Monitoring of rupestrian Peregrine Falcons

Methodology

In the Pyrenees, the observation protocol on known sites corresponds to a minimum of 3 visits per season lasting from 2 to 3 hours during the following periods:
- from February to March: to check the installation and confinement of couples,
- from April to May: to verify the incubation and rearing of chicks,
- from May to June: for the counting of young in flight.

An observer is assigned to monitor one or more sites. Insofar as possible, each observer keeps the same sites for several seasons in a row. A coordinator collects the data, leads the monitoring and writes the annual reports. Currently there are 10 to 15 volunteers regularly involved in monitoring.

The prospection of new nesting sites is carried out in February and March when the couples are the most demonstrative (parades, cries, territorial defence).

Difficulties

This action is carried out by a group of passionate volunteers who do this monitoring in their spare time according to their availability. Consequently, the observations were sometimes variable and heterogeneous over the study periods from 1988 to 2000 and from 2012 to 2017.

In addition, the Nature Midi-Pyrénées association is involved in the monitoring and protection of many species of raptors (Bearded Vulture – *Gypaetus barbatus,* Eurasian Eagle Owl, Egyptian Vulture, Booted Eagle – *Hieraaetus pennatus*, Short-toed Snake Eagle – *Circaetus gallicus*, Golden Eagle – *Aquila chrysaetos*). Depending on the year and priorities, volunteer mobilization can vary from one species to another.

Finally, the search for new sites is sometimes very difficult given the significant snowfall in the Pyrenean massif until April and May. Access to valley bottoms is often impassable before the end of spring.

Analyses

On looking at these data *(Table 1)*, we can identify monitoring periods with a variable level of observations. As previously stated, volunteer involvement in the Peregrine Falcon monitoring has sometimes been reduced, depending on the monitoring priorities of other sensitive species. Because of this, an overall statistical study covering the entire 1988–2017 period is not possible. In addition, the monitoring period is not continuous, with incomplete results in the 2000s *(Table 2)*.

There are nevertheless 2 sets of data that can be compared, with similar and continuous observations: the periods 1988–1994 and 2012–2017 *(Table 3)*. We will try to compare 4 comparable factors between these two periods: brood size, reproduction failure rate, site occupancy rate and the number of known sites.

Assessment

On the basis of these results, we observe that between the periods 1988–1994 and 2012–2017 there was:
- a reproductive failure rate down 12%
- a stable brood size for producing couples
- an increase in the number of known nesting sites by 26%
- a site occupancy rate down 6%
- an increase in the estimate of the breeding population of 17%

Protection measures

Thanks to the mobilization of volunteers in the monitoring and protection of the Peregrine Falcons but also other rupestrian raptors present in the study area (Golden Eagle, Bearded Vulture, Egyptian Vulture and Eurasian Eagle Owl), 3 nesting sites benefited from reinforced regulatory protection through Biotope Protection Prefectural Orders (APPB).

Table 1. Summary of observations during the period 1988–2017 in Pyrenees Ariégoises
1. táblázat A megfigyelések összegzése 1988–2017 között Pyrenees Ariégoises-ban

Year	Number of visited sites (A)	Number of sites occupied by established couples (B)	Number of couples with regular checking (C)	Number of nesting failures (D)	Number of producer couples (E)	Number of juveniles in flight (F)
1988	13	10	9	5	4	8
1989	14	12	12	2	10	23
1990	15	14	10	4	6	10
1991	15	14	9	6	3	7
1992	17	16	15	4	11	20
1993	19	16	15	6	9	18
1994	15	12	12	5	7	15
1995	9	7	5	1	4	9
1996	8	6	6	1	5	9
1997	9	7	7	3	4	6
1998	7	6	5	3	2	4
1999	6	5	5	1	4	7
2000	17	15	13	5	8	12
2012	24	20	17	7	10	21
2013	25	20	16	8	8	15
2014	25	20	18	5	13	29
2015	17	13	10	2	8	16
2016	16	13	9	1	8	12
2017	20	17	14	3	11	23
Average	**15**	**13**	**11**	**4**	**7**	**14**

(A) sites visited at least once during the breeding season, (B) established couples with 2 adults or 1 adult and 1 immature, (C) couples checked until juveniles' flight, (D) couples with regular checking who did not reproduce, (E) couples with at least 1 juvenile

Over a defined area, these orders regulate human activities and prohibit any ravages of species and their habitats. The bans focus on noise pollution, the use of pesticides, the deposition of waste, the over-flight by motorized devices, free flight, forestry, etc. Practices such as hunting or climbing are authorized between dates outside the breeding periods of raptors.

Despite these measures and warning signs put in place, these regulations are not rigorously respected. Site monitoring by birders remains imperative to ensure continued awareness of users.

Many other sites would deserve to have stronger regulatory protections, but many steps are required for the introduction of APPB regulations that make the process heavy and tedious. At least 30% of peregrine breeding sites are equipped for climbing (fixed ropes, pitons, etc.). These climbing routes seem relatively unfrequented, but once again, without continuous surveillance, it is very difficult to know if disturbances are occurring. For the birds' safety, charters with climbers could be established.

Table 2. Comparison of monitoring results and definition of various periods (indicated by different background colours)

2. táblázat A monitoring eredmények összehasonlítása és az egyes időszakok meghatározása (eltérő háttérszínnel jelölve)

Year	**Number of known nesting sites**	**Completeness of sites check**	**Rate of occupied sites (B)/(A) in %**	**Failure rate of couples checked (D)/(C) in %**	**Number of juveniles per producing couple (F)/(E)**
1988	22	56 to 83% of known sites are checked	77	56	2,0
1989	22		86	17	2,3
1990	22		93	40	1,7
1991	22		93	67	2,3
1992	22		94	27	1,8
1993	24		84	40	2,0
1994	24		80	42	2,1
1995	25	23 of 34% of known sites are checked	78	20	2,3
1996	27		75	17	1,8
1997	27		78	43	1,5
1998	27		86	60	2,0
1999	27		83	20	1,8
2000	27	63% of known sites are checked	88	38	1,5
2012	28	55 to 86% of known sites are checked	83	41	2,1
2013	28		80	50	1,9
2014	28		80	28	2,2
2015	29		76	20	2,0
2016	29		81	11	1,5
2017	31		85	21	2,1
Average	**26**		**83**	**35**	**2**

Table 3. Sites and breeding statistics during the 1988–1994 and 2012–2017 periods

3. táblázat Fészkelőhely és költéssiker statisztikák az 1988–1994 és a 2012–2017 közötti periódusokban

Period	**Average breeding success rate (%)**	**Average brood size per producing couple**	**Known sites**	**Average occupancy of sites (%)**	**Density of known sites (site / 100 km^2)**	**Estimation of the breeding population in the study area (1600 km^2)**	**Density of breeding pairs in the study area (1600 km^2) (pairs / 100 km^2)**
1988–1994	59	2	23	87	1.4	20.0 in 1988	1.25
2012–2017	71	2	29	81	1.8	23.5 in 2017	1.47

Monitoring of urban Peregrine Falcons

Wintering Peregrines in Toulouse agglomeration

Peregrine Falcons were first reported wintering in the Garonne plain around Toulouse in the middle of nineteenth century (Companyo 1863, Lacroix 1875). For the recent period, the first Peregrine Falcon data available in Toulouse dates back to November 1981 and was probably related to migratory passage or occasional winter visits (Bousquet 1984, Joachim *et al.* 1997). During the following years, yearly observations were reported during autumn and winter months (Bousquet & Joachim 1987, 1988, 1989, 1991, 1994).

It was not until 1991 that complete wintering in downtown Toulouse was established (Defos du Rau 1992). A falcon was regularly seen on the tower of the Jacobins church and was seen hunting over the Garonne river. For the following 10 years, the species was subject to few detailed observations in the town and all of them concerned passage or wintering.

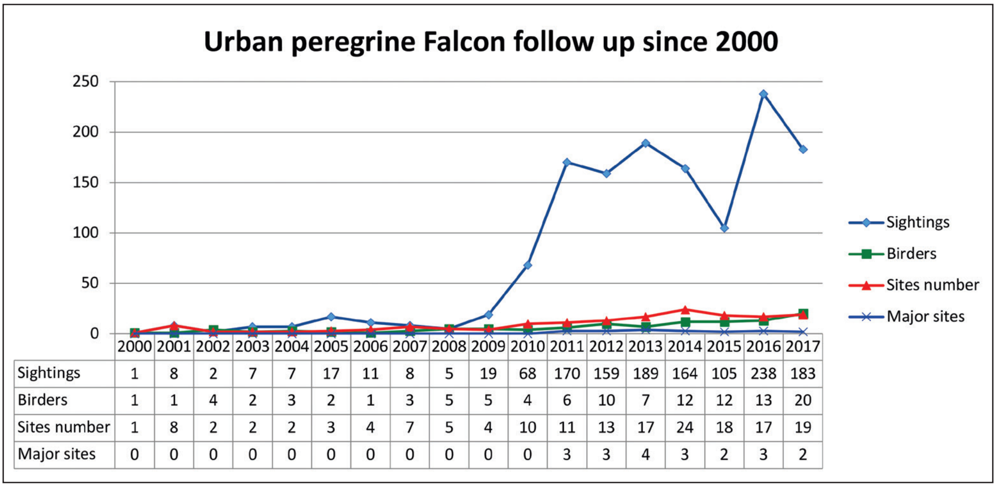
In 2000, an adult Peregrine regularly used a balcony as a platform for an overnight stay and as a regular larder on a tall private building on the banks of the Garonne south of downtown. At the same time two Peregrines, a male and female, were seen in the town (M. Viallet, L. Kergoat, T. Buzzi, pers. com.). A nest box was installed on the top of the private building on March 4th, 2001 by two birders (G. Téhel and P. Fioramonti). However, this nest box was never occupied and had to be removed a few months later because of refection work on the building after the explosion at the AZF chemical plant on September 21st, 2001. Some observations of Peregrines were reported at this site during the winter of 2001–2002 but after that the site was not used again.

A complete new wintering season was documented in 2001 (L. Kergoat, pers. com.) on the same site. In the same year two birds were seen together and stayed in the city centre during the winter until March but there were no further sightings until the month of September when, again, a bird was seen. Wintering seemed regular and at least one bird was present in the following years on the same sites.

Interestingly in 2001, an injured juvenile female Peregrine Falcon was found on the ground 5 km south of Toulouse, 9 days after the AZF explosion (equivalent to 40 tons of TNT) on September 21st. She was scrawny and nearly featherless and was taken to the Toulouse veterinary school for medical care. Close examination confirmed burn lesions on her feet, beak and eyelids. She was able to eat by herself one month after her admission (Bonnet *et al*. 2004).

Resident Peregrines in Toulouse

It was not until 2005 that the annual quartering of an individual was clearly proven. During passage periods (November and February) individuals were regularly observed, sometimes with interactions between birds, but this did not lead to any reproduction. In 2007, two birds were recorded as completely over-wintering in the city centre. In 2008, another bird passed the winter on a site on the outskirts of Toulouse. Its area of presence did not seem to overlap with that of the individual confined to the city centre (A. Balthazar, pers. com.). On this



	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Sightings	1	8	2	7	7	17	11	8	5	19	68	170	159	189	164	105	238	183
Birders	1	1	4	2	3	2	1	3	5	5	4	6	10	7	12	12	13	20
Sites number	1	8	2	2	2	3	4	7	5	4	10	11	13	17	24	18	17	19
Major sites	0	0	0	0	0	0	0	0	0	0	0	3	3	4	3	2	3	2

Figure 3. Urban Peregrine Falcon follow up since 2000. The graph presents for the period 2000 to 2017, the annual number of Peregrine Falcon observations within the Toulouse urban area as registered in the Nature Midi-Pyrénées association database (BazNat) completed with personal data, the annual number of birders involved, the overall number of observation sites and the major sites which are defined as sites with more than 20 observations during the year

3. ábra A vándorsólyom megfigyelések, a megfigyelők száma és a megfigyelési helyek alakulása Toulouseban 2000–2017 között. Az adatok a Nature Midi-Pyrénées Egyesület adatbázisából származnak, kiegészítve egyéni megfigyelésekkel

same site, two birds would be observed until the month of March in 2009 but there was no follow-up and the two individuals were not recorded further.

In 2010, many perch sites were identified downtown because observations increased *(Figure 3)* and thanks to the use of digiscoping individual identification of Peregrines was possible. In addition to occasional observations of migrating individuals, four birds were identified as residents: a male in historic downtown, a small female, who was ringed, on the eastern banks of the Garonne river, a large female localised to the extreme east of the city and a wintering male on the Airbus industries site north of Toulouse, by Blagnac Airport *(Figure 4)*.

The habits and territory of each falcon have been studied. Interactions between the falcons were rarely observed but the Peregrines could observe each other from high perches and were observed as having synchronic feedings. The small female falcon was ringed with a blue plastic ring on her left leg with a white V6 dated April 28, 2002, in Dima, Biscaye, Spain (340 km away from Toulouse). Her territory was between the two other downtown birds. She was last seen in December 2015, and then her territory was taken over by the nearby large female who rapidly reduced her frequentation of the east of the city. She is now the female partner of the couple that attempted breeding in 2017 in the nest box put up in south of Toulouse. During winter she regularly continues to hunt Feral Pigeons *(Columba livia domestica)* and perch in her downtown territory that is 3.3 km north of the nest box. Her male partner was a newcomer in 2016 and stays most of the time in the vicinity of the nest box site. The downtown male has not modified its habits since the disappearance of the ringed female.

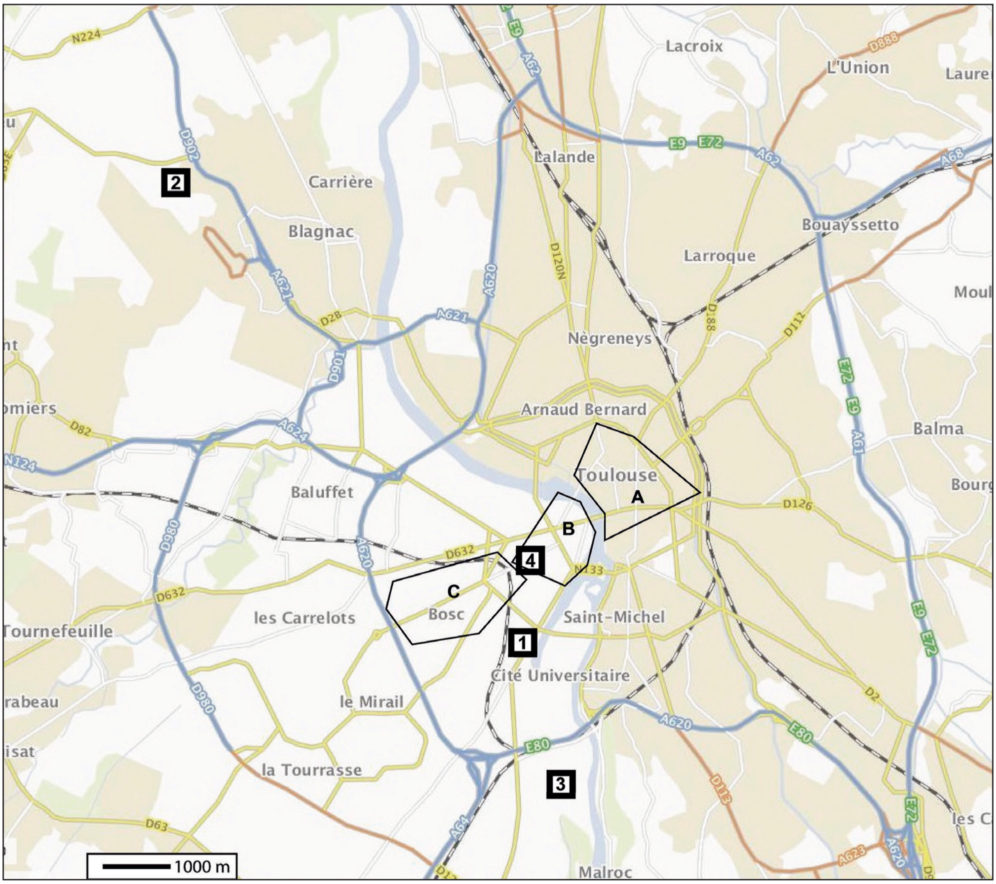


Figure 4. Map of Toulouse city with the localisations of the nest boxes (numbered square 1: 2000, 2: 2010, 3: September 2016, 4: November 2016) and the three historic territories of downtown individuals (A: male, B: ringed female, C: large female)

4. ábra Toulouse térképe a kihelyezett költőládák helyének feltüntetésével (1: 2000, 2: 2010, 3: 2016 szeptember, 4: 2016 november). A betűkkel jelzett területek egy-egy madár régebbi territóriumát tüntetik fel (A: hím, B: gyűrűzött tojó, C: nagy tojó)

Nest boxes and first breeding attempt in Toulouse

The absence of spontaneous breeding in Toulouse led ornithologists to set up nest boxes to try to encourage it. Around 2010, a nest box was set up on the roof of the Airbus A380 assembly workshop north of Toulouse by Blagnac airport by birders working for Airbus Industries *(Figure 4)*. The goal was to retain a wintering Peregrine Falcon on the site to reduce the nuisance associated with the presence of numerous Feral Pigeons. Since then the nest box was moved under the roof to protect it. This nest box was never used for nesting despite the regular nearby wintering of a male Peregrine Falcon. In 2016, a pair of Peregrines was observed on a former industrial site south of the city and monitored *(Figure 4)*.

The two individuals were regularly seen on an 80-metre high industrial chimney used as perch for hunting, as a larder and dormitory. It is situated on the banks of the Garonne River and offers a clear view to the southern plain and to the centre of Toulouse. The site offers an abundant and varied food resource during migration periods and is closely located to downtown (3.3 km) for gathering Feral Pigeons. The Nature Midi-Pyrénées association decided to install nest boxes and two were constructed with the help of municipal services. Thanks to the strong naturalist commitment of the managers of the two selected buildings and the prospect of limiting the cost of the fight against invasive Feral Pigeons, our project has been very well perceived and quickly realized. On September 22nd, 2016, the first nest box was installed during renovation work on the industrial chimney south of Toulouse. During the renovation work the Peregrine pair stayed close to the site, and quickly started visiting and appropriating the nest box. A new flashing security light was installed on the top of the chimney and it took no time for the male to get used to it but it was 10 days before the female perched on rest cavities immediately by the flashing lights. Since then, volunteers have been providing a daily follow-up. At the end of February, a first mating was observed near the chimney and the incubation of eggs began on April 2. The female systematically incubated at night and the male only for short daytime periods with the impression that he had an impatient expectation of being relieved by his mate. Two visits of other Peregrines coming from downtown were observed with, in both cases, a quick response from the couple to keep away the unwanted intruders. Daily matings persisted during changeovers. After a normal incubation period of one month the female was no longer sitting on the eggs but was outside the nest box most of the time and no feeding was observed. We have found no explanation for this breeding failure and no remaining clues when the nest box was visited the following August. The couple was still regularly on the chimney all year long with some visits to downtown buildings. In 2018, monitoring of the breeding period will be carried out: the first couplings were observed on January 28th, 2018.

On November 17th, 2016, with the support of the council of the Department of Haute-Garonne, a second nest box was installed a month later on a downtown building once regularly frequented by a female. Use of this nest box was never observed despite the presence of the female mate of the couple less than five meters away on a balcony used as a larder and perch.

The first city breeding in a nest box in France was in 1989 in Albi, a city that is only 70 km east of Toulouse. The nest box is situated on the tower of Sainte-Cécile cathedral and has been monitored using webcams since 2007. Breeding in Albi has been successful since 2001 with 3 to 4 chicks regularly produced for most breeding seasons. Since then nest boxes are blooming in the region. In Auch, 70 km west of Toulouse, a nest box for Peregrines was installed on the cathedral in 2017 (March 3rd). In Carmaux, 85 km northeast of Toulouse, a nest box was installed on the tower of the cathedral (November 2017). In the city of Montauban, 50 km north of Toulouse, Peregrines are regularly reported downtown with a couple observed since 2016 and a nest box project is on-going.

Discussion

If it is difficult, with the data collected, to precisely define the evolution of the breeding population between 1988 and 2017, but we do not observe any significant variations in the brood size, the occupation rate of the sites or the failure rate of the reproduction between 1988–1994 and 2012–2017. From one season to the next, fluctuations in brood size and failure rate mainly depend on the meteorological factors: significant rainfall in the spring being unfavourable (risk of submersion of eggs, difficulties in prey supply during rearing juveniles).

The only data that has increased significantly is the number of known sites. This increase can be explained by a real increase in the number of breeding pairs, but also by a better knowledge of the territory by observers over time. It should be noted that the western part of the study area is the least explored area and it is therefore possible that the number of breeding pairs is underestimated in this sector.

In the studied area, the carrying capacity of the environment does not seem to be saturated. The best sites are probably all occupied, but birders still identify many potentially favourable cliffs.

Unlike the mountains of eastern France, here in the Ariège, the Peregrine Falcon must, in addition to the Eurasian Eagle Owl and the Northern Raven, coexist with other raptors with territorial behaviour such as the Golden Eagle, the Bearded Vulture and the Egyptian Vulture. The influence of these interspecific competitions on breeding sites is difficult to measure, probably limited, but very real in the most favourable rupestrian areas. Predation on the Peregrines by the Eurasian Eagle Owl has not been sufficiently studied to draw conclusions.

The actions of the Peregrine Falcon monitoring group have led to a clarification of the species status in Ariège and at least shown the stability of the breeding population. Some sites benefit from regulatory protection (APPB), but ensuring the rules are respected by users of rupestrian environments demands constant vigilance, year after year. Finally, periodic monitoring of nesting pairs is still necessary in view of the growth of potentially disturbing human activities around breeding sites.

To date, despite resident and regular wintering Peregrine Falcons for more than 30 years and 3 nest boxes available, no reproduction has occurred in Toulouse. The first reported attempt was in 2017 in a nest box recently installed, but failed for reasons unknown. We will continue monitoring the city Peregrine population in Toulouse and hope for successful nestings in the coming years.

Acknowledgements

Many passionate birders have succeeded each other on these actions for over thirty years. This monitoring was able to exist and remains thanks to the constant mobilization of the observers, the members of the association Nature Midi-Pyrénées but also the agents of the National Office of Forests. May they all be thanked here, especially: Abadie M., Anael T., Baltazart A., Baranco S., Baratieux B., Barbier L., Barrau A., Berne J. J., Bertholin H., Bourcy

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The Danish Peregrine Falcon population: Reestablishment and eggshell thinning

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Abstract Denmark being a country with only a few suitable steep nesting cliffs has only harboured a small population of Peregrine Falcons *(Falco peregrinus)* in historic time. In the previous century, the population gradually declined due to persecution, egg and young collection, and pollution. The last breeding attempt in the 20th century occurred in 1972 in southeastern Denmark. No new breeding attempts were recorded in Denmark until 2001 but since then the population has gradually increased – most rapidly since 2012 – to a peak of 24 territorial pairs in 2018; some of them breeding on man-made structures (nest boxes at bridges and power plants). Here we update the information on the reestablishment of the Peregrine Falcon in Denmark, including origin and dispersal, reproduction, and eggshell thinning.

Keywords: Denmark, recovery, productivity, dispersal, monitoring, eggshell thinning

Összefoglalás Dánia azon országok közé tartozik, ahol nagyon kevés olyan természetes képződmény, sziklaorom található, mely a vándorsólymok *(Falco peregrinus)* fészkelési igényeinek megfelel. Az elmúlt évszázadban a populáció mérete erősen csökkent a zavarás, tojás- és fiókagyűjtés, valamint a szennyezések következtében. A 20. század utolsó költési kísérlete 1972-ben volt, Délkelet-Dániában. Nem volt megfigyelhető költés egészen 2001-ig, amióta azonban a populáció mérete ismét növekedésnek indult – 2012 óta még erőteljesebben – 2018-ban elérve a csúcsot 24 territoriális párral, melyek közül néhány ember által épített helyeken (hidakon és erőműveken) fészkelt. Ebben a tanulmányban tesszük közzé a dán vándorsólyom populáció helyreállításának eredményeit, beleértve az egyedek eredetét és mozgási mintázatait, szaporodásukat és a tojáshéjak vékonyodását.

Kulcsszavak: Dánia, helyreállítás, produktivitás, terjedés, monitorozás, tojáshéj vékonyodás

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Introduction

As reported by Andreasen (2009) the Peregrine *(Falco peregrinus)* in Denmark suffered from the same effects of environmental pollutants and persecution as the population in the neighbouring countries and was absent as breeding bird from 1972 until 2001 when the first (unsuccessful) clutch of eggs was laid at the classical breeding site, the chalk cliffs of Møns Klint. In this paper, we summarize the recovery and expansion of the population in Denmark, report on the exchange of breeding birds with Sweden, Germany and Poland, and analyse the eggshell thickness as an indicator of the pollutant levels that first led to the extirpation.

Material and Methods

Under the auspices of Birdlife Denmark, volunteers have been engaged in various projects to monitor rare and endangered bird species in Denmark; a sub-group have been focusing on the Peregrines under the coordination of the first author. The ‘classical’ historical breeding sites known from the 1900s have been visited irregularly in the 2000s and, when reoccupied, monitored annually to assess breeding success. Other likely breeding sites, often on man-made structures, have been reported by birders and the public and, when occupied by Peregrines, included in the monitoring scheme.

In roughly half of the successful nesting sites the young have been ringed since 2009 (several sites were inaccessible for various reasons, including landowners, security at power plants); young were aged according to Clum *et al*. (1996) and colour ringed in coordination with the Nordic Peregrine ringing programmes. Observations of ringed birds reported by photographers, observers and falcon researchers in neighbouring countries etc. has made it possible to determine the origin of several breeding Peregrines in Denmark and abroad.

In nests visited for ringing, the nest scrape was carefully searched for eggshell fragments deriving from the hatched eggs; all fragments were collected and later measured and analysed according to the procedures described by Falk *et al*. (2006) and Vorkamp *et al*. (2017).

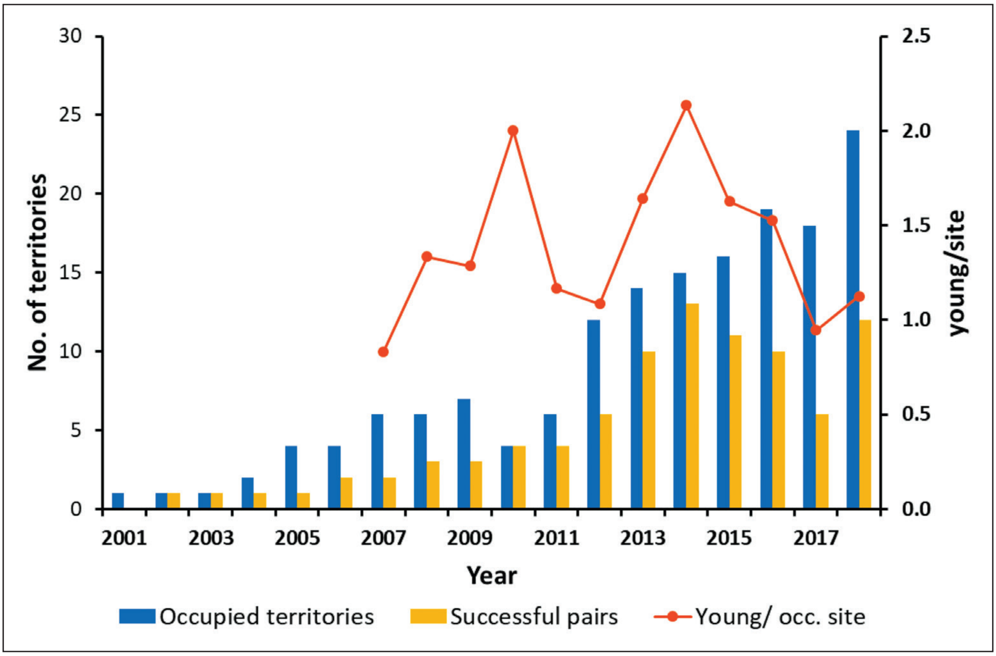

Figure 1. Population increase and productivity in the Danish Peregrine Falcon population 2001–2018
1. ábra A dániai vándorsólyom populáció növekedése és produktivitása 2001 és 2018 között

Results and Discussion

Since the Peregrine returned to Denmark and started breeding by 2001, the population has increased to a peak of 24 territorial pairs in 2018 with up to 13 (in 2014) successfully producing young *(Figure 1)*. The apparent dip in 2010–11 may have been caused by less thorough field surveys. Since 2007 more than 5 sites have been occupied and on average 60% have been successful.

Andreasen (2009) estimated that the Danish breeding population in the past centuries probably was around 6–8 pairs/year on average, maximum 10–15 pairs, so the population can be considered to be fully recovered and now beyond historical levels which, however, was probably artificially low, i.e. below environmental carrying capacity, due to centuries of persecution (Andreasen 2008).

Denmark is largely a flat country so a typical cliff-nester as the Peregrine mainly have access to suitable breeding sites at the few chalk and limestone cliffs in eastern Denmark, on the rocky coasts and stone quarries of the island Bornholm and, increasingly, on man-made

Figure 2. Example of Peregrine breeding sites in Denmark: limestone cliffs such as Møns Klint (a), rocky coastal cliffs (b) and stone quarries (c) at the isle of Bornholm (only part of Denmark with bedrock) and man-made structures like Ensted power plant (d)

2. ábra Példák a vándorsólyom fészkelőhelyeire Dániában: mészkőszirtek, mint a Mana Klint (a), sziklás partoldalak (b) és kőfejtők (c) Bornholm szigetén, valamint mesterséges épületek, mint az Ensted erőmű (d) structures like tall power plants or bridges *(Figure 2)* similar to the population in the Czeck Republic, where industrial structures, not city centre buildings, are main man-made breeding sites (Beran *et al.* 2018). With less persecution of raptors compared to decades ago, man-made structures may offer opportunities for an expanding breeding population; several tall buildings in cities hold wintering Peregrines (according to citizen science database, Birdlife Denmark) and, at some point, may turn into breeding sites.

Average productivity (2007–18 – excluding the early years with less than 5 occupied sites) was 1.4 young/occupied site (range 0.8 to 2.1), or 2.4 young/successful pair *(Figure 1)*. The productivity of Danish Peregrines is thus well above the critical limit (1.0 young/occupied site, USFWS 2003) where concerns may be raised. Based on backdating from the age of young when they were ringed, the average hatching date of first egg in 36 clutches was May 8 (SD = 14.4).

Ringed Peregrines originating from neighbouring countries have in 11 cases been observed breeding in Denmark *(Figure 3)*: three from Sweden, six from Germany and two from Poland. Similarly, Peregrines ringed in Danish nests have been observed as territorial or breeding in Sweden (two cases) or at other locations in Denmark (five cases). Hence, the recovery of the Danish population relies on the reestablishment of healthy populations in neighbouring countries – and the ringing recoveries verify continued exchange and gene flow within the region.

Not much is known about contaminant loads in Danish Peregrines in the past. One of the eggs from the breeding attempt in 1970 was analysed for DDT and PCB and the result showed very high values, comparable to those known from England and Germany (Andreasen 2012).

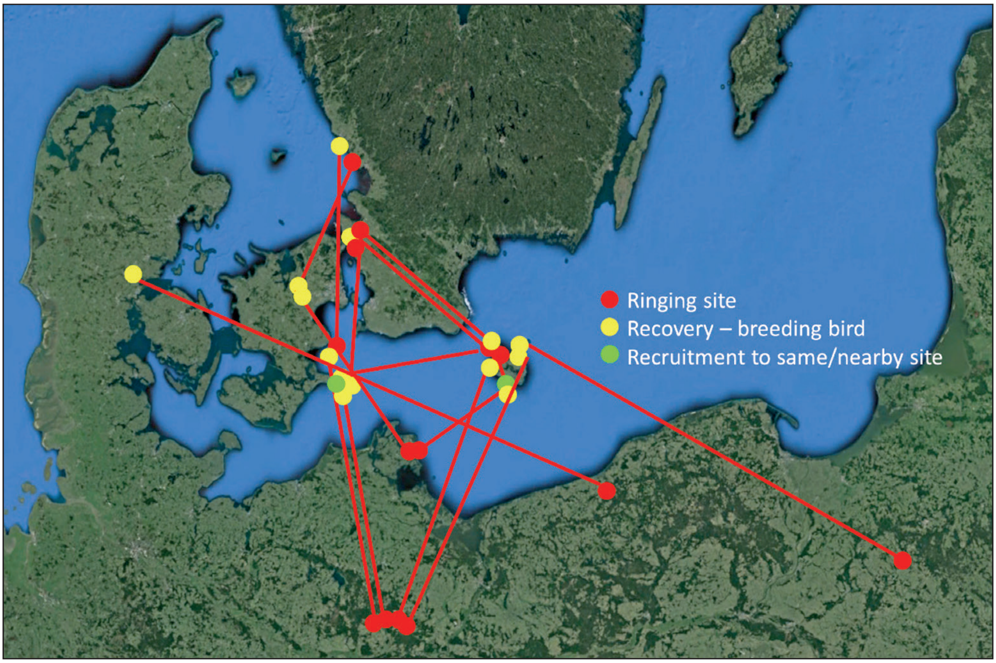

Figure 3. Origin and dispersal of ringed Peregrines from/to the breeding population in Denmark 2001–2018 (map source: Google Earth)

3. ábra A gyűrűzött vándorsólymok jelölési helyei és útvonalai a dán költőpopulációból 2001 és 2018 között (térkép forrása: Google Earth)

The eggshell fragments collected in 11 successful Danish nests 2009–16 had on average normal thickness when compared to pre-DDT eggs available at Zoological Museum, Natural History Museum of Denmark (0.335 mm, SD = 0.0181, N = 11). The pre-DDT eggs used for comparison also had a thickness of 0.335 mm, SD = 0.0183, N = 16 (Falk & Møller 1990). This indicates that the load of eggshell thinning contaminants, especially DDT and its degradation products, in the Peregrines is low and no longer of concern. This is consistent with findings from Germany where Peregrine Falcon shell thinning was back to normal 30 years after the legal ban of DDT in 1972 (Wegner *et al.* 2005), in contrast to some populations in the Nearctic where normal shell thickness is still decades away (Falk *et al.* 2018).

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A summary of intentional poisoning of Peregrine Falcons in Switzerland during the last decade

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Abstract In May 2011, a webcam in Zurich, Switzerland, registered the sudden death of a Peregrine Falcon. Analyses revealed that poison had been applied to the nape feathers of the pigeon captured by the bird. This case really raised the awareness of Peregrine Falcon poisoning by pigeon fanciers in Switzerland. BirdLife Switzerland, with the help of numerous partners, started researches on the subject that pigeon fanciers began a "war" against Peregrine Falcons and other raptors. Between 2006 and 2017, BirdLife Switzerland listed 7 cases of proven intentional poisonings of birds of prey where analyses confirmed the use of poison; and 19 suspected cases with the presence of dead pigeons and birds of prey simultaneously or other suspicious deaths in Switzerland. Three decoy pigeons with poison on the neck could be secured before they were captured by the target species. Two pigeon fanciers who used poisoned pigeons were convicted in 2016 and 2017. Although the numbers of proven and suspected cases are still low, we believe that the phenomenon may be much more widespread. We think that the poisoning may have a negative effect on the population of the Peregrine Falcon in Switzerland.

Keywords: intentional killing, persecution, poaching, pigeon fanciers

Összefoglalás 2011 májusában egy zürichi (Svájc) webkamera rögzítette egy vándorsólyom hirtelen elhullását. Az elemzések kimutatták, hogy a sólyom által megfogott galamb tarkótollait méreggel kezelték. Ez az eset országszerte felhívta a figyelmet a vándorsólymok galambászok általi mérgezésére. A BirdLife svájci szervezete együttműködők bevonásával kutatásokba kezdett a galambászok által a ragadozó madarak ellen indított "háború" kapcsán. 2006 és 2017 között hét, bizonyítottan mérgezéses esetet regisztráltak, és további 19 esetben feltételezhető a méreg használata, mivel mind elhullott galambokat és ragadozókat is rögzítettek Svájcban. Három csaliként alkalmazandó galambot sikerült a ragadozók előtt elfogni. Két galambászt mérgezős vétségében elítéltek 2016-ban és 2017-ben. Annak ellenére, hogy a bizonyított és feltételezett mérgezések száma alacsony, úgy hisszük, hogy ezek az esetek gyakoribbá válhatnak. Meglátásunk szerint a mérgezések kártékony hatással lehetnek a svájci vándorsólyom populációra.

Kulcsszavak: szándékos mérgezés, orvvadászat, törvénykezés, galambászok

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Introduction

In May 2011, a webcam in Zurich, Switzerland, registered the sudden death of a Peregrine Falcon *Falco peregrinus* at its nesting box. The bird died while plucking a pigeon. Analyses revealed that a poison had been applied to the nape feathers of the pigeon. The three young were brought to a rehabilitation centre, reared to independence and released afterwards. The male survived but was found poisoned three years later at another nesting site in Zurich.

This death registered by a webcam was the case that really raised the awareness of Peregrine Falcon poisoning by pigeon fanciers in Switzerland. Thus, BirdLife Switzerland, with numerous partners initiated a Peregrine group dealing with the intentional poisoning. The group started researches on the subject and gathered information on suspicious cases also from the past years. The first publication described the phenomenon of the intentional poisoning of Peregrine Falcons in Switzerland (Vogler *et al.* 2015), but in the last years new cases sadly had to be added to the list. In the following, we present the conflict between pigeon fanciers and birds of prey, the data on poisoning that could be gathered from 2006 to 2017, the cases that have come to justice, the activities of the Peregrine group to counter the poisoning and lastly, we place the poisoning in relation to the status of the Peregrine Falcon population in Switzerland in recent years.

The conflict between pigeon fanciers and birds of prey

Pigeons count among the prey items of Peregrine Falcons and other raptors and the birds do not differentiate between wild pigeons and domestic pigeons. Domestic pigeons may even be easier targets because they are less adapted to the life in the wild and may have a lower ability to escape predators.

There are at least two different groups of pigeon fanciers that are concerned by the predation of their pigeons by Peregrine Falcons: the keepers of homing pigeons that are released at a remote place and must travel long distances to their home loft (Riviere 1923) and the keepers of high flyers or tippler pigeons. This second group of pigeons is trained to fly in the air above the loft and to remain airborne in the same place for long hours (Gessaman *et al.* 1991). High flyers and tipplers are very predictable prey items since they are flying in flocks regularly at the same place for several hours. Even if less predictable, homing pigeons are also regularly captured by Peregrine Falcons and other birds of prey. In the case of the high flyers and tippler pigeons, the pigeon fanciers often observe the raptor attacks. In the case of homing pigeons, when the pigeons do not return home, the causes may be multiple and an attack by a bird of prey can generally not be proven.

For pigeon fanciers, it is of course a loss, if their pigeons are injured or killed by birds of prey. They are flying races with them and pigeons that win races and their offspring are worth several thousand dollars (up to $5,000). There may also be high stakes in some races and a Peregrine Falcon attack will interrupt the flight of high flyers or tippler pigeons even without the loss of a pigeon. In such a case, the pigeon fancier will lose his chances to win the race. Some pigeon fanciers give recommendations to deal with Hawks and Falcons: according to Sewall (2017), the golden rules when dealing with raptors are to be flexible and to be unpredictable. It means not to train the pigeons every day at the same hour at the same place in order to get the raptors to move to other hunting grounds. Other pigeon fanciers choose illegal methods: the poisoning or shooting of their enemies. Illegal killing of Peregrine Falcons, especially by pigeon fanciers is one of the known threats for the species in a lot of countries (Olsen & Olsen 1980, Haas 1995, Monneret 2000).

The Peregrine Group, with the help of a Serbian falcon specialist, found out that pigeon keepers, native from South-eastern Europe started a "war" against Peregrine Falcons and other birds of prey in Switzerland and in other countries. They had a blog in Serbian where they explained how to kill the Peregrine Falcons with the help of poisoned pigeons released outside and prevented from returning to the loft. On the blog, they also wrote about numerous successful attempts to kill Peregrine Falcons. A pigeon fancier from the Balkans, resident in Switzerland, who regularly wrote on this blog under a nickname was discovered and controlled by the police. But there was too little evidence for prosecution.

As the following data shows, the problem of poisoning of Peregrine Falcons and other raptors exists in Switzerland and it is mainly, if not entirely due to pigeon fanciers. They are the group exhibiting the greatest conflict with these birds.

Data on poisoning

Between 2006 and 2017, the Peregrine Group listed 7 cases of proven intentional poisoning of birds of prey (5 Peregrine Falcons, 1 Northern Goshawk *Accipiter gentilis*, 1 indeterminate bird of prey) were analyses confirmed the use of poison. Three living decoy pigeons with poison on the neck could be secured before they were captured by the target species.

In 19 cases, 15 Peregrine Falcons, 2 Eurasian Sparrowhawks *(Accipiter nisus)*, 2 Eurasian Buzzards *(Buteo buteo),* the use of poison was not proven, but the deaths are suspicious. In four cases, the raptors were found together with a dead pigeon, in one additional case, the raptor had a pigeon wing feather in the throat. In the other cases, the dead raptors were found at their feeding or breeding places without a visible injury. In three cases the male and female were found dead simultaneously. Since the rising of the awareness through the images taken by the webcam at the breeding site in 2011, analyses are normally made in all suspicious cases, if the carcasses are fresh enough. In cases before 2011, analyses to detect a poison were not usually made. *Table 1* summarizes the cases of sure and suspected intentional poisoning of birds of prey in Switzerland. We do not give indications about the location of the cases because we do not want to give the pigeon fanciers too much clues were they are mainly under control and where it is less the case.

While the numbers of proven and suspected cases are still low, we suspect that the phenomenon may be much more widespread. The detection probability of the poisoned Peregrine Falcons is probably very low.

Table 1. Cases of certain and suspected intentional poisoning of birds of prey in Switzerland from 2006 to 2017

1. táblázat A bizonyított és feltételezett ragadozó madár mérgezések Svájcban 2006 és 2017 között

Year	**Dead raptor species**	**Poison detected**	**Presence of pigeon**	**Comments**
2017	None	Carbofuran	Yes	Decoy pigeon captured alive
2017	None	Carbofuran	Yes	Decoy pigeon captured alive
2017	*Falco peregrinus*	–	Lot of pigeon remains but not entire pigeon	Suspect death of Peregrine on its feeding place. Carcass too old to detect poison
2016	None	Carbofuran	Yes	Decoy pigeon captured alive
2016	Unknown	Carbofuran	Yes	Feeding place with some pigeon feathers with poison. Carcasses were removed
2016	*Falco peregrinus*	–	Yes	Carcasses too old to detect poison
2015	*Accipiter gentilis*	Furadan	Yes	
2015	*Falco peregrinus*	Formetan/ Carbofuran	Yes	
2015	*Falco peregrinus*	Carbofuran	Yes	
2015	*Falco peregrinus*	Carbofuran	Yes	
2015	*Accipiter nisus*	–	Yes	Carcasses too old to detect poison
2015	*Accipiter nisus*	–	–	Carcass not secured
2014	*Falco peregrinus*	Methomyl	Yes	
2014	*Falco peregrinus*	–	–	Suspect death at the breeding place. Carcass too old to detect poison
2014	*Falco peregrinus*	–	–	Blog post that said a peregrine was intentionally killed
2014	*Falco peregrinus*	–	–	Suspect death at the breeding place. Carcass too old to detect poison
2014	*Falco peregrinus*	–	–	Suspect death at the breeding place. Carcass too old to detect poison
2011	*Falco peregrinus*	Methomyl	Yes	Registered by webcam
2010	*Falco peregrinus*	–	–	Suspect death of Peregrine on its feeding place. Carcass too old to detect poison
2010	*Falco peregrinus*	–	–	Suspect death at the breeding place. Carcass too old to detect poison
2009	*Falco peregrinus*	–	Yes	At the breeding place. No analyses made
2009	*Falco peregrinus*	–	Yes	At the breeding place. No analyses made
2009	*Falco peregrinus*	–	–	Suspect death. Carcass too old to detect poison
2009	*Falco peregrinus*	–	–	Suspect death. Carcass too old to detect poison

Year	Dead raptor species	Poison detected	Presence of pigeon	Comments
2009	*Buteo buteo*	–	With a pigeon wing feather in the throat	Suspect death. No analyses made
2008	*Buteo buteo*	–	–	Suspect death. Carcass too old to detect poison
2008	*Falco peregrinus*	–	–	Suspect death at the breeding place. Carcass too old to detect poison
2007	*Falco peregrinus*	–	–	Suspect death. No analyses made
2006	*Falco peregrinus*	–	–	Nest abandoned by adults, one nestling died later with symptoms of poisoning, but no analyses made

Cases that have come to justice

In some regions, Police are actively involved in collecting evidence and in persecuting subjects that poison raptors or try to do so. Thanks to this help, two pigeon fanciers who used poisoned pigeons were convicted in 2016 and 2017. The first pigeon fancier succeeded in killing in 2015 a Northern Goshawk with a decoy pigeon. The dead birds were found in the vicinity of the pigeon loft and the police was called. The poison used could be found in the loft. The pigeon fancier admitted the crime and was condemned to a fine of 4,000 CHF (around $4,000) and a conditional prison sentence of 11 months. He also had to cover the costs of the court of around 10,000 CHF. Before the trial, he was in jail for investigative custody for 5 weeks.

In the second case, a pigeon with coloured feathers and poison on its nape was secured by the police on a loft. The poison used was not found in the loft and the pigeon fancier did not admit the crime. But another illegal poison was found in the loft. This type of poison was used between 2011 and 2014 for several cases of poisoning of Peregrine Falcons in Switzerland. The fact that the pigeon tried to get back to this loft is a strong indication that it belongs to this loft. Accordingly, the court of first instance, as well as the cantonal court (second instance) decided that the pigeon fancier was guilty and condemned him to a fine of 1,500 CHF and a conditional prison sentence of 15 months. He was also condemned to cover the costs of the court of more than 20,000 CHF. Before the trial, he was in jail for investigative custody for 4 weeks. At the time of writing, it is as yet unknown, whether the pigeon fancier will appeal to the Federal Court.

Activities to counter the poisoning

The Peregrine Group that was formed by BirdLife Switzerland after the case filmed by the webcam, has produced a leaflet about the intentional poisoning of Peregrine Falcons and other birds of prey. The leaflet explains the problem, how to recognise suspicious cases and how to react in the case of a dead bird of prey or a probable decoy pigeon. The group is largely diffusing the leaflet to inform the public and the authorities about the topic. With this information, we hope to raise the awareness about the poisoning, to obtain clues of poisonings or the use of decoy pigeons that may lead to more condemnations. We also want to send a message to pigeon fanciers that may consider the use of poison against birds of prey: this is a cowardly, unacceptable behaviour that will be prosecuted by the authorities.

BirdLife Switzerland is also lobbying with authorities for stricter control of currently almost unregulated pigeon breeding. Furthermore, volunteers are surveying suspicious pigeon lofts.

Status of the Peregrine Falcon population in Switzerland and impact of the poisoning

As in many other regions in Europe and North America, the population of the Peregrine Falcon recovered in Switzerland after the collapse between the 1950s and the 1970s. After the turn of the millennium the situation changed: in the South West part of Switzerland, the population decreased 35% between 2008 and 2015, in the Northern Jura Mountains 43% between 2009 and 2015 and 50% in the canton of Zurich between 2002 and 2015 (Kéry *et al.* 2018). As causes for the decline, Kéry *et al.* mention the predation by the Eagle Owl, whose populations are recovering in Switzerland, and the persecutions by humans, i.e. the intentional poisoning. In addition, growing human disturbance at the breeding sites (e.g. through climbers) and collisions with glass, power lines, or other energy infrastructure may also contribute to the population decline.

The few cases of poisoning may seem too sporadic to have an influence on the Peregrine Falcon population. But firstly, we certainly detect only a proportion of cases and secondly as Altwegg *et al.* (2014) and Kéry *et al.* (2018) could show in their publications, given the low numbers of birds composing the population, removing only a few individuals can lead to a critical decline in the population level.

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Raptors are still affected by environmental pollutants: Greenlandic Peregrines will not have normal eggshell thickness until 2034

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Abstract The DDT-induced effects, eggshell thinning and breeding failure in Peregrine Falcon *(Falco peregrinus)* populations were reverted with restrictions on the use of the compound from the 1970s, and in most studied populations, the eggshell thickness is back to normal. In Greenland, a previous study of eggshell thinning in Peregrines found that shells had not yet reached pre-DDT levels. In this study, we extend the time series and reinterpret shell thinning data for 196 clutches covering a 45-year time span (1972–2017). There was a significant (P<0.001) increase in the eggshell thickness of 0.23% per year. This corresponds to a change in eggshell thinning from 14.5% to 5.4% in 2017 compared to the pre-DDT mean. With the current rate of change, pre-DDT shell thickness is predicted to be reached around the year 2034. However, a few clutches are still below the critical limit. The relatively slower recovery of the shell thickness in the Greenland population is likely indicative of the slower phasing out of DDT in the Greenlandic Peregrines' wintering grounds in Latin America. The shell thinning in the Greenlandic population probably never crossed the 17% threshold associated with population declines, contrary to the populations in many other parts of the world.

Keywords: Arctic, Greenland, DDT, pollutants, egg, shell thinning, monitoring

Összefoglalás A DDT okozta hatások, tojáshéj-vékonyodás és költési sikertelenség visszaállítása a vándorsólyom *(Falco peregrinus)* populációiban a szer használatának korlátozásával (betiltásával) az 1970-es évek óta eredményesnek bizonyul, hiszen a legtöbb vizsgált populáció esetében a tojáshéj vastagsága visszaállt a normális szintre. Azonban egy korábbi tanulmány kimutatta, hogy Grönlandon a tojáshéjak vastagsága még nem érte el a DDT-használat előtti időszakra jellemző értékeket. Jelen tanulmányban a vizsgálati időszak kiterjesztésével egy 45 évet átölelő (1972–2017) időszakban igyekszünk a tojáshéj-vékonyodás adatait áttekinteni 196 fészekalj bevonásával. Jelentős növekedés figyelhető meg (P<0,001) a héjak vastagságában, ami körülbelül 0,23%-os változást jelent évente. Ez az érték megfelel a tojáshéjak vékonyodásában mutatkozó változásnak, hiszen 2017-re 14,5%-ról 5,4%-ra változott a DDT használat előtti időszak átlagához viszonyítva. Ekkora mértékű változás hatására 2034-re a tojáshéjak vastagsága elérheti a normál értéket. Azonban néhány fészekalj továbbra is a kritikus érték alatt van. A tojáshéj vastagságának lassú helyreállítódása valószínűleg a grönlandi vándorsólymok dél-amerikai telelőterületein kimutatható hatásoknak köszönhető, ahol a DDT viszonylag lassan tűnik el. A héjvékonyodás mértéke a grönlandi populációban valószínűleg soha nem érte el a kritikus, 17%-os tűréshatárt, amely határ összefüggésben lehet a vándorsólyom populációk világméretű csökkenésével.

Kulcsszavak: sarkvidék, Grönland, DDT, szennyezőanyagok, tojás, héjvékonyodás, monitorozás

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Introduction

Ever since it was first shown that the insecticide DDT caused eggshell thinning and breeding failure in wild Peregrine Falcon *(Falco peregrinus)* populations (Ratcliffe 1970) the effects of persistent organic pollutants (POPs) on the eggshell thickness and breeding success in high-trophic level birds have been widely documented. Especially DDT and its degradation products have been identified as a key group of POPs responsible for the widespread reduction in breeding success and subsequent population decline in the Peregrine Falcon in large parts of its distribution area (Hickey 1969, Cade *et al*. 1988) and in other top predators (e.g. Newton, 1979). The top predators turned out to be sensitive indicators of certain environmental pollutants and the discoveries of those side effects of pesticide usage led to the phasing out of DDT and subsequently a global ban on the use (except for restricted disease vector control) with the 2001 UN Stockholm Convention on Persistent Organic Pollutants taking effect in 2004 (UNEP 2009).

Over the past 40 years Peregrine (and other top predator) populations have recovered from the setback caused by the most harmful pollutants. But the top predators still serve as indicators of the pollutant level and in the case of DDT it was not until early in this millennium – 30 years after the ban in Europe – that eggshell thickness in German Peregrines and Swedish Ospreys *(Pandion haliaetus)* were back to normal (pre-DDT) levels (Wegner *et al*. 2005, Odsjö & Sondell 2014). In Greenland the shell-thinning in Peregrines has been much slower to recover (Falk & Møller 1990, Falk *et al*. 2006, Vorkamp *et al*. 2017), suggesting a slower change rate of DDT in the Greenlandic Peregrines' environment – from the Arctic breeding grounds to wintering areas in Latin America (see mapping of wintering grounds in Vorkamp *et al*. 2017) – compared to northern Europe.

In this study we extend the time series for eggshell measurements and reinterpret data for a 45-year time span (1972–2017) for the Greenlandic Peregrines *(F. p. tundrius)*.

Material and Methods

Samples

The Greenland Peregrine Falcon population has been the subject of long-term studies since the 1970s (Burnham & Mattox 1984, Falk & Møller 1988, 2018, Mattox & Seegar 1988), which have provided samples of eggshells over decades. This study combines samples from two study areas: West Greenland (samples from 1972–1988) and South Greenland (samples from 1981–2017).

Active nests were visited at least once post-hatching and the nest scrape carefully searched for eggshell fragments deriving from the hatched eggs. In addition, shells from whole dead eggs sampled and analysed for contaminants (Vorkamp *et al*. 2017, Vorkamp *et al*. 2018) were included in this analysis. Egg clutches from Greenland Peregrines collected between 1881 and 1930 (before DDT was introduced) stored at the Zoological Museum, University of Copenhagen, were used as the reference for normal eggshell thickness in the pre-DDT era (Falk & Møller 1990), so the total samples available cover a 136 year time span.

Measurements and statistical analyses

The eggshell thickness was determined as in previous studies (Falk *et al*. 2006, Vorkamp *et al.* 2017), in summary:

The shell fragments were measured with a computer-connected Mitutoyo Digital Micrometer (type 293-521-30) with a small stainless steel ball glued to the rotating jaw in order to fit the inner curved surface of the eggshell fragments. Measurements were performed only on (parts of) fragments without any membrane. We included only clutches that provided 20 or more measurable fragments, assuming they represent the thickness of the entire clutch (cf. Odsjö & Sondell 1982).

Whole, addled eggs were opened in the laboratory and the content removed for the contaminant analyses; the eggs were cut along the equator and the empty half shells washed with water before left to dry for 3 months at room temperature before measurements were taken along the equator cut line.

In this analysis, mean shell thickness was estimated for 196 clutches providing at least 20 fragments, and for 56 whole addled eggs from 44 clutches (a total of > 6600 measurements). From 19 clutches samples from both fragments and whole eggs were available; a paired t-test showed no significant difference ($t = 0.38$, $p = 0.71$) between those two sub-samples, thus data from fragments and whole eggs were combined for analysis. When comparing measurements with and without membranes, a membrane factor of 0.071 mm was applied, based on measurements of neighbouring shell areas with and without membranes (Falk *et al*. 2006).

For the analyses of the temporal trend, the mean annual shell thickness was analysed by log-linear regression analysis (AMAP 2016, Rigét *et al.* 2016) using the free software R version 3.13 (R Core Team 2015).

Results and Discussion

Over the 45-year time span 1972–2017 there was a significant increasing trend in the average eggshell thickness ($P < 0.001$). The slope of the linear regression shows an average increase of 0.23% per year, corresponding to a change in eggshell thinning from 14.5% in 1972 to 5.4% in 2017 when compared to pre-DDT eggs; these values are a slight adjustment to earlier estimates (Falk *et al*. 2006, Vorkamp *et al*. 2017). Shell thickness may continue to increase and level out when normal, pre-DDT average (0.336 mm) will be reached; based on the current rate of change it is predicted to be in 2034. However, the 95% confidence limit on the predicted value (black dotted lines) indicates that the year for the eggshell to obtain unaffected thickness can also be earlier or much later. A few clutches are still below the critical limit, as indicated by the red dashed line in *Figure 1*.

Some studies suggest that embryo development may affect shell density and/or thickness (Ratcliffe 1970, Bunck *et al*. 1985, Bennett 1995, Castilla *et al*. 2010) and shell thickness varies across different parts of the shell. The potential error introduced by those factors might slightly influence the reported *value* of the shell thickness in Greenlandic Peregrine Falcons and, hence, the predicted timing of full recovery. But since it is a random error across the years and the same methods have been applied over the entire 45-year study period, the *trend* remains unaffected. The empirical threshold for shell thinning causing negative population effects is around 17% (Peakall & Kiff 1988). As discussed by Falk *et al*. (2006), the shell thinning in the Greenlandic Peregrine population was probably near or below that

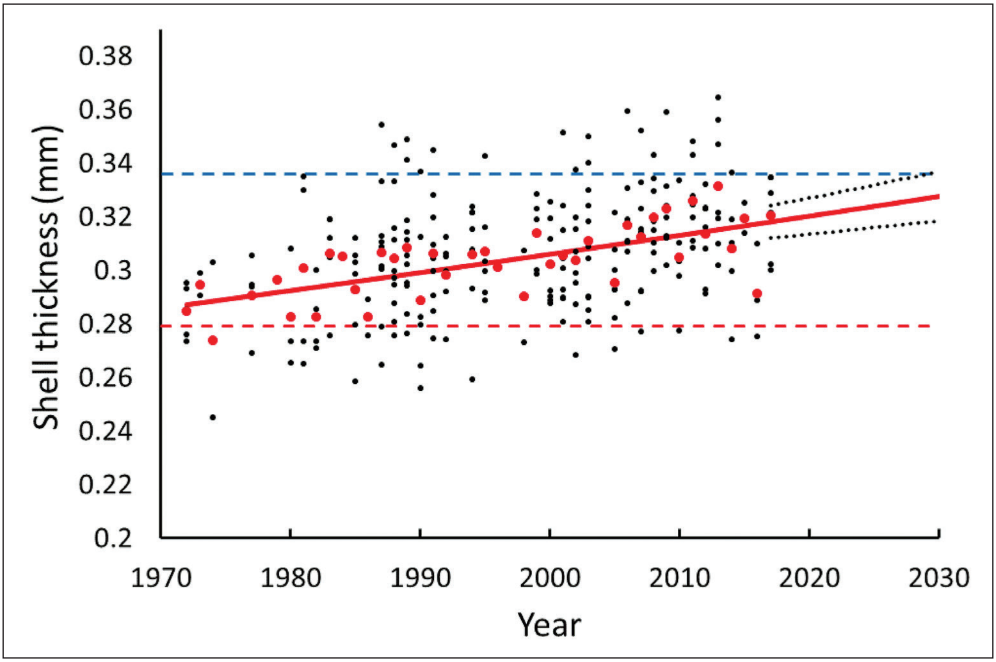

Figure 1. Shell thickness of Peregrine Falcons eggs from Greenland shown as clutch means (black symbols), annual means (red symbols) and projected trend line (red) with confidence limits (black dottet lines) for projections according to which the mean shell thickness may reach pre-DDT normal thickness in 2034 (0.336 mm, blue line, Falk & Møller 1990, Falk *et al*. 2006). The red dashed line indicates the empirical "17% threshold" (0.279 mm) associated with population declines across the world (Peakall & Kiff 1988)

1. ábra A grönlandi vándorsólyom tojások héjvastagsága a fészekaljak átlagában (fekete jelek), évenkénti átlag (vörös jelek) és a változás becsült mintája (vörös vonal) a megbízhatósági határértékekkel (fekete szaggatott vonalak), miszerint az átlagos héjvastagság 2034-re éri el újra a DDT-használat előtti időszakra jellemző értékeket (0,336 mm, kék vonal, Falk & Møller 1990, Falk *et al*. 2006). A szaggatott vörös vonal jelöli a 17%-os tűréshatárt (0,279 mm), amivel a világ vándorsólyom populációinak csökkenését hozták összefüggésbe (Peakall & Kiff 1988) critical limit only for a very short time span, if ever, and avoided the population crash that effected many other populations.

In Germany, Peregrine Falcon shell thinning was back to normal 30 years after the legal ban of DDT in 1972 (Wegner *et al*. 2005). Similarly, a long term study of shell thinning in Swedish ospreys showed that it took 30 years to reach full thickness again after the lowest level in 1973; from the beginning of the decrease it took more than 50 years to reach unaffected conditions (Odsjö & Sondell 2014). Hence, the much slower recovery of the shell thickness in the Greenland Peregrine population in this study might be indicative of the slower phasing out of DDT in the Americas (Vorkamp *et al*. 2009).

The continued change in exposure to DDT and its metabolites in the areas the Peregrines inhabit during their annual cycle can be monitored by continued low-cost collection of eggshell material. Although the Peregrine populations around the world are recovering from the pesticide-related population collapse, they continue to be important indicator species for environmental contaminants.

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A 20-year study investigating the diet of Peregrines, *Falco peregrinus*, at an urban site in south-west England (1997–2017)

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Abstract Until relatively recently Peregrines have been regarded as a rural bird. As their populations have increased over the past 20 years, Peregrines have increasingly become urban birds. One of the earliest locations to be occupied by Peregrines in the UK was on a church in Exeter, in the county of Devon. Over the past 20 years we have studied their diet, collecting prey remains on a regular basis. The results reveal that Feral Pigeons *Columba livia* comprise one third of the diet by frequency and just over half of the diet when measured by mass. The remainder of the diet comprises a wealth of other species including wading birds, other doves and pigeons, ducks, gulls and terns, and rails. A selection of species eaten by the Peregrines reveal that they are hunting at night, taking certain wading birds, rails and grebes, that would be difficult to catch by day and are known to migrate at night. This study is the most comprehensive to date and reveals that while the Feral Pigeon is an important part of the diet, contrary to public opinion, it is by no means the only species that Peregrines eat. In fact, the remaining half of the diet, by mass, comprised 101 other species of bird and three species of mammal. Such dietary studies help dispel myths about peregrines feeding habits and ensure that their conservation and protection is based on evidence.

Keywords: prey, food, nocturnal, hunting, church

Összefoglalás A vándorsólymot egészen mostanáig egy városokon kívül élő fajnak tekintették. Az elmúlt 20 évben, ahogy a vándorsólyom állományok növekedtek, egyre inkább városi madárrá vált. Az Egyesült Királyságban az egyik első városi költőhely, amit vándorsólymok foglaltak el, a Devon megyei Exeterben, egy templomon volt. Az elmúlt 20 évben tanulmányoztuk a táplálkozásukat rendszeres táplálékmaradvány gyűjtéssel. Az eredmények azt mutatják, hogy táplálékuk egyharmadát parlagi galambok teszik ki, ha a tömegét tekintjük, akkor annak valamivel több, mint felét. A táplálék többi része különböző fajok nagy változatosságából áll, többek között partimadarakból, más galambokból és gerlékből, sirályokból és csérekből, valamint guvatfélékből. A vándorsólymok által fogyasztott fajok egy része azt mutatja, hogy a vándorsólymok éjszaka is vadásznak, mivel olyan fajokat, pl. partimadarakat, guvatféléket és vöcsköket zsákmányolnak, amelyeket nappal nagyon nehéz lenne elfogniuk, és amelyek éjszaka vonulnak. Ez a tanulmány eddig a legátfogóbb, és kimutatja, hogy a parlagi galambok a sólymok táplálékának ugyan jelentős részét teszik ki, de a közhiedelemmel ellentétben messze nem az egyetlen táplálék, amit fogyasztanak. Valójában a táplálékuk másik részét 101 különböző madárfaj és három emlősfaj adja. Az ilyen táplálékvizsgálatok segíthetnek eloszlatni a vándorsólymok táplálkozási szokásairól terjedő téveszméket és biztosítani, hogy védelmük és megőrzésük tényeken alapuljon.

Kulcsszavak: zsákmány, táplálék, éjszakai vadászat, templom

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Introduction

In the late 1990s Peregrines, *Falco peregrinus*, were just beginning to appear in towns and cities in southern England. Two decades later, in 2014, 1,769 pairs were recorded across the UK. Out of these approximately 211 pairs now breed on man-made structures, with many currently populating city centres (Wilson *et al.* 2018, pers. com.). One of the earliest cities to be occupied was Exeter in Devon, where Peregrines tenanted St. Michael's Church, Mount Dinham. This is very close to the city centre and 6 km from where the River Exe begins to open out in the Exe Estuary.

Urban sites such as St. Michael's Church have had different Peregrines in residence over a 20-year period. During this time there has been a growing interest and commitment by individuals, groups and organisations to observe and share with the general public the comings and goings of Peregrines that may be nesting in their local city centre. The Exeter Peregrines have been watched by a worldwide audience, following the installation of a camera to watch the nest by the wildlife surveillance company, Eco-watch Ltd; this was in use between 2001 and 2007. They have also been part of the Royal Society for the Protection of Birds' (RSPB) 'Aren't Birds Brilliant' Campaign between 2005 and 2008.

Urban nesting Peregrines provide a unique chance to study different aspects of their lives and behaviour in close detail, and, in particular, their diet. When they bring prey back to buildings, fallen remains end up on the ground, on the roofs and in the gutters (Drewitt & Dixon 2008). This provides an opportunity – not generally available at traditional cliff nest sites – to regularly collect remains all year round with no disturbance to the Peregrines to determine prey selection and diet. Nick Dixon has been collecting prey remains since June 1997 at St. Michael's, and has been investigating the diet of the Peregrines, with the help of Ed Drewitt. This study covers the period 1997 to 2017, and is the largest single-site study of prey by Peregrines in the world.

The study of the diet of any animal gives researchers the potential to find out what that species is eating and what is important for their survival. While peregrines are mainly generalist avian feeders, there are patterns to their diet. Discovering what Peregrines eat, and how their diet changes throughout a year and over a longer period, is important for the species' conservation. It gives us a better understanding of how they fit into the ecology of our rural and urban landscapes. While the Peregrine has been increasing in urban areas across England, there have been declines across the UK, particularly in northern England and Scotland (Wilson *et al.* 2018). Therefore, knowing what Peregrines are feeding on is an important part of understanding what may be affecting population numbers in certain regions.

A brief history of the peregrines at St. Michael's Church

Peregrines have been associated with St. Michael and All Angels Church at Mount Dinham in Exeter City Centre since July 1988, when a second summer male first took up residence. He was joined by an adult female in the spring of 1989 and the pair was regularly observed hunting over the city, feeding and perching on the many stone pinnacles on the church tower.

The Devon Bird Watching & Preservation Society (DBWPS) installed a nest box. However, the falcons were never observed entering it. The pair dispersed in late 1990, but other single Peregrines were occasionally recorded up until 1992. This behaviour is typical of Peregrines and how they colonise urban areas over time (the pattern of urbanisation) (Taranto 2009). No Peregrines were recorded at the church from 1993 until 1997.

A pair of Ravens *Corvus corax* had previously been nesting in tall cedar trees to the west of the church and, in 1997, built a stick nest on an 45cm wide east-facing ledge at the base of the spire, about 30m above ground level. It is not known if the Ravens used the nest. However, a new pair of Peregrines took up residence in early April, laid eggs and successfully reared three young, in what was the first record of urban nesting on a man-made structure in Devon.

During the following winter, the lightning conductor, upon which the Ravens had constructed their nest, had to be replaced. The stick nest was in poor condition, having been flattened by the three juvenile Peregrines during their development, and subsequently fell apart and was removed. During the works, DBWPS replaced it with a purpose-built shallow tray containing loose substrate, with sticks wired around the exterior to replicate the original nest. The falcons immediately took to the new nest tray, and in 1998 they again fledged three young and continued to use this site over the following years.

In 2001, the wildlife surveillance company Eco-Watch Ltd. designed and installed a camera to film the birds at the nest, enabling all to watch the developments via the Worldwide Web. The RSPB, Devon Wildlife Trust and Exeter City Council also ran guided watches for the public from a tall car park overlooking St. Michael's Church during many of the breeding seasons.

In 2008, the camera became obsolete when a new female arrived and opted to use the original nest box erected in 1989 on the southern face. This new site required the falcons to enter a wide stone trefoil, 2 m above the south-facing ledge, to access an internally mounted nest box set within the bell chamber.

A new web camera was installed prior to the breeding season in 2013 by Jason Fathers, of 'Wildlife Windows', a wildlife surveillance company. Jason has also ringed the juvenile peregrines in the south face nest since 2013.

The peregrines at St. Michael's Church have bred every year since 1997, rearing 57 young over the period, with all but two successfully fledging into the wild. In 1997, one juvenile came down to the ground prior to fledging and was taken into care by a rehabilitator and later reported as released into the wild. In 2008, a newly fledged female became entangled in anti-bird netting on a nearby roof, damaging its wing and many primary feathers. This bird was also taken into care and subsequently released into the wild after she had moulted into her adult plumage and been trained into peak fitness for hunting (Dixon 2017).

Materials and methods

When feeding, Peregrines leave behind lots of evidence of what they have been eating. Feathers, wings, beaks, heads, legs, and whole or partially eaten corpses are dropped or left on and around the structures where Peregrines reside.

Over the past 20 years, prey remains have been collected at least once a week from the ground beneath St. Michael's Church by Nick Dixon. Collections have also been undertaken from Exeter Cathedral and another church within the city from 2006, with careful comparisons of dates and species caught, so that the same individual prey items remains are not counted twice. Sometimes prey may be plucked at one site and then taken to another site to be eaten.

Since 2009, local residents have been helping to collect feathers and, also in 2009, an MSc student from the University of Exeter, Lin Chen Yu, undertook daily collections for three months as part of a more detailed study (Chen Yu 2009). This close scrutiny retrieved dropped or discarded material, including whole or part carcasses, feathers, heads/skulls, wings, legs, rings and pellets (Oro & Tella 1995, López-López *et al.* 2009). While pellets have been collected, they usually reveal just powdery pigeon feathers and little else; sometimes a bird ring.

Every autumn, the gutters have been cleared by steeplejacks and the remains from this – mainly skulls and carcases – have been dried and identified. Searching for remains on the ground requires a thorough scan close to the church and up to 20m away to find feathers that have been blown down paths and alleys. A wider search, up to 50m from the roost/nest site, is carried out after strong winds. While every effort is made to collect as much prey as possible, many remains may be lost to the wind, scavengers and street cleaning. Some prey items such as the larger prey captures may be eaten away from the church and not carried back to be stored or eaten.

Remains were dried after each collection and bagged for subsequent analysis. Prey species were identified from experience and with the help of reference material. These included:

- Jenni & Winkler 1994
- Brown *et al.* 2003
- Dutch feather website, michelklemann.nl/verensite/start/index.html
- The online library for bird feathers, featherbase.info

Occasionally, items were confirmed by comparison with museum specimens, either at the Natural History Museum (Tring) or at Bristol's City Museum & Art Gallery. Average weights were taken from Snow and Perrins (1998).

The similar species Common Tern *Sterna hirundo* and Arctic Tern *Sterna paradisea*, and Common Chiffchaff *Phylloscopus collybita* and Willow Warbler *Phylloscopus trochilus*, have been grouped together. This is because key distinguishing feathers, such as the outer primary feathers in the terns and the outer wings of the warblers, were missing and/or earlier identifications of remains was done without knowledge of distinguishing features. Therefore, in the early years, prey remains could have been from either of the two species in each pair. The books by Svensson (2005), Baker (2016) and Demongin (2016), have since helped with identifying all four species more accurately where the feathers/wings allow.

Some prey is cached by Peregrines and eaten over a period of time, so that the remains of individual items were sometimes found over a number of days. The minimum number of individual prey items was established by checking, for example, for duplication of the same wing feathers or legs as well as for feathers from birds of a different age or sex class. Feather condition and weather-related damage was important in assessments of how fresh the remains were.

Results

During the past 20 years 5, 426 remains of 102 species of bird and three species of mammal have been found and identified. *Figure 1* (by frequency) and *Figure 2* (by biomass) summarise the main groups of prey taken by the peregrines. Feral Pigeon includes just *Columba livia* while doves and pigeons include common Wood Pigeon *Columba palumbus*, Eurasian Collared Dove *Streptopelia decaocto*, European Turtle Dove *Streptopelia turtur* and Stock Dove *Columba oenas*.

Within the passerines, the top species to be eaten in the Common Blackbird *Turdus merula* (5.18% by frequency and 2.76% by biomass), followed by Redwing *Turdus iliacus* (4.68% and 1.52%) and the Common Starling *Sturnus vulgaris* (9.31% and 3.63%). Within the waders, Common Snipe *Gallinago gallinago* was the most common prey item (2.82% and 1.61%), followed by European Golden Plover *Pluvialis apricaria* (1.36% and 1.56%), Eurasian Woodcock *Scolopax rusticola* (1.22% and 1.90%) and Northern Lapwing *Vanellus vanellus* (1.11% and 1.32%). See *Appendix 1* for all species and totals taken during this 20-year period.

Regular (often annual) yet unusual prey includes nocturnal migrants such as Spotted Crake *Porzana porzana* and Corn Crake *Crex crex*, and other species such as Common Cuckoo *Cuculus canorus*, Pied Avocet *Recurvirostra avosetta* and Common Kingfisher *Alcedo atthis*.

Discussion

These preliminary descriptive results of our 20-year study reveal a huge breadth in the diet of the urban Peregrine at one location. Through personal communications with other Peregrine workers across the UK, the results from our study appear to reflect what urban Peregrines at other sites are also eating. Certainly, our comparison with data from the cities of Bath and Bristol also showed this (Drewitt & Dixon 2008).

The results also reveal more about what many of the prey species are doing, for example, that rare Corncrakes, Spotted Crakes and Turtle Doves are passing over this part of England. The study builds further on our paper published after 15-years in the Devon Bird Report (Drewitt & Dixon 2012), where we discuss nocturnal birds, Feral Pigeons, estuary birds and scarce species, in more detail.

Our findings at St. Michael's Church in Devon contributed towards the theory that Peregrines hunt at night in the UK, later confirmed by web camera footage from Derby cathedral, England (Drewitt 2008). Since then many sites across the UK and other parts of Europe have discovered a range of nocturnally migrating species that are most likely to be caught at night (per. comms. with various peregrine workers). Night-hunting has also been recorded in many other parts of the world (Drewitt & Dixon 2008, Drewitt 2014). These suggest night hunting is happening on a wide scale, and is often supported by web camera recordings at night where prey is still obviously still alive when it is brought in. Night feeding of young has also been recorded in Poland and the UK, and may be more widespread (Rejt 2004, Kettle *et al.* 2016). Our 20-year study and beyond, continues to develop this remarkable story and reveal how adaptable the Peregrine is.

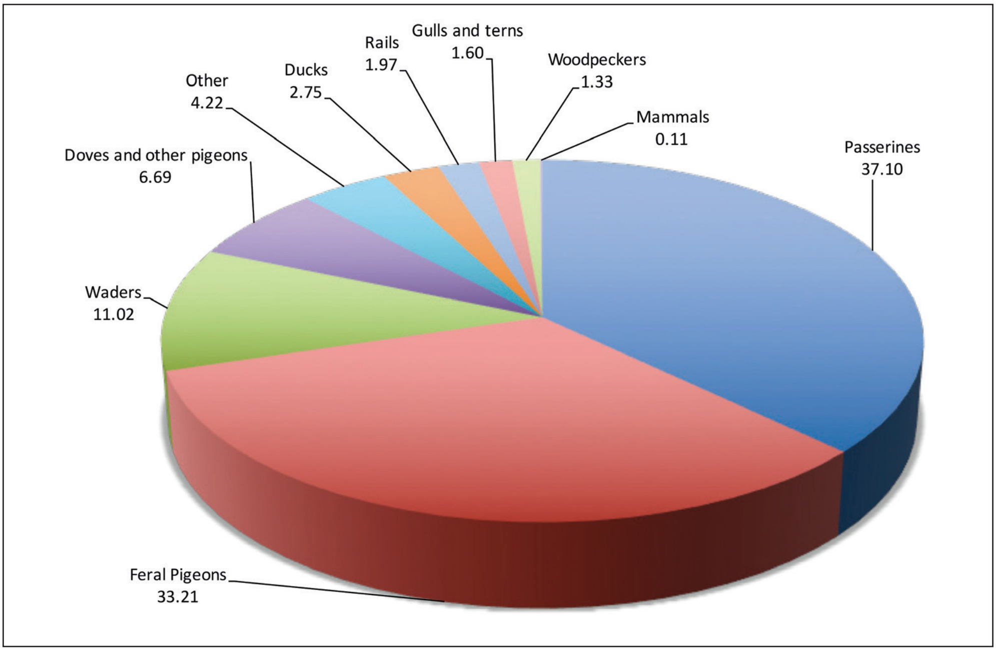

Figure 1. Frequency of prey taken by urban Peregrines in Exeter, England, 1997–2017 (n = 5,426)
1. ábra A városi vándorsólymok prédáinak gyakorisága – Exeter, Anglia, 1997–2017 (n = 5426)

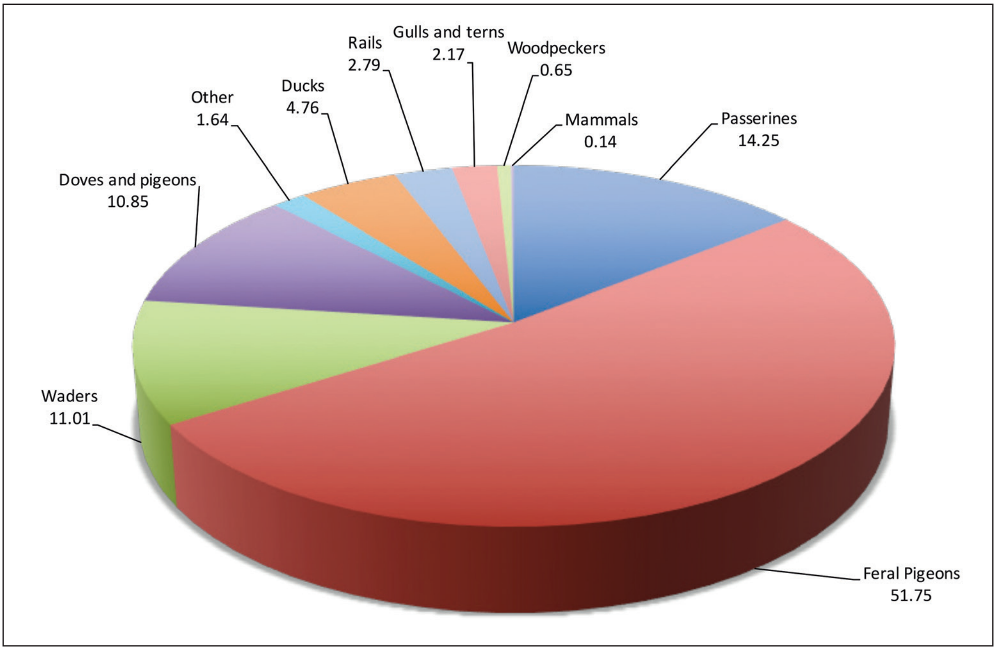

Figure 2. Prey (by biomass) taken by urban Peregrines in Exeter, England, 1997–2017 (n = 5,426)
2. ábra A városi vándorsólymok prédái (biomassza szerint) – Exeter, Anglia, 1997–2017 (n = 5426)

Next steps

In 2018–2019 Ed Drewitt will be studying this comprehensive diet work in more detail, using detailed statistics to look at the diversity of prey across time and whether there are significant differences in prey throughout the year and comparing with other sites such as Bath and Bristol, in the west of England. This will also compliment Ed's 10-year study on the movements of Peregrines and natal dispersal using colour rings.

Conclusion

The Exeter Peregrines have provided us with the largest single site study of the prey of this species in the world, in both longevity and sample size. The results provide an insight not only into what the Peregrines themselves are eating but also into the bird species that are occurring locally around Exeter. We will continue to collect prey remains from this site until we have data for a 25 years period and meanwhile, Ed will be analysing the current results in more detail.

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Appendix 1. Prey species identified from remains at St. Michael’s Church, Exeter, Devon, 1997–2017. Average weights taken from Snow & Perrins (1998)

1. melléklet A Szent Mihály templomban talált táplálék-maradványok alapján azonosított prédafajok – Exeter, Devon, 1997–2017. Átlag tömegek Snow & Perrins (1998) alapján számolva

Name	n	%	Unit mass (g)	Total biomass (g)	% biomass
Mareca stepera	1	0.02	775	775	0.07
Mareca penelope	1	0.02	750	750	0.07
Anas crecca	146	2.69	325	47450	4.54
Aythya fuligula	1	0.02	750	750	0.07
Coturnix coturnix	12	0.22	105	1260	0.12
Oceanodroma leucorhoa	1	0.02	45	45	0.004
Puffinus puffinus	1	0.02	417	417	0.04
Tachybaptus ruficollis	21	0.39	161.5	3391.5	0.32
Accipiter nisus	5	0.09	226	1130	0.11
Rallus aquaticus	23	0.42	130	2990	0.29
Crex crex	9	0.17	160	1440	0.14
Porzana porzana	2	0.04	90	180	0.02
Gallinula chloropus	72	1.33	330	23760	2.27
Fulica atra	1	0.02	800	800	0.08
Haematopus ostralegus	10	0.18	540	5400	0.52
Recurvirostra avosetta	8	0.15	275	2200	0.21
Vanellus vanellus	60	1.11	230	13800	1.32
Pluvialis apricaria	74	1.36	220	16280	1.56
Pluvialis squatarola	1	0.02	235	235	0.02
Charadrius hiaticula	22	0.41	64	1408	0.13
Numenius phaeopus	18	0.33	480	8640	0.83
Numenius arquata	1	0.02	920	920	0.09
Limosa lapponica	9	0.17	340	3060	0.29

Name	n	%	Unit mass (g)	Total biomass (g)	% biomass
Limosa limosa	46	0.85	320	14720	1.41
Arenaria interpres	2	0.04	117.5	235	0.02
Calidris canutus	17	0.31	135	2295	0.22
Calidris alba	5	0.09	57	285	0.03
Calidris alpina	47	0.87	47.5	2232.5	0.21
Scolopax rusticola	66	1.22	300	19800	1.90
Lymnocryptes minimus	6	0.11	70.5	423	0.04
Gallinago gallinago	153	2.82	110	16830	1.61
Actitis hypoleucos	2	0.04	55	110	0.01
Tringa ochropus	4	0.07	86	344	0.03
Tringa totanus	36	0.66	117.5	4230	0.2
Tringa nebularia	4	0.07	200	800	0.08
Chroicocephalus ridibundus	39	0.72	300	11700	1.12
Larus argentatus	4	0.07	974	3896	0.37
Thalasseus sandvicensis	13	0.24	245	3185	0.3
Sternula albifrons	1	0.02	56	56	0.01
Sterna dougallii	2	0.04	112.5	225	0.02
Sterna hirundo/S. paradisea	28	0.52	237.5	3572.5	0.34
Columbia livia	1802	33.21	300	540600	51.75
Columba oenas	4	0.07	300	1200	0.11
Columba palumbus	161	2.97	449	72289	6.92
Streptopelia turtur	12	0.22	140	1680	0.16
Streptopelia decaocto	186	3.43	205	38130	3.65
Cuculus canorus	17	0.31	117.5	1997.5	0.19
Athene noctua	4	0.07	180	720	0.07
Apus apus	126	2.32	43.5	5481	0.52
Alcedo atthis	11	0.20	40	440	0.04
Dendrocopos major	65	1.20	85	5525	0.53
Picus viridis	7	0.13	185	1295	0.12
Falco tinnunculus	1	0.02	204	204	0.02
Garrulus glandarius	27	0.50	165	4455	0.43
Pica pica	49	0.90	227	11123	43106.00
Coloeus monedula	54	1.00	220	11880	43114.00
Corvus frugilegus	1	0.02	310	310	0.03
Corvus corone	8	0.15	510	4080	0.39
Corvus corax	1	0.02	657.5	657.5	0.06
Cyanistes caeruleus	19	0.35	11	209	0.02
Parus major	21	0.39	18	378	0.04

Name	n	%	Unit mass (g)	Total biomass (g)	% biomass
Alauda arvensis	25	0.46	38	950	0.09
Riparia riparia	2	0.04	13.5	27	0.002
Hirundo rustica	6	0.11	19	114	0.001
Delichon urbicum	11	0.20	19	209	0.02
Phylloscopus collybita/ Ph.trochilus	4	0.07	9	36	0.003
Acrocephalus shoenobaenus	1	0.02	9	9	0.0008
Sylvia atricapilla	13	0.24	23.5	305.5	0.03
Sylvia communis	2	0.04	19	38	0.003
Regulus regulus	1	0.02	5.75	5.75	0.0005
Troglodytes troglodytes	1	0.02	9.5	9.5	0.0009
Sitta europaea	1	0.02	22.5	22.5	0.002
Sturnus vulgaris	505	9.31	75	37875	3.63
Turdus merula	281	5.18	102.5	28802.5	2.76
Turdus pilaris	90	1.66	100	9000	0.86
Turdus philomelos	76	1.40	82.5	6270	0.6
Turdus iliacis	254	4.68	62.5	15875	1.52
Turdus viscivorus	22	0.41	125	2750	0.26
Muscicapa striata	2	0.04	17	34	0.003
Erithacus rubecula	10	0.18	17.5	175	0.02
Oenanthe oenanthe	8	0.15	23.5	188	0.02
Cinclus cinclus	4	0.07	66.5	266	0.03
Passer domesticus	112	2.06	31	3472	0.33
Prunella modularis	20	0.37	20.50	410	0.04
Motacilla cinerea	1	0.02	18	18	0.001
Motacilla alba	59	1.09	21	1239	0.12
Anthus pratensis	19	0.35	18.5	351.5	0.03
Fringilla coelebs	92	1.70	23.5	2162	0.21
Fringilla montifringilla	3	0.06	23.5	70.5	0.01
Pyrrhula pyrrhula	9	0.17	21	189	0.02
Chloris chloris	114	2.10	28.5	3249	0.31
Linaria cannabina	3	0.06	18.5	55.5	0.01
Acanthis caberet	1	0.02	10.5	10.5	0.001
Carduelis carduelis	59	1.09	16.5	973.5	0.090
Serinus canaria	1	0.02	28	28	0.002
Spinus spinus	4	0.07	14.5	58	0.01
Emberiza citrinella	2	0.04	30.5	61	0.01
Emberiza schoeniclus	4	0.07	20.5	82	0.01

Name	n	%	Unit mass (g)	Total biomass (g)	% biomass
Feral or escaped cagebirds					
Psittacula krameri	3	0.06	117.5	352.5	0.03
Nymphicus hollandicus	15	0.28	90	1350	0.13
Melopsittacus undulates	11	0.2	28	308	0.03
Unidentified birds					
Unidentified cage bird	1	0.02	28	28	0.002
Unidentified wader	7	0.13	110	770	0.07
Unidentified passerine	11	0.2	32	352	0.03
Mammals					
Sciurus carolinensis	1	0.02	550	550	0.05
Rattus norvegicus	2	0.04	397.5	795	0.08
Nyctalus noctula	3	0.06	29.5	88.5	0.01
TOTAL	**5426**	**100.00**			**100.00**

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Diet of Peregrine Falcons *(Falco peregrinus)* in relation to temporal and spatial variation in racing pigeon availability in Wales

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Abstract The relative frequency of Common Pigeons *Columba livia* in the diet of Peregrine Falcons differed across three areas of south-central Wales in line with racing pigeon availability. Peregrines exhibited a functional response to spatial and temporal availability of racing pigeons. During the pigeon-racing season (April–September), pigeons comprised 63% of kills in South Wales where pigeons were most available, 43% in the Brecon Beacons with intermediate availability and 30% in Central Wales, where availability was lowest. The corresponding values outside the pigeon-racing season were 18%, 6% and 5% respectively. We estimate that 92% of pigeons killed by Peregrines were racing pigeons, 7% were feral pigeons and the remainder were other domestic pigeon varieties.

Keywords: *Columba livia*, predator-prey, functional response, human-wildlife conflict

Összefoglalás A vándorsólyom étrendjében három dél-közép-walesi területen eltérést mutat a parlagi/házi galamb *Columba livia* hozzávetőleges gyakorisága, összefüggésben a galambászok által tenyésztett példányok elérhetőségével. A vándorsólymok funkcionális választ mutatnak az ilyen galambok térbeli és időbeli elérhetőségére. A galamb-versenyek időszakában (április-szeptember) Dél-Walesben, ahol a versenyekre tenyésztett galambok száma a legmagasabb, az elejtett prédák 63%-a volt galamb, Brecon Beacons térségében 43%, míg ahol a legkevesebb ilyen galamb volt (Közép-Wales), csupán 30% volt ez az arány. Ugyanezen területeken a versenyidőszakon kívül az arányok 18%, 6% és 5% körül alakultak. Felméréseink alapján elmondható, hogy az elejtett galambok 92%-át versenyekre tenyésztették, 7%-a vadon élő volt, a többi pedig más, háziasított formákból származott.

Kulcsszavak: *Columba livia*, ragadozó-préda, funkcionális válasz, ember és vadon élő állatok közti konfliktus

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Introduction

In the United Kingdom, Common Pigeons *Columba livia* comprise a significant proportion of the Peregrine diet in many regions (Ratcliffe 1993, Drewitt & Dixon 2008). Ratcliffe (1993) proposed that high Peregrine breeding densities found in Snowdonia, Lakeland and Galloway reflected the large, but seasonal supply of racing pigeons that pass through these areas. In South Wales, it has been suggested that Peregrines are largely dependent on racing pigeons for successful breeding (Richards & Shrubb 1999). Euphemistically described as ‘domestic’ or ‘feral’, the pigeons killed by Peregrines comprise mostly racing pigeons (Dixon & Richards 2003, Dixon *et al.* 2003, Parrott *et al.* 2008), to the extent that changes in racing pigeon availability is considered a causal factor of Peregrine population changes in some UK regions (Dixon *et al.* 2010, Wilson *et al.* 2018). While the influence of racing pigeons on Peregrine ecology is of interest to ornithologists, the potential impact of Peregrine predation on racing pigeons is of concern to pigeon racing enthusiasts (Scottish Homing Union 1998), creating a human-wildlife conflict (Shawyer *et al.* 2000, Dixon 2002, Henderson *et al.* 2004).

Common Pigeons exist in various forms and most studies on the diet of Peregrines do not distinguish between them. There is the ‘wild-type’, the Rock Dove, which has a very restricted range in Britain as a result of inter-breeding with domesticated varieties (Gibbons *et al.* 1993). Rock Doves have largely been replaced by ‘feral pigeons’, most of which are wild-bred rather than captive-bred pigeons living a feral existence (Shawyer *et al.* 2000). Feral pigeons have a predominantly coastal and urban distribution, though there is some evidence of an expansion into rural arable areas (Gibbons *et al.* 1993). Captive-bred varieties of Common Pigeon, can often be identified by leg-rings and are kept as decorative pets in dovecotes or as sporting pigeons in the form of racers, show-pigeons, tipplers and rollers; the most abundant of these various ‘domestic pigeons’ is the racing pigeon. Racing pigeons can occur either on passage or as strays in most areas of Britain during the race season (April–September) and home lofts are widespread with concentrations in certain areas.

In this paper we describe the diet of Peregrines inhabiting south-central Wales, focussing particularly on spatial and temporal variation in the availability of racing pigeons. We also examine spatial variation in the ‘home origin’ of racing pigeons killed at a regional level in south-central Wales and at a finer local scale within South Wales.

Materials and methods

Study area

Peregrine sites within our south-central Wales study region were allocated to three areas i.e. South Wales, the Brecon Beacons and Central Wales *(Figure 1)*. The South Wales area is the main centre of pigeon racing in Wales and holds approximately 2350 racing pigeon lofts distributed across most of

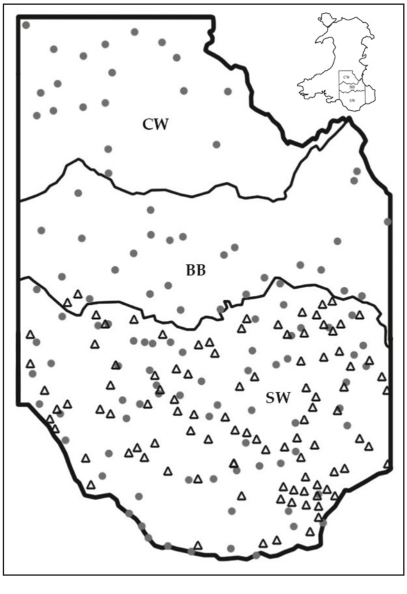

Figure 1. Map showing the division of south-central Wales into three regions; Central Wales (CW), Brecon Beacons (BB) and South Wales (SW). Grey circles mark Peregrine breeding sites and triangles show the location of racing pigeon clubs

1. ábra Dél-Közép-Wales területi felosztásának térképe: Közép-Wales (CW), Brecon Beacons (BB) és Dél-Wales (SW). A szürke körök a vándorsólymok költőhelyeit, a háromszögek a sportgalambász egyesületek elhelyezkedését jelölik the valley towns. Individual lofts in a local area are organised into clubs; the distribution of these local clubs in south-central Wales is shown in *Figure 1.* The Brecon Beacons area includes Peregrine breeding sites within the boundary of the Brecon Beacons National Park. The Brecon Beacons area holds few pigeon lofts (probably less than 50). The Central Wales area lies to the north of the Brecon Beacons National Park and holds very few racing pigeon lofts (probably less than 10).

Racing pigeon availability

The racing pigeon population in Britain varies in time and space which makes quantitative assessment difficult. The abundance of racing pigeons not only varies seasonally between the race season and the off-season, but also within the race season on a daily basis because most races take place on weekends. In addition to this temporal variation, the abundance of racing pigeons varies spatially depending on the geographical location of lofts, training routes and race routes. Nevertheless, it is still possible to make a qualitative assessment of their availability as prey for Peregrines. The availability of pigeons as prey is related to their activity. We have designated four activities to describe the circumstances of racing pigeons that are available as prey for Peregrines. (1) Pigeons on race flights, (2) pigeons on training flights, (3) pigeons exercising around the loft and (4) stray pigeons that have failed to return to lofts. The availability of racing pigeons in each of these four classes differed between study areas *(Table 1)*.

Pigeons on race flights are normally only available on weekends along routes between the liberation point and the home loft. Race distances vary in length and pigeons can deviate significantly from a direct flight route yet still home successfully (Dall 'Antonia *et al.* 1999). Thus, pigeons on races have an ephemeral, but potentially very widespread, availability. Training flights are of shorter length and occur more frequently than races, but are normally conducted at the same bearing from the home loft. Thus, pigeons on training flights have more frequent but less widespread availability than pigeons on races. During the race season, pigeons are normally released daily from their lofts for exercise flights in the local area. Pigeons on exercise flights have a very frequent but spatially restricted availability. Finally, stray racing pigeons can potentially occur anywhere at any time, though their availability may vary both in time and space. It is likely that there are more strays in the environment immediately following a race weekend and that some of these birds eventually make their way home. Furthermore, it is possible that strays are attracted

Table 1. Qualitative assessment of the availability of racing pigeons as prey within three study areas of south-central Wales

1. táblázat Minőségi értékelés a versenyzésre tenyésztett galambok, mint prédaállatok elérhetőségéről a három vizsgálati területen, Dél-Közép-Walesben

Study Region	Pigeon Availability	Circumstance of Availability
South Wales	Highest	Exercising : Training : Racing : Stray
Brecon Beacons	Intermediate	Training : Racing : Stray
Central Wales	Lowest	Racing: Stray

to particular areas, perhaps to localities where there are large aggregations of lofts or arable areas with a rich food supply. We had no means of assessing the relative availability of stray pigeons between our study areas, but we believe that they were more abundant in South Wales, possibly having been attracted to the area by resident pigeons returning home from races.

Peregrine diet

Over the period 1985–2018, we identified the remains of avian prey at Peregrine breeding ranges in south-central Wales. Prey remains consisted of plucked feathers and partially eaten carcasses. In most cases, in the absence of whole or partially eaten carcases, we categorized the remains based on the condition and number of feathers found at plucking sites, judging them to be either 'recent kills' allocated to the month when they were found or else killed within one of two seasons, 'summer' (April–September; corresponding with the timing of the pigeon race season in Britain) or 'winter' (October–March). Avian prey remains that could not be allocated to a particular month or season were not included in our analyses.

The use of prey remains to characterise raptor diets has a number of potential biases (e.g. Newton & Marquiss 1982). However, as we are only using prey remains to compare the relative frequency of prey species between study areas our approach should not be biased in any particular direction. In order to account for variation in sampling effort, for major prey species, we calculated their percentage of total prey items in each month of the year.

Results

Diet of Peregrines in south-central Wales

We identified 95 species killed by Peregrines in our study areas *(Appendix 1)*, including three that could not be assigned to a specific season i.e. Manx Shearwater *Puffinus puffinus*, Sandwich Tern *Thalasseus sandvicensis* and Canary *Serinus canaria* (the former two being vagrants in south-central Wales and the latter an escaped exotic). In South Wales we identified 79 species from 2869 prey remains, in the Brecon Beacons 60 species from 1215 prey remains and in Central Wales 61 species from 922 prey remains. Common Pigeons were the most important prey species in all three study areas. Apart from Common Pigeons, Jackdaws *Coloeus monedula*, were frequently killed throughout the year, comprising more than 5% of prey by frequency and weight in summer and winter across all three study areas. Starlings were also an important prey species, comprising more than 5% of prey by frequency in both seasons in each study area. In winter across all three study areas, Wood Pigeons *Columba palumbus* and Woodcock *Scolopax rusticola* comprised more than 5% of prey by weight, while Fieldfare *Turdus pilaris*, Redwing *T. iliacus* and Blackbird *T. merula* comprised more than 5% of prey by frequency.

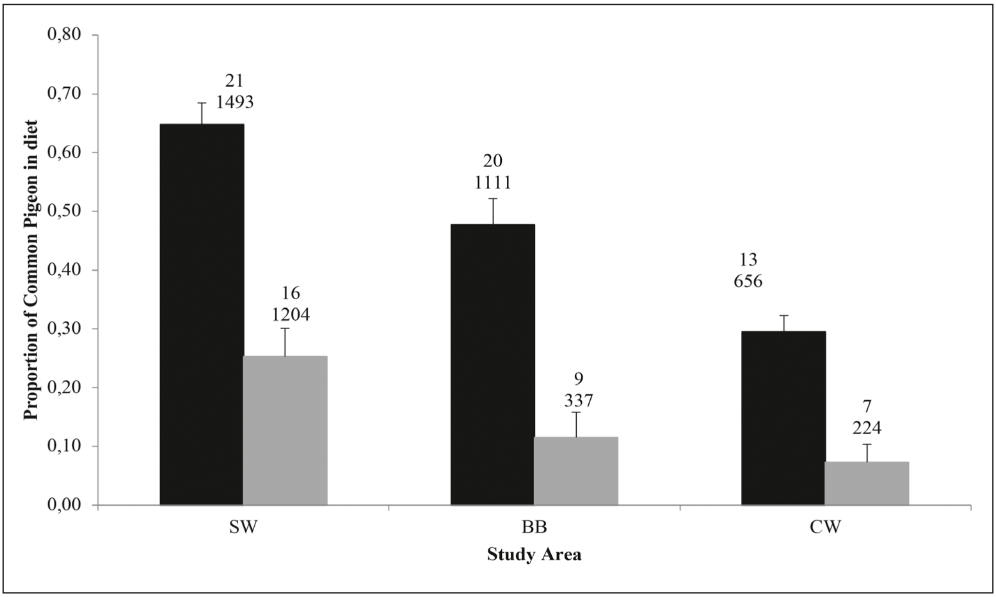

Figure 2. Proportion of Common Pigeons in the diet of Peregrines in each of the three study areas (SW = South Wales, BB = Brecon Beacons, CW = Central Wales). Black columns represent summer period and grey columns winter period. Values above SE bars refer to the number of Peregrine territories sampled and the number of prey items identified

2. ábra A parlagi/házi galamb gyakoriság a vándorsólymok étrendjében a három vizsgálati területen (SW = Dél-Wales, BB = Brecon Beacons, CW = Közép-Wales). A fekete oszlopok a nyári, a szürkék pedig a téli időszakot jelentik. A hibaértékeket jelölő sávok fölötti értékek a vizsgált vándorsólyom territóriumok számát és az azonosított prédák számát mutatják

The frequency of Common Pigeons in prey remains in south-central Wales varied significantly throughout the year. Pigeons are killed much more frequently during the pigeon race season than outside it (Fisher's exact test $P < 0.0001$), highlighting the importance of racing pigeons in the diet. During the pigeon race season, there was a significant difference in the frequency of pigeons killed in South Wales (63% of kills), the Brecon Beacons (43%) and Central Wales (30%; $\chi^2 = 238$, 2 *df*, $P < 0.00001$) *(Figure 2)*. In terms of prey mass the corresponding percentages were 84%, 67% and 50% respectively. Outside the pigeon race season, the frequency of common pigeons killed was lower overall, but still significantly higher in South Wales (18% of kills), than the Brecon Beacons (6%) and Central Wales (5%; $\chi^2 = 57$, 2 *df*, $P < 0.00001$) *(Figure 2)*; in terms of prey mass, the corresponding percentages were 38%, 14% and 14% respectively.

The proportion of Common Pigeons in the diet increased and decreased sharply in April and September respectively *(Figure 3a)*. The proportion of Jackdaws in the diet ranged from 5% to 17% of monthly prey items *(Figure 3b)*, Starlings were killed most frequently in June and during the winter months *(Figure 3c)*. Fieldfare and Redwing appeared in the diet in October, peaked in December and were last found among prey remains in May *(Figure 3d)* and the proportion of Woodcock in the diet exhibited a similar pattern *(Figure 3e)*.

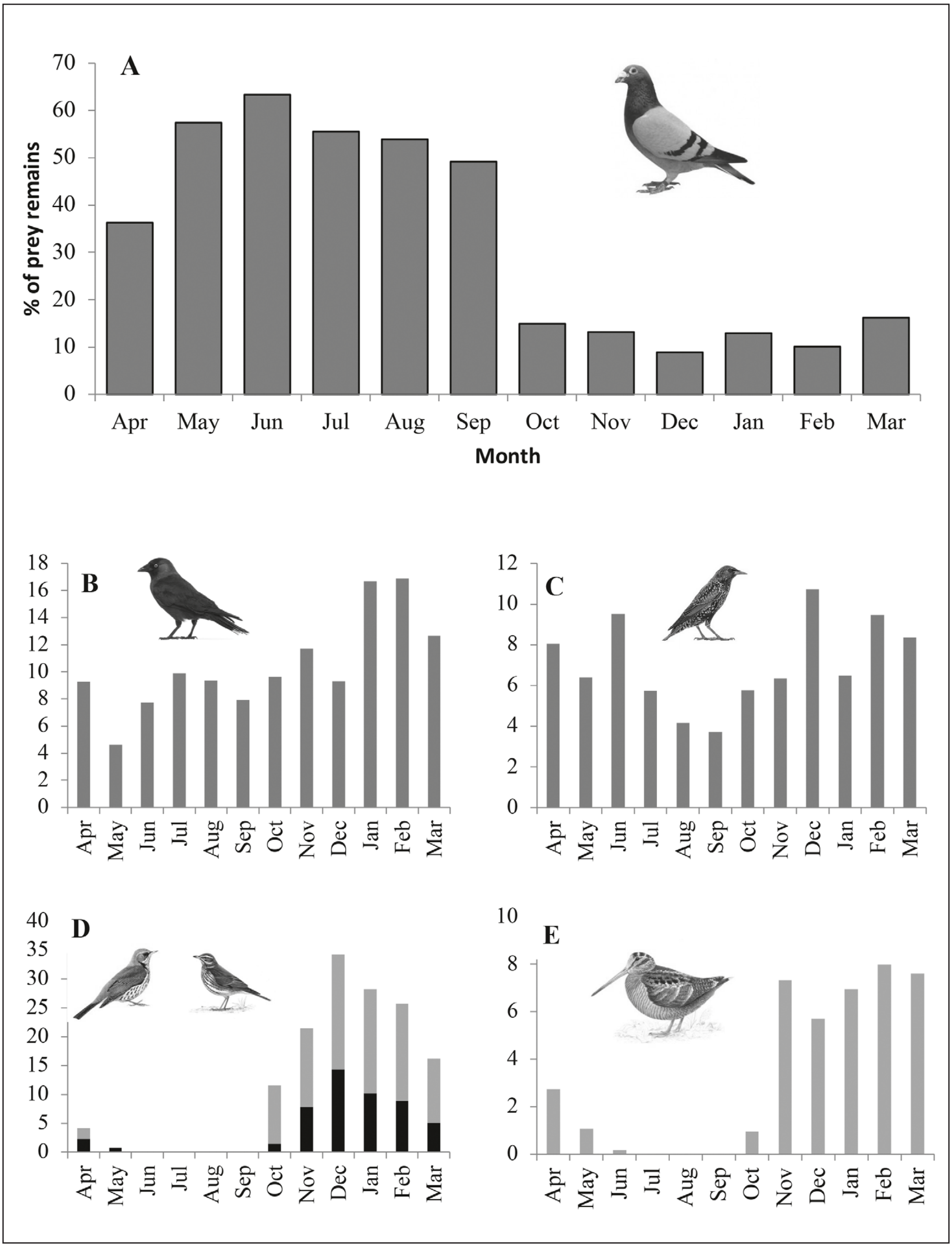

Figure 3. Proportion of Common Pigeon (A), Jackdaw (B), Starling (C), Fieldfare (black column) and Redwing (grey column) (D) and Woodcock (E) in the diet during each month of the year across south-central Wales

3. ábra. A parlagi/házi galamb (A), a csóka (B), a seregély (C), a fenyőrigó (fekete oszlop) és a szőlőrigó (szürke oszlop) (D), valamint a szalonka (E) aránya a vándorsólymok táplálékában hónapokra lebontva, Dél-Közép-Wales területén

Types of Common Pigeon killed by Peregrines

Of 30 Common Pigeon carcasses with both legs present, 28 were ringed indicating that in south-central Wales nearly 7% of pigeon kills were 'feral pigeons' and 93% were domestic pigeons. All but two of these carcasses, both of which were ringed domestic pigeons, were found during the pigeon race season and both feral pigeons were found at Peregrine sites in South Wales.

In a sample of 5049 domestic pigeon rings collected at Peregrine sites in south-central Wales 98.7% (N = 4984) were from racing pigeons, 0.8% (*n* = 40) were from tipplers, 0.3% (*n* = 15) were rollers, 0.2% (*n* = 10) were show pigeons. Most tippler rings were recovered from Peregrine nesting sites in the Swansea, Neath and Port Talbot districts (73%).

Discussion

Diet of Peregrines in south-central Wales

The diet of Peregrines in south-central Wales varied in line with spatial and temporal variation in the availability of racing pigeons: where and when racing pigeons were most available they comprised a greater proportion of the diet. Peregrines respond to changes in relative availability of racing pigeons and thus behave like opportunistic generalist avian predators, but it remains an unanswered question as to whether Peregrines selectively specialized on racing pigeons (e.g. Dawson *et al.* 2011). Fixation by Peregrines on particular prey species may lead to increased skill in capture, while certain species may be particularly vulnerable prey because of their mass, flight behaviour and their occurrence in unfamiliar habitats (White *et al.* 2002). Racing pigeons, with a typical mass of 435 g (Irvine *et al.* 2007), fall within the range of 50–500 g suggested to represent optimal prey mass for Peregrines (Ratcliffe 1993, White *et al.* 2002) and are selectively bred to home accurately and rapidly, and thus are unlikely to exhibit the range of predator avoidance strategies found in wild birds, or find refuges from attack when in unfamiliar habitats on long distance races or if they have strayed from the loft region.

Despite the wide range of prey species killed by Peregrines, the main part of the diet in south-central Wales comprises a relatively small number of species. In summer, in Central Wales where racing pigeons are less available, corvids are an important component of the diet, particularly Jackdaws but also Magpie *Pica pica* and Rook *Corvus frugilegus*, along with Wood Pigeon, Mistle Thrush *Turdus viscivorus* and Starling. In winter, when racing pigeons are less available across all regions, the same species are important with the addition of species that winter in south-central Wales, especially migratory thrushes such as Fieldfare, Redwing and Blackbird, along with Woodcock.

The monthly proportion of Common Pigeons in the diet varied in line with the timing of the pigeon race season, as would be expected when most Common Pigeons killed are racing pigeons. Jackdaws are the next most important prey species for Peregrines in south-central Wales, killed in relatively consistent proportions across the year. Starlings were killed most frequently in June when post-fledging summer flocks were formed and during winter when resident flocks were augmented by winter migrants. Migrant thrushes and Woodcock are important prey species that arrive in south-central Wales at the end of the pigeon season and make up, at least partially, for the loss of racing pigeon biomass from the environment.

Types of Common Pigeon killed by Peregrines

There is little arable land in any of our three study areas to attract roving flocks of feral pigeons, thus their distribution is mainly restricted to human settlements. Feral pigeons are abundant in most of the larger towns throughout South Wales (Tyler *et al.* 1987, Hurford & Lansdown 1995). They are less abundant in the Brecon Beacons and Central Wales, but they do occur in many of the larger towns within these regions (Gibbons *et al.* 1993). Most of the Common Pigeons killed were racing pigeons, though there were a few other varieties of domestic pigeon represented in our ring sample, mainly tipplers, rollers and show pigeons. Their occurrence was highly localised to Peregrine sites in the Swansea, Neath and Port Talbot districts. Tippler pigeons, whose purpose is to fly high above the loft for long periods, must be particularly susceptible to predation. Musgrove (1994) reported that in Bristol, tippler flying all but ceased following colonisation of the city by Peregrines. We note that a similar decline in tippler flying in the Swansea area was reflected in the decreasing frequency of tippler rings recovered from local Peregrine sites over time (tipplers comprised 1.3% of domestic pigeons ringed between 1992–1996 and only 0.5% that were ringed between 1997–2001).

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Appendix 1. Prey species identified at Peregrine breeding sites in the Central Wales, Brecon Beacons and South Wales study areas during summer (April–September) and winter (October–March). %N is the percentage of prey items by frequency (N = number of prey items) and % wt. is the percentage of total prey mass for each species

1. függelék Azonosított prédafajok a vándorsólyom költőhelyeken a közép-walesi, Brecon Beaconsi és dél-walesi vizsgálati területeken a nyári (április-szeptember) és téli (október-március) időszak alatt. A % N a zsákmányállatok aránya gyakoriság szerint (N = zsákmányállatok száma), a % wt. pedig a teljes zsákmány tömegének százalékos aránya minden fajra

Species	**Central Wales**				**Brecon Beacons**				**South Wales**			
	Summer		**Winter**		**Summer**		**Winter**		**Summer**		**Winter**	
	%N (N)	**% wt.**	**%N (N)**	**% wt.**	**%N (N)**	**% wt.**	**%N (N)**	**% wt.**	**%N (N)**	**% wt.**	**%N (N)**	**% wt.**
Willow Grouse *Lagopus lagopus*	0.2 (1)	0.4	0.0 (0)	0.0	0.1 (1)	0.3	0.5 (2)	1.6	0.0 (0)	0.0	0.0 (0)	0.0
Red-legged Partridge *Alectoris rufa*	0.0 (0)	0.0	0.4 (1)	1.2	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.1	0.0 (0)	0.0
Pheasant *Phasianus colchicus*	0.2 (1)	0.7	0.4 (1)	2.9	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.4
Mallard *Anas platyrhynchos*	0.3 (2)	1.2	0.0 (0)	0.0	0.1 (1)	0.5	0.0 (0)	0.0	0.1 (1)	0.2	0.2 (3)	1.2
Teal *Anas crecca*	0.3 (2)	0.4	1.5 (4)	3.2	0.1 (1)	0.1	0.7 (3)	1.3	0.0 (0)	0.0	0.2 (2)	0.2
Tufted Duck *Aythya fuligula*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.3
Common Pigeon Columba livia	29.5 (195)	50.4	5.0 (13)	13.7	42.5 (328)	67.1	5.8 (24)	13.9	63.2 (1005)	83.9	17.9 (228)	37.7
Stock Dove *Columba oenas*	0.0 (0)	0.0	0.4 (1)	0.7	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.1	0.2 (3)	0.3
Wood Pigeon ***Columba palumbus***	4.2 (28)	**7.5**	2.7 (7)	**7.7**	2.0 (16)	3.3	2.4 (10)	**6.0**	1.8 (29)	2.5	3.9 (50)	8.5
Collared Dove *Streptopelia decaocto*	0.2 (1)	0.1	0.4 (1)	0.5	0.3 (2)	0.2	0.2 (1)	0.3	0.3 (4)	0.2	0.5 (6)	0.5
Common Swift *Apus apus*	1.4 (9)	0.2	0.0 (0)	0.0	0.9 (7)	0.1	0.0 (0)	0.0	0.6 (9)	0.1	0.0 (0)	0.0
Common Cuckoo *Cuculus canorus*	0.5 (3)	0.2	0.0 (0)	0.0	0.3 (2)	0.1	0.0 (0)	0.0	0.3 (4)	0.1	0.0 (0)	0.0
Eurasian Coot *Fulica atra*	0.2 (1)	0.5	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Grey Heron *Ardea cinerea*	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.7	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Oystercatcher *Haematopus ostralegus*	0.0 (0)	0.0	0.4 (1)	1.3	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Lapwing *Vanellus vanellus*	0.6 (4)	0.5	0.0 (0)	0.0	0.4 (3)	0.3	1.2 (5)	1.5	0.3 (5)	0.2	0.9 (11)	1.0
Golden Plover Pluvialis apricaria	1.5 (10)	1.3	1.9 (5)	2.7	0.0 (0)	0.0	1.2 (5)	1.5	0.1 (1)	<0.1	1.2 (15)	1.2
Grey Plover Pluvialis squatarola	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.1
Woodcock ***Scolopax rusticola***	1.4 (9)	1.5	4.6 (12)	**8.2**	0.5 (4)	0.5	**7.7 (32)**	**11.9**	0.5 (8)	0.4	**6.1 (78)**	8.2
Common Snipe *Gallinago gallinago*	0.8 (5)	0.3	0.4 (1)	0.3	0.4 (3)	0.2	1.7 (7)	1.0	0.2 (3)	0.1	1.9 (24)	1.0
Curlew *Numenius arquata*	0.3 (2)	1.1	0.0 (0)	0.0	0.4 (3)	1.2	0.0 (0)	0.0	0.1 (1)	0.2	0.0 (0)	0.0

Species	Central Wales				Brecon Beacons				South Wales			
	Summer		Winter		Summer		Winter		Summer		Winter	
	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.
Common Redshank *Tringa totanus*	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Greenshank *Tringa nebularia*	0.2 (1)	0.1	0.0 (0)	0.0	0.3 (2)	0.2	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Little Stint *Calidris minuta*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1
Dunlin *Calidris alpina*	0.2 (1)	<0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0
Sanderling *Calidris alba*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.2 (2)	<0.1
Kittiwake *Rissa tridactyla*	0.0 (0)	0.0	0.4 (1)	1.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Black-headed Gull *Chroicocephalus ridibundus*	0.9 (6)	1.0	0.8 (2)	1.4	1.4 (11)	1.4	0.7 (3)	1.1	0.1 (2)	0.1	0.5 (7)	0.8
Common Gull *Larus canus*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.2 (1)	0.5	0.0 (0)	0.0	0.0 (0)	0.0
Common Tern *Sterna hirundo*	0.2 (1)	0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0
Arctic Tern *Sterna paradisaea*	0.0 (0)	0.0	0.0 (0)	0.0	0.3 (2)	0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1
Barn Owl *Tyto alba*	0.0 (0)	0.0	0.8 (2)	1.4	0.0 (0)	0.0	0.2 (1)	0.4	0.3 (5)	0.3	0.2 (2)	0.2
Tawny Owl *Strix aluco*	0.2 (1)	0.3	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Long-eared Owl *Asio otus*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.1
Short-eared Owl *Asio flammeus*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.1
Eurasian Sparrowhawk *Accipiter nisus*	0.0 (0)	0.0	0.0 (0)	0.0	0.4 (3)	0.3	0.2 (1)	0.3	0.1 (2)	0.1	0.0 (0)	0.0
Kingfisher *Alcedo atthis*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1
Great Spotted Woodpecker *Dendrocopos major*	2.7 (18)	0.9	0.4 (1)	0.2	2.9 (23)	0.9	2.6 (11)	1.2	0.9 (15)	0.2	1.8 (23)	0.7
Green Woodpecker *Picus viridis*	0.9 (6)	0.7	0.4 (1)	0.4	1.0 (8)	0.7	1.2 (5)	1.2	0.8 (12)	0.4	1.2 (15)	1.0
Common Kestrel *Falco tinnunculus*	0.0 (0)	0.0	0.0 (0)	0.0	0.3 (2)	0.2	0.0 (0)	0.0	0.1 (1)	<0.1	0.1 (1)	0.1
Merlin *Falco columbarius*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.1
Hobby *Falco subbuteo*	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Cockatiel *Nymphicus hollandicus*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (2)	<0.1	0.2 (2)	0.1
Budgerigar *Melopsittacus undulatus*	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0	0.3 (5)	0.1	0.0 (0)	0.0
Rosy-faced Lovebird *Agapornis roseicollis*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0
Jay *Garrulus glandarius*	1.4 (9)	0.9	0.4 (1)	0.4	1.6 (13)	1.0	1.4 (6)	1.3	0.9 (14)	0.4	1.6 (21)	1.3

Species	Central Wales				Brecon Beacons				South Wales			
	Summer		Winter		Summer		Winter		Summer		Winter	
	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.
Eurasian Magpie ***Pica pica***	3.3 (22)	2.9	1.2 (3)	1.6	1.3 (10)	1.0	4.8 (20)	**5.9**	1.1 (17)	0.7	3.6 (46)	3.8
Jackdaw ***Coloeus monedula***	12.0 (79)	10.7	11.6 (30)	16.6	11.3 (90)	9.3	17.1 (71)	21.4	7.2 (114)	5.0	13.2 (168)	14.4
Rook *Corvus frugilegus*	3.2 (21)	3.9	0.4 (1)	0.8	0.4 (3)	0.4	1.0 (4)	1.6	0.0 (0)	0.0	0.0 (0)	0.0
Carrion Crow *Corvus corone*	1.1 (7)	2.1	0.4 (1)	1.2	1.0 (8)	1.8	1.4 (6)	4.0	0.3 (4)	0.4	0.5 (7)	1.3
Coal Tit *Periparus ater*	0.3 (2)	<0.1	1.9 (5)	0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.2 (3)	<0.1
Great Tit *Parus major*	0.0 (0)	0.0	0.0 (0)	0.0	0.3 (2)	<0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.2 (2)	<0.1
Blue Tit *Cyanistes caeruleus*	0.3 (2)	<0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Skylark *Alauda arvensis*	1.5 (10)	0.2	0.8 (2)	0.2	2.1 (17)	0.3	0.7 (3)	0.2	1.5 (24)	0.2	0.7 (9)	0.1
Sand Martin *Riparia riparia*	0.2 (1)	<0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Barn Swallow *Hirundo rustica*	0.6 (4)	<0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.3 (5)	<0.1	0.1 (1)	<0.1
House Martin *Delichon urbicum*	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0	0.1 (2)	<0.1	0.0 (0)	0.0
Willow Warbler *Phylloscopus trochilus*	0.2 (1)	<0.1	0.0 (0)	0.0	0.4 (3)	<0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Goldcrest *Regulus regulus*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.2 (2)	<0.1
Wren *Troglodytes troglodytes*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (2)	<0.1	0.2 (2)	<0.1
Nuthatch *Sitta europaea*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1
Treecreeper *Certhia familiaris*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0
Starling ***Sturnus vulgaris***	**7.9 (52)**	2.6	**12.4 (32)**	**6.5**	**8.4 (67)**	2.6	**9.1 (38)**	4.2	**6.9 (109)**	1.8	**6.6 (84)**	2,7
Ring Ouzel *Turdus torquatus*	0.2 (1)	0.1	0.0 (0)	0.0	0.4 (3)	0.2	0.2 (1)	0.2	0.1 (1)	<0.1	0.1 (1)	<0.1
Blackbird ***Turdus merula***	**5.8 (38)**	2.3	**6.9 (18)**	4.4	4.8 (38)	1.8	**5.0 (21)**	2.8	3.3 (53)	1.0	4.2 (54)	2.1
Fieldfare ***Turdus pilaris***	1.7 (11)	0.7	**12.4 (32)**	**8.5**	0.3 (2)	0.1	**9.9 (41)**	**5.9**	0.2 (3)	0.1	**7.2 (92)**	3.8
Redwing ***Turdus iliacus***	0.8 (5)	0.2	**20.1 (52)**	**8.2**	0.6 (5)	0.1	**13.9 (58)**	**5.0**	0.2 (2)	<0.1	**12.9 (164)**	4.0
Song Thrush *Turdus philomelos*	1.8 (12)	0.6	2.3 (6)	1.2	2.3 (18)	0.7	2.9 (12)	1.3	1.1 (18)	0.3	2.3 (29)	0.9
Mistle Thrush ***Turdus viscivorus***	**5.8 (38)**	2.8	3.5 (9)	2.7	3.8 (30)	1.7	2.6 (11)	1.8	1.0 (16)	0.4	1.6 (21)	1.3
Robin *Erithacus rubecula*	0.2 (1)	<0.1	0.0 (0)	0.0	0.1 (1)	<0.1	0.2 (1)	<0.1	0.1 (1)	<0.1	0.1 (1)	<0.1
Black Redstart *Phoenicurus ochruros*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1
Redstart *Phoenicurus phoenicurus*	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0

Species	Central Wales				Brecon Beacons				South Wales			
	Summer		Winter		Summer		Winter		Summer		Winter	
	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.	%N (N)	% wt.
Whinchat *Saxicola rubetra*	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
Stonechat *Saxicola rubicola*	0.2 (1)	<0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.1 (1)	<0.1
Northern Wheatear *Oenanthe oenanthe*	0.9 (6)	0.1	0.0 (0)	0.0	0.9 (7)	0.1	0.0 (0)	0.0	0.4 (6)	<0.1	0.1 (1)	<0.1
Dipper *Cinclus cinclus*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.2 (1)	0.1	0.0 (0)	0.0	0.0 (0)	0.0
House Sparrow *Passer domesticus*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1
Dunnock *Prunella modularis*	0.0 (0)	0.0	0.4 (1)	0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
White Wagtail *Motacilla alba*	0.3 (2)	<0.1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.2 (3)	<0.1	0.1 (1)	<0.1
Meadow Pipit *Anthus pratensis*	1.4 (9)	0.1	1.2 (3)	0.1	3.4 (27)	0.2	0.5 (2)	0.1	1.6 (25)	0.1	1.6 (21)	0.2
Rock Pipit *Anthus petrosus*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0
Chaffinch *Fringilla coelebs*	2.0 (13)	0.2	1.5 (4)	0.2	0.8 (6)	0.1	1.4 (6)	0.2	1.6 (25)	0.1	2.6 (33)	0.3
Brambling *Fringilla montifringilla*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1
Greenfinch *Carduelis chloris*	0.2 (1)	0.1	0.4 (1)	0.2	0.1 (1)	<0.1	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0
Siskin *Carduelis spinus*	0.2 (1)	<0.1	0.8 (2)	0.1	0.0 (0)	0.0	0.2 (1)	<0.1	0.1 (2)	<0.1	0.4 (5)	<0.1
Goldfinch *Carduelis carduelis*	0.3 (2)	<0.1	0.4 (1)	<0.1	0.0 (0)	0.0	0.2 (1)	<0.1	0.5 (8)	<0.1	0.3 (4)	<0.1
Common Redpoll *Carduelis flammea*	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0	0.1 (1)	<0.1	0.0 (0)	0.0
Linnet *Carduelis cannabina*	0.2 (1)	<0.1	0.0 (0)	0.0	0.3 (2)	<0.1	0.0 (0)	0.0	0.2 (3)	<0.1	0.2 (2)	<0.1
Common Crossbill *Loxia curvirostra*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1	0.1 (1)	<0.1
Bullfinch *Pyrrhula pyrrhula*	0.3 (2)	<0.1	0.4 (1)	0.1	0.0 (0)	0.0	0.2 (1)	<0.1	0.1 (1)	<0.1	0.2 (3)	<0.1
Reed Bunting *Emberiza schoeniclus*	0.2 (1)	<0.1	0.0 (0)	0.0	0.3 (2)	<0.1	0.0 (0)	0.0	0.2 (3)	<0.1	0.2 (3)	<0.1
Snow Bunting *Plectrophenax nivalis*	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.1 (1)	<0.1

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Onset of natal dispersal in Peregrine Falcon from Mediterranean islands (Italy)

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Abstract Basic information on natal dispersal of Peregrine Falcons is virtually lacking in Europe, despite increased attention on this species, and the sensitivity of this stage in the Peregrines' life history. In this study, we collected satellite telemetry data during the onset of natal dispersal of 19 Peregrine Falcons tagged in Sicily and the Aeolian archipelago (Italy). We divided the onset of dispersal into the following 3 periods: post-fledging dependence period (PFDP), wandering, and wintering. PFDP lasted on average 47±16 days, during which young peregrines moved very little (0.167 km), and explored small areas (0.226 km^2) far from the nest cliff, and showed no sex differences. The wandering phase was highly individualistic, with median net displacements of 23.97 km. Both PFDP and wandering bearings were oriented towards NNE-ESE. Only five individuals went sporadically outside the island borders. During their first winter, Peregrines had a mean home range of 135.65±82.31 km^2 spatially scattered across Sicily and mainly composed of open habitats, like cereal steppes, arboreal crops and agri-mosaics. Individuals had a dissimilar assortment in habitat composition, however the urban habitat was the most selected and the woodland the least. At night, during both wandering and wintering phases Peregrines used rocks, cliffs and electricity pylons in frequencies not statistically different between sex, phase and type of roost. Only two individuals had significant use of pylons and one of rocks. The multifaceted framework of Peregrine Falcon's natal dispersal was described here for the first time in a Mediterranean population.

Keywords: natal dispersal, Mediterranean islands, Peregrine Falcon, satellite telemetry, Sicily

Összefoglalás A kirepülés utáni diszperzió egy meghatározó szakasza a vándorsólyom életmenetének, azonban, a fokozott kutatási aktivitás ellenére sem ismerünk alapvető információkat erről a periódusról az európai populációk esetében. Tizenkilenc Szicíliában és a Lipari-szigeteken (Olaszország) műholdas jeladóval jelölt vándorsólymot követtünk kirepülés utáni diszperziójuk során. Ezt az életszakaszt három periódusra osztottuk: kirepülés utáni korai periódus (post-fledging dependence period, PFDP), kóborlás és telelés. A PFDP periódus átlagosan 47 ± 16 napig tartott, mialatt a fiatal sólymok nagyon kis távolságra (0,167 km) távolodtak el a fészektől, annak csak a közvetlen környékét fedezték fel (0,226 km^2), és az ivarok sem különböztek ezekben a paraméterekben. A kóborlási fázis jelentős egyedi variabilitást mutatott 23,97 km medián eltávolodással. Mind a PFDP, mind a kóborlási fázisban a sólymok mozgása ÉÉNY-KDK irányt vett fel. Mindössze 5 egyed hagyta el rövid időkre Szicíliát. Az első telükön a fiatal vándorsólymok átlagosan 135,65 ± 82,31 km^2 területen, elszórtan tartózkodtak a szigeten, jellemzően nyílt élőhelytípusokat – mint a gabonaföldek, gyümölcsfás ligetek és egyéb mozaikos mezőgazdasági területek – preferálva. Bár az egyedek különböztek az elfoglalt élőhelytípusok összetételében, a városi élőhely volt a leggyakrabban, míg az erdei élőhely a legritkábban használt. Éjszakázóhelynek sziklákat, sziklafalakat és elektromos oszlopokat használtak, a kóborló és a telelő időszakban egyaránt. Ezen helyek használatának gyakorisága azonban statisztikailag nem különbözött az egyedek, ivarok és életszakaszok között. Csupán két fiatal sólyom használta kimagaslóan gyakran az elektromos oszlopokat, míg egy a sziklákat preferálta éjszakázóhelyként. Tanulmányunk elsőként közöl részletes leírást a vándorsólyom mediterrán populációjának kirepülés utáni diszperziójáról.

Kulcsszavak: kirepülés utáni diszperzió, mediterrán szigetek, vándorsólyom, műholdas telemetria, Szicília

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Introduction

Biologging technologies, primarily satellite data-loggers, have opened new frontiers in the study of animal ecology, via the access to mass of high resolution data recorded on the daily activity and behaviour of single individuals moving in their habitats (Cooke *et al.* 2004, Cagnacci *et al*. 2010). This new scientific branch, called movement ecology (Nathan *et al.* 2008), applies to the investigation of all the relevant aspects of a species' life history, such as migration, space use, prospecting and dispersal (Bowler & Benton 2005, Ponchon *et al.* 2013).

The movement of an individual from one natal or living site to a new living site, currently defined as dispersal (Bullock *et al.* 2002, Ronce 2007), is an ecological process which has multi-level effects on the permanence, evolution and conservation of species (Bullock *et al.* 2002), because it determines individual survival, fitness costs, gene flow among populations, and species ranges (Bullock *et al.* 2002, Kokko & Lopéz-Sepulcre 2006, Nevoux *et al.* 2013). Furthermore, the spatial structure and connectivity of populations are directly linked to dispersal (Clobert *et al.* 2004).

Dispersal is basically the pattern of movements associated with both daily needs (e.g. foraging, roosting) and the search for a new habitat where to establish and reproduce (Doligez *et al*. 2002, Van Dyck & Baguette 2005). This adaptive force driving animal life can be further divided in 'natal dispersal', i.e. movement from the birthplace to the first breeding site; and 'breeding dispersal', i.e. movement between successive breeding sites (Greenwood 1980, Greenwood & Harvey 1982). Currently, the variety of movements associated with breeding biology and dispersal behavior in raptors and other bird species have been categorized in sequential, but distinct, phases, coded with a rather variable terminology (Bennetts *et al*. 2001, Andreassen *et al*. 2002, Bowler & Benton 2005, Penteriani & Delgado 2009), that Morrison and Wood (2009) tried to standardize.

A complex interaction between genetic and condition-dependent environmental forces gives rise to the development of animals' dispersal strategies (Bowler & Benton 2005). Indeed, individuals' behavioural characteristics may complement such an interaction and shape flexible dispersal strategies (Penteriani & Delgado 2009) with the ultimate purpose of settling in areas similar to the natal site (Doligez *et al*. 2002). In many species, including raptors, young birds collect public information by prospecting the quality of future breeding sites during their post fledging explorations (Boulinier *et al.* 1996, Reed *et al.* 1999, Doligez *et al*. 2002, Serrano *et al*. 2004, Nocera *et al*. 2006), or likewise explore the possibility for pair formation after a vacancy has occurred in natal areas (e.g. Ferrer 1996). Such an evaluation has a potentially relevant role in breeding habitat selection and helps individuals making optimal dispersal decisions often through prospecting and previous information of future reproductive success (Ponchon *et al.* 2013).

Since dispersal has also important consequences in raptor populations and community composition it is necessary to identify the factors that constrain (e.g. spatial distribution of appropriate habitat, avoidance of territorial adults, etc.) the movement of young raptors when floating in search of stable settlement areas and/or breeding territories, as well as the effects they have on the communities of the settling area (Morrison & Wood 2009, Penteriani & Delgado 2009). Such effects can extend beyond their role as future breeders, as pointed out by Penteriani and Delgado (2009), in the case of predator-prey relationships and intra-guild predation of dispersing top predators.

In this context, a never addressed issue concerns how strategies of one species' natal dispersal can affect the occupancy patterns of species with similar ecological requirements, and hence can influence the competitive interactions among related species. This might occur between the Peregrine *(Falco peregrinus)* and the Lanner Falcon *(Falco biarmicus)* in Sicily, because the large and increasing population of the former species produces every year more offspring than the small and declining population of the latter one (Sarà *et al.* 2014). Hence, it might be the case that large numbers of Peregrine floaters could saturate the spatial niche available for Lanner Falcons in the medium- or long-term. Within the framework of an extensive investigation on the ecological interactions between the two species in Sicily (Amato *et al.* 2014, Sarà 2014, Sarà *et al.* 2016), we compare natal dispersal patterns of both species by satellite telemetry. We report here on the onset of natal dispersal occurring in juvenile Peregrine Falcons. In particular, in this first contribution we describe the individual patterns and sex differences during: i) the post-fledging dependence period, ii) the wandering phase, iii) the settling during the first winter of life and the related land-uses, iv) the nocturnal roosts used during wandering and wintering phases.

Material and Methods

Study area

Sicily is the largest Mediterranean island, as it extends over an area of 25,832 km^2 and is one of the most populated regions of Italy (193 inhabitants per km^2). Its typically Mediterranean climate has remarkable variation from the northern areas facing the Tyrrhenian Sea, that mostly fall within the meso-Mediterranean sub-humid and meso-Mediterranean dry bioclimate to the southern areas that mostly fall within the thermo-Mediterranean dry bioclimate. Almost 24.4% of the Sicilian territory is mountainous, 61.4% is composed of highlands, while 14.2% of the surface is lowland. Deciduous forests and Mediterranean vegetation, of which almost 6–8% burns every year, cover 8.4% of the surface area, and are widespread mostly in the north-eastern part of the island, with beech *(Fagus sylvatica)* forests extending from 1200–1400 m a.s.l. in the northern ridge. Hilly and flat inland areas show great habitat heterogeneity, with cultivation zones (especially arable land, fodder, vineyards and olive orchards) intermingled with forest patches of non-native species (*Pinus* spp. and *Eucalyptus* spp.), natural evergreen woodlands (*Quercus* spp.), Mediterranean xeric grasslands, garrigues and shrub vegetation.

The Aeolian archipelago is a volcanic arch formed in the last 300,000 years before present and composed by seven major islands and several islets. Most of the archipelago stretches in a more or less parallel way along the north eastern coasts of Sicily, from which is clearly visible. The nearest island (Volcano) is about 20 km from Sicily while the farthest (Stromboli) is about 50 km *(Figure 1)*. Strongly exploited by agricultural activities in the past and by tourism today, the islands have lost most of the original vegetation that has been replaced by vineyards and non-native species. Nonetheless, significant patches of Mediterranean evergreen woodland and shrubland remain in the steep sides and at the top of the volcanos.

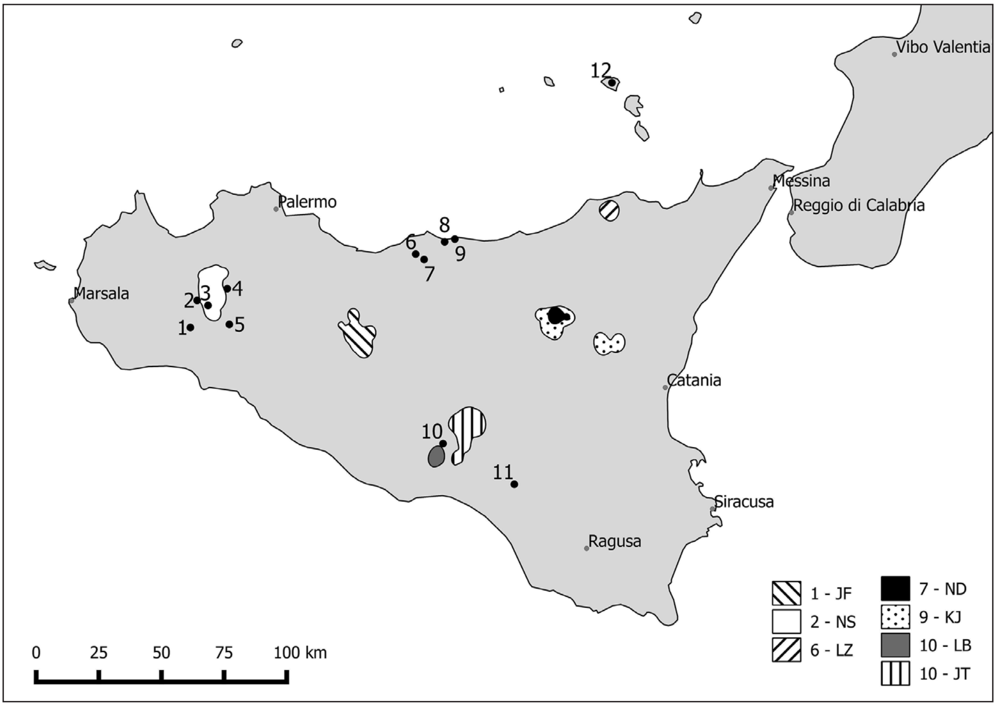

Figure 1. Map of study area with main towns, the twelve sampling sites (1-11 in Sicily and 12 in Salina, Aeolian archipelago) and 7 wintering areas (black, white and stippled or dashed) of juvenile Peregrine Falcons. Wintering individuals have been coded from both their natal site and lecture ring. For instance, 2-NS refers to falcon NS born in site 2 and wintering in the very close white area, etc., individuals have been listed in Table 2. All individuals but 10-JT are females, and all but 9-KJ had a single wintering area. The second wintering area of 9-KJ was used the year before by 7-ND, so the overlap is only spatial. Stromboli the foremost north-eastern Aeolian island, not showed because is out of map limits

1. ábra A vizsgálati terület térképe a jelentősebb városok, a 12 mintavételi (1-11 Szicíliában, a 12. Salina-n, – Lipari-szigetek) és 7 telelő terület feltüntetésével (fekete, fehér és pöttyözött vagy sávozott). A telelő egyedek jelölését a költőterület és a gyűrűszám kombinációja adja meg. Például, 2-NS az NS-sel jelölt sólymot jelenti, amelyik a 2-es mintavételi területen kelt ki, és a közeli, fehérrel jelölt területen telelt. Az egyedek listája a 2. táblázatban található. A 10-JT egyeden kívül minden sólyom tojó, és mindnek, kivéve a 9-KJ egyednek, csak egyetlen telelő területe volt. 9-KJ második telelő területét az előző évben a 7-ND jelölésű sólyom használta, ezért átfedés kizárólag térben történt. A Stromboli, a Lipari-szigetcsoport legészakabbra fekvő szigete a lépték miatt nincs ábrázolva a térképen

Study species

The nearly-cosmopolitan Peregrine Falcon (White *et al.* 2013) is a sedentary and quite common species in both Sicily and Aeolian Islands, where it breeds in diverse coastal and inland habitats at altitudes up to 1300 m a.s.l. The Sicilian population currently assigned to *F. p. brookei* (White *et al.* 2013, but see Mengoni *et al.* 2018), was very likely only slightly hit by the massive world-wide decline occurring in the 20th century due to organochlorine pesticides (Cade *et al.* 1988, White *et al.* 2013). Past censuses (e.g. Schenk *et al.* 1983) estimated the population to be around 150 pairs, some 195–205 pairs were recorded after a review of local literature, and this baseline value was used to estimate a potential population of 216±52 pairs by modeling the species' occupancy (Sarà 2008). Recent monitoring in 2014–2017, mapped the presence of 166 territories in nearly 65–70% of Sicily (Sarà *et al.* unpublished data), that would produce a prudential estimate of 240–250 territories in the whole island. Further 4–5 pairs are known in the Aeolian archipelago (Lo Cascio 2017). In both Sicily and Aeolian archipelago, the species is mainly threatened by direct human persecution (illegal shooting) and marginally by nest despoliation for illegal trading of eggs and chicks.

Field procedures and data treatment

To investigate the onset of natal Peregrine Falcon dispersal, we used a sample of known breeding sites, 11 distributed in northern, western and southern Sicily and 1 in Salina (Aeolian Island) during the 2014–2017 breeding seasons. Four northern sites and the Salina are coastal, while the others are located inland in Sicily *(Figure 1)*. The entire sample was formed by natural nests, located on vertical cliffs in cavities, rocky ledges or old nests of Raven *Corvus corax*. Nests were accessed by a rock climber expert in raptor handling, who delivered the chicks to the base or to the top of the cliff for processing (collection of biometric data and genetic samples, ringing and tagging). We deployed 19 GPS-GSMs (model Saker ultra-light, Ecotone, Poland, weight 20 g) on juvenile Peregrine Falcons (6 males, 13 females, including duos of siblings from 4 sites), about 33–36 days old. Sex was inferred by body biometrics and then confirmed by genetic analysis (Mengoni *et al*. 2018). Transmitters were fixed as a backpack using a teflon harness (Rodríguez *et al.* 2009) and birds were released into their nest a maximum of 30–45 minutes after capture. The complete backpack weighted about 21 g, well below the 3% limit of body weight. Tagged birds were monitored once a week for the first month after marking, to check both bird and tag conditions. The satellite transmitters had a solar battery and were programmed to collect a GPS position every 6 of 24 hours of signal reception while chicks were in the nest, and every 1–2 hours after they have fledged out. To avoid biases associated to the non-independence of the data, positions obtained less than 2 hours after the previous one, were excluded from the analyses (Limiñana *et al.* 2007). Bird locations and routes were retrieved in geographical coordinates and then converted to UTM WGS84 coordinates for further calculation by QGIS 2.16 (QGIS Development Team 2016).

In this first contribution, we considered only locations corresponding to the period from the first fledging flight till the end of first winter of the young Peregrine Falcons. This 9-month period, describing the onset of natal dispersal, was divided in three different phases, according to current literature (Weathers & Sullivan 1989, Morrison & Wood 2009, Penteriani & Delgado 2009): 1) post-fledging dependence period (hereafter PFDP), from the fledging day to the first day of leaving the natal area; 2) wandering, from the day of leaving the natal area until 30 November, was conventionally terminated by the start of next phase; and 3) first settling and wintering. As suggested for early-spring breeder species (Spina & Volponi 2008), this phase was considered from 1 December to 28 February.

To establish the end of PFDP and the start of wandering phase, we used both a visual observation of QGIS maps, and two standardized and quantitative methods: 1) net displacement (hereafter ND, Kareiva & Shigesada 1983, Turchin 1998), and 2) the cumulated coefficient of variation (hereafter ΔCV, Limiñana *et al.* 2008). For every individual, the ND procedure determines the Euclidean distance between the initial location and each subsequent relocation. We preferred not to transform ND values into squared NSD values (i.e. net squared displacement), because the nonlinearity of squared transformation alters distance values, so that the obtained movement timing would initiate and terminate later in the NSD framework compared to the ND scale (Beatty *et al.* 2013). ND differs by season, hence its interpretation depends on the timing and location of marking (Bunnefeld *et al.* 2011). This implies that the movement pattern for every individual marked in the nest shows an increase of ND values representing the onset of wandering or dispersal movements from the nest, followed by a second phase in which these values become quite stable and fluctuate around a maximum value, once the individuals have reached a given settling area (e.g. wintering grounds). In order to verify the start of wandering phase recorded by both visual observations and the ND method, we looked for the abrupt change in the movement pattern of every Peregrine Falcon, as expressed by the incremental coefficient of variation (ΔCV) between two subsequent bird locations. ΔCV shows a peak when the animal leaves the natal site and is flat when wandering movements become more continuous. This procedure allowed us to precisely identify both the start and duration of wandering movements per every tagged Peregrine Falcon *(Figure 2)*.

To identify the geographical areas of both PFDPs and overwintering period, and their extensions, we calculated the 95% kernel (KDE95) using kernel density estimation and the Minimum Convex Polygon (MCP95) of the AniMove tool for ArcGis 9.3, by data obtained from ND and ΔCV calculations.

We used circular statistics (Batschelet 1981) to analyze whether PFDP and wandering directions, with respect to the geographic North and taking as reference the nest-site location of every individual, were different from a random dispersion and whether they differ by sex and siblings. Both PFDP and wandering directions obtained by QGIS were first transformed to rectangular polar coordinates to obtain the mean angle (azimuth) and the mean vector r. This latter measure of angular dispersion ranges from 0 (uniform dispersion) to 1 (complete concentration in one direction). Then, we used the Rayleigh's z statistics to test the null hypothesis that there is no mean direction of dispersion during the PFDP and wandering phases. The Watson-Williams' U statistics was used to test whether the male and female, as well as siblings Peregrine Falcons are significantly different in their main PFDP and wandering azimuths.

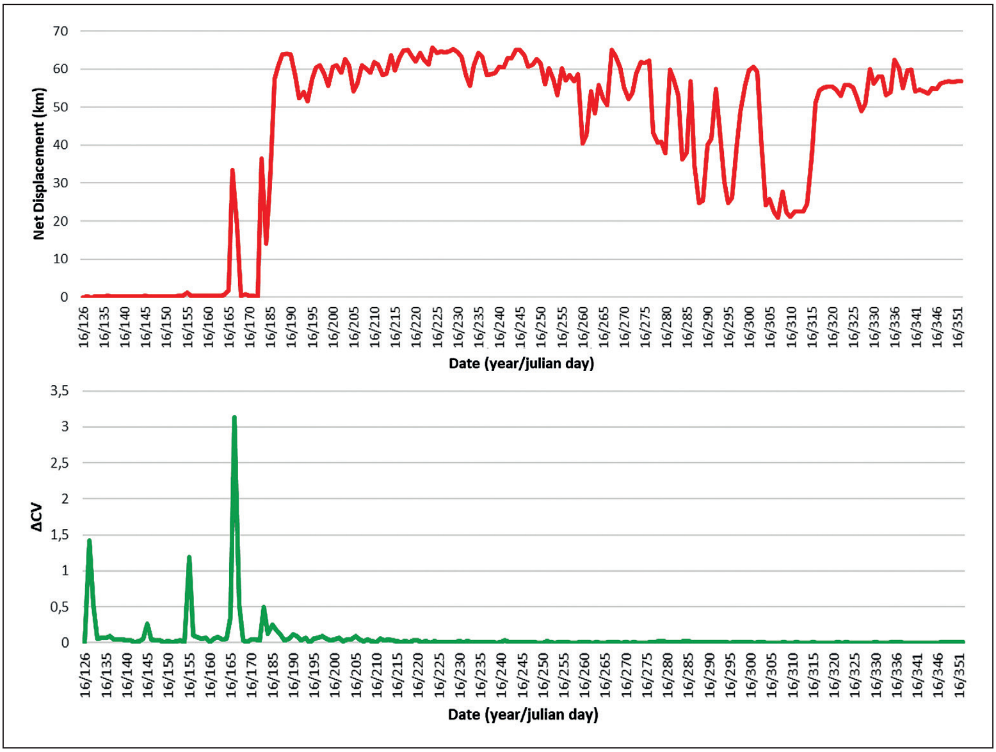

Figure 2. The end of PFDP and the start day of Peregrine Falcon LJ wandering is presented here as an example of the methodology followed to distinguish between the two phases. Above the first peak of movement from the nest cliff (Net Displacement). Below the highest increment of coefficient of variation (ΔCV) between two consecutive displacements. Both occurring on day 14 June 2016 (16/165), when wandering started after 32 days of PFDP

2. ábra Az LJ jelölésű vándorsólyom PFDP periódusának végét és a kóborlási periódus kezdetét mutatja az ábra illusztrálva a módszert, amit a két periódus elkülönítésére használtunk. A felső panel a fészektől való első elmozdulási csúcsot mutatja (Net Displacement). Az alsó panel két egymást követő elmozdulás közötti legnagyobb variációs koefficiens növekményt (ΔCV) ábrázolja. Mindkettő 2016. június 14-én (16/165) történt, amikor a fiatal sólyom 32 napnyi PFDP után elkezdett kóborolni

We assessed whether net displacements, NDs, among individuals changed during dispersal phases (PFDP, wandering and wintering), by means of a general linear mixed model with ‘ND’ as dependent variable, ‘sex’ and ‘phase’ as fixed factors, ‘individual’ as a random factor, and a normal error distribution. To account for the predictor relationships, we employed a nested ANOVA design where ‘sex’ and ‘phase’ interact each other and are both nested in individual, sex was also nested in phase: so the resulting model was phase + sex(phase) + individual (sex*phase).

To investigate land use during winter we categorized land-cover as coded at the second or third hierarchical level (EEA, 2000) and acquired from GIS databases of CORINE Land Cover (CLC) digital maps (scale 1:25,000) of Sicily (http://dataservice.eea.europa.eu/dataservice). We considered the following 7 land-use categories: cereal steppes, grazeland, shrubland, agri-mosaic (most herbaceous crops on irrigated land intermingled with other arboreal and herbaceous crops), arboreal crops (including vineyards), woodland (including both artificial and natural formations), and urban areas. To explore individual similarity of habitat uses during winter, we analyzed the diurnal locations (i.e. excluding nocturnal fixes, see below) per every individual in each land-use class using a multidimensional scaling (MDS) ordination. This procedure found the eigenvalues and eigenvectors of a matrix containing the similarities between all individuals' locations as expressed by the Bray-Curtis index of similarity, currently used for abundance data. Then to estimate the preference for land-use classes we compared KDE95, considered as used areas by Peregrine Falcons, with available areas as identified by MCP95s. We used a design of first type (i.e. used compared with known proportions of available units) and evaluated whether the use and availability of space differed among land-use classes by the standardized selection ratio B_i and the related chi-square test (Manly *et al.* 1993).

Finally, we made an analysis of nocturnal roost sites, by extracting all data recorded between 21:00 pm and 04:00 am, which corresponds to the darkness period through the whole year at the latitude of Sicily. We considered only the wandering and wintering phases and excluded the PFDP, because the roosts used at this stage are in or nearby the natal cliff, and hence depend from the habitat features of a given nesting site. We categorized nocturnal roosts as: a) trees, including bushes; b) cliffs and rock piles; c) electricity pylons, in order to perform a general linear mixed model with 'number of nocturnal fixes' as dependent variable, 'type of roost' and 'phase' as fixed factors, 'individual' as a random factor, and a normal error distribution. The 'individual*phase', 'individual*type of roost' and 'phase*type of roost' interactions were also modelled.

We used QGis 2.6.1 to perform all spatial analyses, STATISTICA 10.0 (Statsoft inc.) and PAST 3.18 (Hammer *et al.* 2001) for all statistical analyses, setting the statistical significance threshold at $P < 0.05$. Dates were expressed as Julian calendar days (1st January = 1). To avoid overestimation of sample means due to averaging extreme values, we preferred to use the median and lower-upper (Q25-Q75) quartiles of ND values.

Results

Post-fledging dependence period

The mean fledging day of the 19 Peregrine Falcons tagged during 2014–2017 was 17 May, without sex difference (Student's test $t_{17} = 1.03$; $P = 0.32$), although males fledged on average four days earlier than females. The mean (±SD) duration of PFDP was 47±16 days (min-max: 27-84), again without sex difference ($t_{17}= 0.06$; $P = 0.95$). The juvenile falcons ended their PFDP (and started their wandering phase) on average the 3 July (min-max: 10/6-10/8). Males tended to become independent four days earlier than females, although this difference was statistically not significant ($t_{17} = 0.52$; $P = 0.61$). The PFDP length did not show any linear correlation with fledging date of juvenile falcons (Pearson's $r = –0.109$; $P = 0.67$; $n = 19$); besides, the Julian day of fledging did not significantly correlate with the Julian day of wandering (Pearson's $r = 0.371$; $P = 0.13$; $n = 19$).

The GLM used to assess the factors predicting the net displacements of Peregrine Falcons was statistically significant (F_{47} = 6674.183; P = 0.000) and explained most of the original variability in the ND data set (Adjusted R^2 = 0.874). Two of the fixed factors, i.e. the intercept (F_1 = 32.654; P = 0.000) and the phase (F_2 = 5.881; P = 0.006), together with the random factor individual(sex*phase) (F_{42} = 5401.04; P = 0.000) were statistically significant, whereas the sex(phase) was not (F_3 = 0.982; P = 0.410).

The NDs during the PFDP were statistically shorter than those during wandering (Tukey's HSD with unequal N: P = 0.00002), and wintering (Tukey's HSD with unequal N: P = 0.00002). Nonetheless, all the 171 ND combinations among individuals during the PFDP are not statistically significant in the post hoc tests (Tukey's HSD with unequal N: P range = 0.196-1.000). The four pairs of siblings included in these 171 ND combinations were not significantly different, therefore displaying analogous net displacements from the natal cliffs.

Overall, their median displacement was 0.167 km from the natal cliff, and males did not differ from females (Tukey's HSD with unequal N: P = 0.633) *(Table 1, Figure 3)*. Some individuals performed long flights, over 48 km in females and over 37 km in males, while still dependent on their parents *(Table 1, Figure 3)*. During their PFDP the juvenile falcons stayed nearby the natal cliff, because the median KDE95 area explored was 0.226 km^2 (Q25-Q75: 0.087-0.454 km^2) with a maximum value of 3.782 km^2. Males tended to explore smaller areas around the cliff than females, although this difference was not significant (0.17 km^2 in males vs 0.24 km^2 in females, Kruskal-Wallis $H_{1,19}$ = 0.377; P = 0.539).

The directions of movements around the cliff site were statistically different from a uniform circular dispersion (Rayleigh's z value = 7.61; P = 0.0002; n = 19), as all individuals showed a clear tendency to explore more the northern, eastern and southern quadrants with

Table 1. Median values in kilometres of male and female juvenile Peregrine Falcons during onset of their natal dispersion in Sicily. All net displacement values (n fixes) have been calculated with respect to the nest-site of each individual. PFDP = Post-fledging dependence period; Q25 = lower quartile, Q75 = upper quartile

1. táblázat Szicíliai vándorsólymok költés utáni diszperziójának kezdeti fázisai alatt mért medián értékek kilométerben kifejezve. Minden nettó elmozdulási érték az egyedek fészkéhez van viszonyítva. PFDP = kirepülés utáni korai periódus (post-fledging dependence period), Q25 = alsó kvartilis, Q75 = felső kvartilis

Phase	Sex	N individuals	N fixes	Q25	Median	Q75	Minimum	Maximum
	F	13	7033	0.070	0.249	1.215	0.000	48.502
PFDP	M	6	3286	0.040	0.073	0.212	0.000	37.907
	Total	19	10319	0.055	0.167	0.897	0.000	48.502
	F	12	20085	7.024	24.879	64.849	0.004	218.405
Wandering	M	6	4864	8.330	18.548	147.469	0.004	249.786
	Total	18	24949	7.090	23.969	66.003	0.004	249.786
	F	9	7798	8.675	47.859	72.714	0.060	116.646
Wintering	M	2	2013	15.931	16.571	151.123	1.210	153.822
	Total	11	9811	8.734	41.117	75.739	0.060	153.822

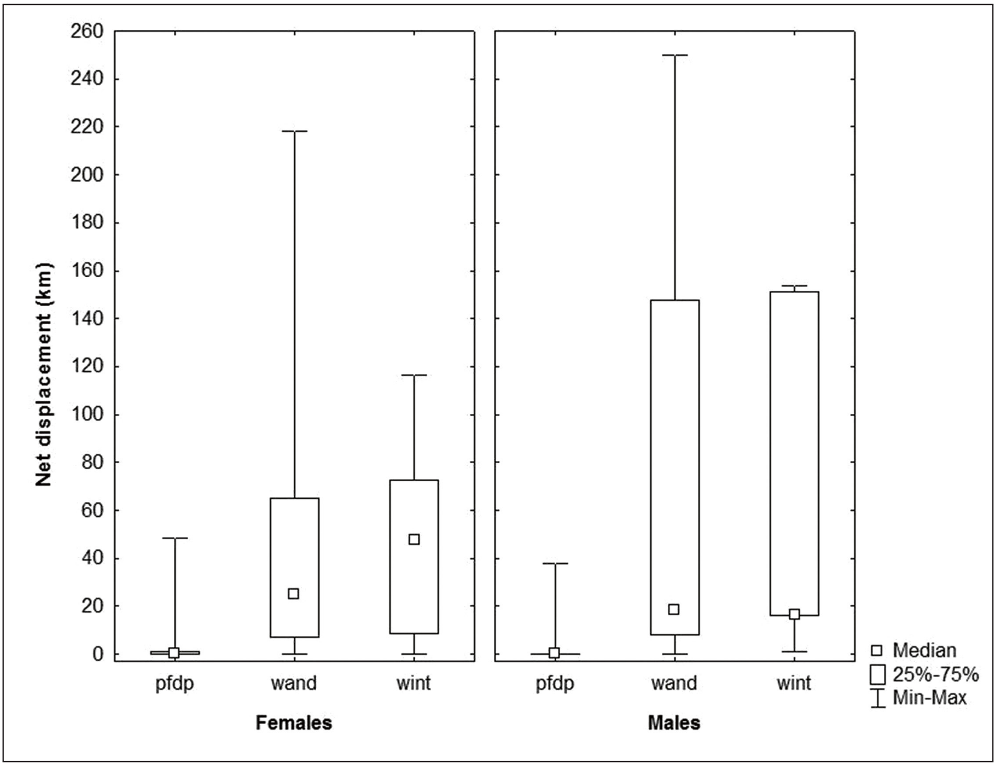

Figure 3. Median displacements values in kilometres of male and female Peregrine Falcons across the three initial phases of natal dispersal. All displacements have been related to the nest-site position of every individual. pfdp = post-fledging dependence period, wand = wandering, wint = wintering

3. ábra Hím és tojó vándorsólymok medián elmozdulásai (km) a kirepülés utáni diszperzió első három szakaszában. Minden elmozdulási érték az egyedek fészkéhez van viszonyítva. pfdp= kirepülés utáni korai periódus (post-fledging dependence period, PFDP), wand = kóborlás (wandering), wint= telelés (wintering)

respect to the natal cliff location (*Figure 4* above). The pattern for the total sample of juvenile falcons showed a quite high concentration of dispersion (mean vector r = 0.633) headed for directions with mean azimuth α = 95.49° (bootstrapped 95% confidence = 66.16°–121.4°). Males and females not differ in this pattern (Watson-Williams' $U_{1,17}$ = 2.483; P = 0.131). Siblings from three pairs behaved heterogeneously, flying with bearings distant 22.5° (n = 1) and 67.5° (n = 2) each other, while those of the fourth pair tended to fly more or less with the same bearing (< 10°), however the mean azimuth angles of the four sibling duos did not statistically differ (Watson-Williams' $U_{1,6}$ = 0.002; P = 0.881).

Wandering

This second temporal segment, which is the first true dispersal moment in the life of young falcons, proved to be an idiosyncratic phase, and no pattern is actually emerging in our sample, as juvenile falcons dispersed from the natal cliff in several ways *(Table 2)*. Some of them (e.g. individuals KP and JA in *Table 2*) did short (4–7 days) nomadic explorations then came back to natal site, to move progressively far (JA) or to stand always close in following days (KP). Other individuals (NF black, LV, KL) stayed always very close (0.49-1.63 km) to natal site, moving back and forth the natal cliffs rather than beginning a true wandering phase, with maximum travel bouts of 40–60 km *(Table 2)*, the remainders moved gradually far away. All individuals during wandering came back one or many times to natal cliffs, as showed by the minimum values in *Table 2*.

The total median net displacement during wandering was 23.969 km *(Table 1, Figure 3)*, however the NDs during the wandering phase were statistically shorter than those during wintering (Tukey's HSD with unequal N: P = 0.00002). Females travelled significantly more

Table 2. Summary of net displacements in kilometres from natal cliffs during the wandering phase in Peregrine Falcons from Sicily and Salina Island (NP black and JL black). Every individual is named by its lecture ring code; same letter specifies the sibling duos. JL black was recovered and died in Salina island after a summer windstorm when still in PFDP. NA = not available

2. táblázat Nettó elmozdulások összesítése a kikelés helyétől számítva kilométerben a kóborlási periódus alatt Szicíliából és Salina-ról (NP black és JL black). Minden egyed a gyűrűkódja alapján van elnevezve; ugyanaz a betű testvérpárokat jelöl. A JL black jelölésű sólyom még a kirepülés utáni korai periódus alatt pusztult el Salina-n egy nyári szélvihar után. NA = nem hozzáférhető

Name	Sibling duo	Year	Sex	n	Q25	Median	Q75	Minimum	Maximum
NF black		2017	M	377	0.08	0.49	9.77	0.01	43.58
LV	a	2016	M	209	0.04	0.68	1.14	0.01	58.96
KP		2014	M	709	0.40	0.72	3.93	0.00	249.79
KL		2015	F	1988	1.48	1.63	2.35	0.00	62.81
LB	a	2016	F	2219	1.16	5.69	6.85	0.02	82.85
NS		2016	F	1852	6.56	8.68	8.86	0.03	51.71
LB black		2017	F	288	8.69	15.84	18.19	0.22	42.03
JT	b	2015	M	1526	14.83	15.94	17.18	0.00	128.28
JA		2014	F	2731	6.84	18.43	36.17	0.14	124.93
LP	b	2015	F	2346	16.59	19.95	43.43	0.06	149.74
NP black	c	2017	F	676	2.58	25.87	28.08	0.03	73.76
LJ		2016	F	2117	50.21	56.62	64.60	0.05	91.46
JF	d	2016	F	2096	61.14	64.18	73.74	0.01	101.21
ND		2016	F	1922	65.44	73.94	106.66	2.99	218.41
LZ		2016	F	1648	84.26	90.53	121.51	0.06	156.86
KJ black		2017	M	1894	147.42	147.50	149.32	0.79	164.85
JB	d	2016	M	149	18.93	177.06	210.76	0.02	236.20
KN		2015	F	202	192.35	194.49	196.54	27.47	198.76
JL black	c	2017	F	0	NA	NA	NA	NA	NA

than males with median displacement values of 24.879 km and a maximum of 218.405 km with respect to males, which nonetheless showed the highest upper quartile (Q75) and the maximum absolute displacement of 249.786 km far from the nest cliff *(Table 1, Figure 3)*. Only two pairs of siblings *(*b and d in *Table 2)* had statistically different travelling distances (Tukey's HSD with unequal N: P = 0.00005), but not the third pair *(*a in *Table 2;* Tukey's HSD with unequal N: P = 0.980*)*.

The directions of leaving for the initial dispersal travel from the natal cliff (i.e. first day of wandering, see *Figure 2*) were statistically different from a uniform circular distribution (Rayleigh's z value = 14.51; P = 0.0002; n = 18), as all but one individual showed a clear tendency to fly away more to the northern, eastern and southern quadrants with respect to the nest-cliff location (*Figure 4* below). The pattern for the total sample of juvenile falcons showed a quite high concentration of dispersion (mean vector r = 0.650) headed for wandering directions with mean azimuth α = 101.85° (bootstrapped 95% confidence = 76.4°–125.9°). Males and females did not differ in this pattern (Watson-Williams' $U_{1,16}$ = 0.019; P = 0.892), as well as sibling duos (Watson-Williams' $U_{1,4}$ = 0.009; P = 0.928). We found no significant correlation (circular correlation coefficient r = –0.112; P = 0.61; n = 18) between the individual azimuths of PFDP movements and those of the first day of wandering, meaning that the main direction of exploration during PFDP did not influence the direction of leaving the natal site.

Only five falcons exited the natal island borders and only for short periods.

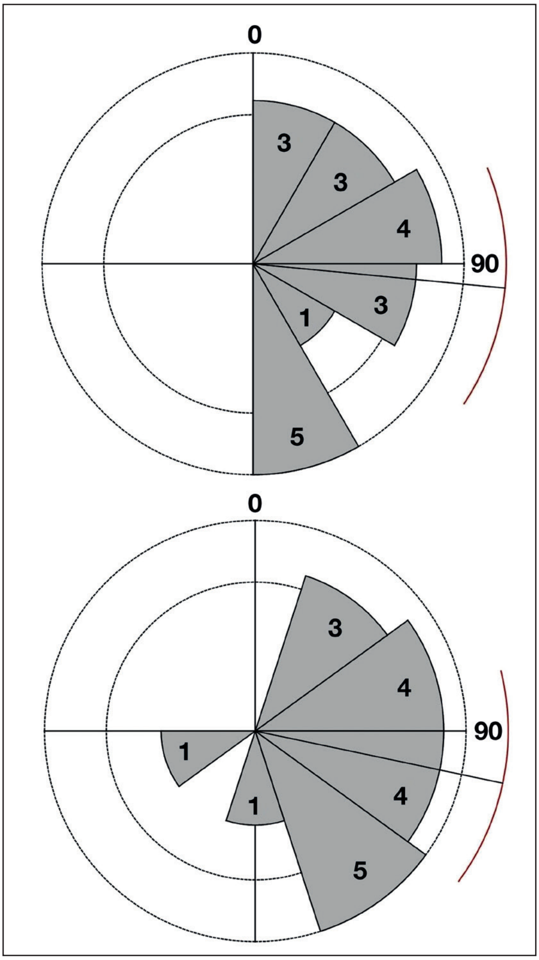

Figure 4. Polar histogram of bearings, ordered clockwise from north (0°) and mean resultant bearing (with respect to East, 90°) taken by Peregrine Falcons during their post-fledging dependence period (above) and wandering phase (below) flights. The number of individuals taking a similar bearing is reported inside the grey inserts

4. ábra Elmozdulások iránya északról (0˚) az óramutató járásának irányába rendezve, és ezeknek átlaga poláris hisztogrammal kifejezve. A felső panel a sólymok kirepülés utáni korai periódusát (PFDP) mutatja, míg az alsó a kóborló periódust. A hasonló irányba elmozduló egyedek száma a szürke cikkelyekben látható

Peregrine Falcon LZ did four short visits of 3-4 days each to Aeolian Island, from 24 August to 3 October 2016. Notably, two out the four visits of Falcon LZ were done reaching the Aeolian Island by nocturnal flights. Contrariwise, Falcon LJ did only a 4-hours trip to the Aeolian island of Filicudi, the 18 October 2017. Falcon ND crossed the Messina Strait the 15 July 2016 and went to Southern Calabria (Italy) for exactly one day before to come back Sicily. Falcon KJ flew over open sea for 4 hours to a maximum distance of 14 km, from the south-eastern coasts (far-off Siracusa, see *Figure 1*) and then came back. Eventually, Falcon NP, born in Salina island, from the 10 of August 2017, started moving back and forth among all the archipelago island but the far away Stromboli. The 20 of October 2017 reached in less than 2 hours inland eastern Sicily, near the Aetna volcano, where was unfortunately shot two days after the arrival, thus hampering us to gather information about its successive movements.

First wintering

Eleven of the 19 Peregrine Falcons provided complete (6 females, 1 males) or partial (3 females, 1 male) wintering data. Their median displacement value was 41.117 km distant from natal cliffs, with a maximum displacement of 153.822 km. Females displaced significantly farther than males during winter (Tukey's HSD with unequal N: $P = 0.00002$), but as in the case of wandering phase, a male had the highest upper quartile (Q75) and maximum winter displacement *(Table 1, Figure 3)*. However, the net displacements of males referred to only two individuals and these results should be taken with caution *(Table 1, Figure 3)*.

Complete data of seven falcons allowed focusing in more detail about the overwintering phase. All the seven falcons but one had a single wintering range, as falcon KJ had a double range in two nearby areas of 99.5 and 169.8 km^2, which it visited intermittently throughout the winter *(Figure 1)*. Their average ± SD home range during winter extended 135.65 ± 82.31 km^2 (min-max: 50.8-234.3) and is on average composed by cereal steppes (48%), arboreal crops (20%), agri-mosaics (12%), shrubland (9%), grazeland (7%), then urban areas (2%) and woodlands (2%). Such a quantitative composition is statistically different between all the seven falcons ($X^2_{36} = 3701.4$, $P = 0.0001$) as can be appreciated by the scatter in the bi-variate space of multidimensional scaling *(Figure 5)*. The scatter arranges the individuals according to the decreasing quantity of cereal steppes used during winter (F1) and to the decrease of shrubland and increase of arboreal crops uses (F2). Thus, on F1 individuals JT and NS have 76.1% and 79.6% of cereal steppe composing their winter habitats while LZ has only 1.5%. On F2, shrubland decreases from 43.0% and 41.4% in ND and JA to 16.2% in LZ. This latter individual has on the contrary the highest quantity (i.e. 62.8%) of arboreal crops.

Despite these quantitative features of habitat configuration, the Peregrine Falcons were not randomly selecting the habitat in proportion to availability ($X^2_6 = 63.280$, df = 72, $P = 0.000$) and the standardized selection ratio Bi ranked the land-use classes by the probability of use such as: $B_{i\text{-urban}} = 0.21$, both $B_{i\text{-agri-mosaic}}$ and $B_{i\text{-cereal}} = 0.18$, $B_{i\text{-arboreal crops}} = 0.17$, $B_{i\text{-shrubland}} = 0.13$, $B_{i\text{-grazeland}} = 0.10$ and $B_{i\text{-woodland}} = 0.05$. Thus the probability of using the urban habitat, independently from its relative quantity in every individual's home range, is only slightly superior to that of agri-mosaics, cereal and arboreal crops, but two times more than grazeland and four times more than woodlands.

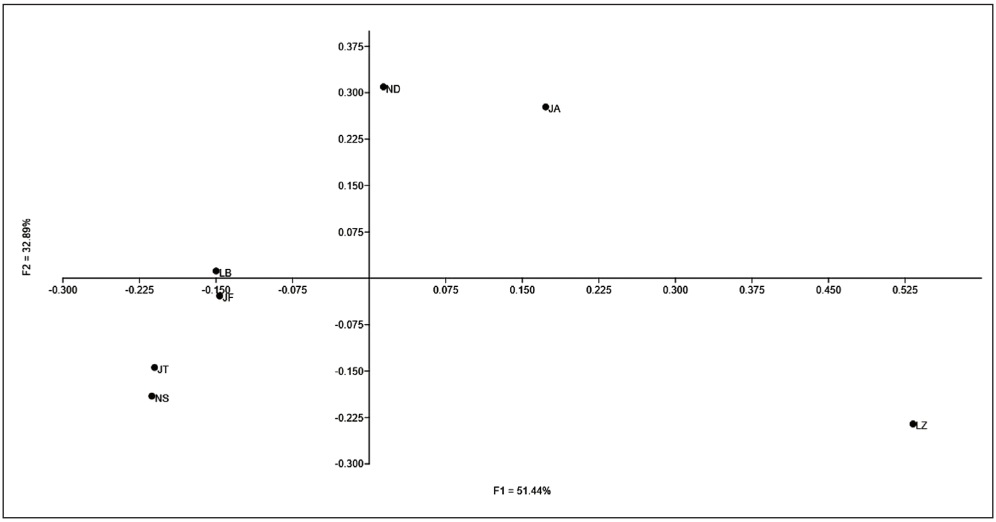

Figure 5. Scatter of seven juvenile Peregrine Falcons plotted in the bi-variate coordinate system of multidimensional scaling. The F1 and F2 axes express the percentage of variance accounted for by these factors and indicate their relative importance in explaining the spread in the data. Ordination along F1 expresses the decrease of cereal steppes use (from left to right), while along F2 expresses the decrease of shrubland and increase of areboreal crop use (from top to below) during winter. Each axis is scaled using the square root of its respective eigenvalue

5. ábra Fiatal vándorsólymok élőhelyválasztása kétváltozós koordinátarendszerben ábrázolva, többdimenziós skálázás segítségével. Az F1 és F2 tengelyek fejezik ki a két változó által magyarázott variancia százalékát és jelzik azok relatív fontosságát az eredmények kialakításában. Az F1 tengely mentén történő ordináció a gabonaföldek használatának csökkenését jelzi (balról jobbra), míg az F2 tengely csökkenő preferenciát jelez a bokros élőhelyek irányába és növekvőt a gyümölcsfás ligetek felé (fentről lefelé) a téli időszakban. Mindkét tengely a sajátértékeinek négyzetgyökével lett standardizálva

Data collection of nocturnal roost sites provided 4,475 locations during the wandering phase of 18 individuals, and 2,636 locations of 10 individuals during the wintering phase. At night during wandering juvenile falcons used 41.23% trees, 33.36% pylons and 25.41% rocks. These frequencies changed during wintering, with a decrease of tree use (24.09%) and an increase of pylon use (52.81%), while the frequency of rock use was similar (23.10%). Nonetheless, the GLMM yielded no significant results ($R^2 = 0.413$; $F_{65} = 1.898$; $P = 0.065$), as none of the tested single fixed effects (phase: $F_1 = 4.629$; $P = 0.06$; type of roost: $F_2 = 0.377$; $P = 0.688$), except for the intercept ($F_1 = 25.077$; $P = 0.000$), and neither the fixed interaction term (type of roost*phase: $F_2 = 1.682$; $P = 0.214$) were statistically significant. The random effect of ‘individual’ was not statistically significant either ($F_{17} = 0.897$; $P = 0.588$), and neither was its random interaction with phase (individual*phase: $F_9 = 0.785$; $P = 0.633$). Only the random interaction ‘individual*type of roost’ was statistically significant ($F_{34} = 2.297$; $P = 0.032$). This was occurring because few individuals, like for instance KL, disproportionately used more pylons (e.g. Tukey’s HSD with unequal N: P of KL vs JB = 0.042; P of KL vs NS = 0.039; P pf KL vs = 0.035, etc.) than the others.

Discussion

The onset of juvenile dispersal is a vital moment in the life history of raptors, since it is the time when juveniles definitively leave the nest but are still vulnerable and inexperienced (Newton 1979). Upon reaching independence, the foraging skills they acquire, as well as the moment they choose to leave, the places they visit, the distances they cover, and the general behavioural patterns they display will probably affect their chances of surviving and the severity of mortality rates (Bowler & Benton 2005, Walls *et al*. 2005, Kitowski 2009).

The availability of individual-based biologging technologies has produced an exponential increase of published papers on bird movements in the last 30 years (e.g. *Figure 2* in López-López 2016). Nonetheless, most dispersal studies on Peregrine Falcons are still based on recoveries of banded birds (but see Dixon *et al*. 2012), besides focusing on migrating populations located in North America and North Eurasia (Dixon *et al*. 2012, Katzner *et al*. 2012, Dennhardt & Wakamiya 2013, Faccio *et al*. 2013, Mattox & Restani 2014), with few exceptions for the rest of Europe, like Zuberogoitia *et al*. (2009) who provided recovery distances from Spain.

Natal dispersal data presented here are the first study by satellite telemetry concerning juveniles from a Peregrine Falcon population living in Mediterranean island of Southern Europe. We distinguished a post-fledging dependence period (Morrison & Wood 2009, Penteriani & Delgado 2009) close to the natal cliff, including the temporary excursions (Walls & Kenward 1995) made by fledglings back and forth the natal cliff and usually within the same day. Departure from natal area, as indicated by a net displacement increase (Kareiva & Shigesada 1983, Turchin 1998) and peaks of cumulated coefficient of displacement variation (Limiñana *et al.* 2008), specified the first true step in the dispersal process of Peregrine Falcons, that we called wandering as in Penteriani and Delgado (2009). The third step related to the onset of natal dispersal we have analyzed, is the settlement in a territory during winter, when Peregrine Falcons occupy their first home-range choosing one or many roosts to exploit the habitat during the non-breeding season.

During post-fledging dependence period, altricial birds rely on their parents for food, while simultaneously developing the flight, foraging and social skills necessary for independent survival (Weathers & Sullivan 1989, Wheelwright & Templeton 2003). After fledging, Sicilian Peregrine Falcons stayed very close to the natal cliff and explored small areas nearby. In agreement with the few studies on raptors recording PFPD distances between sex (Seaton *et al*. 2008, López-López *et al*. 2014), we did not find significant difference between females and males. The duration of post-fledging dependence period differs among raptor species, ranging from 143-231 days in the Bearded Vulture *Gypaetus barbatus* (López-López *et al*. 2014) to 2–8 days in Lesser Kestrel *Falco naumanni* (Bustamante & Negro 1994). It likely does not only depend on body-size and/or lifespan, as it lasts longer in the smaller, magpie-size New Zealand Falcon *Falco novaeseelandiae* (76 days, Seaton *et al*. 2008), than in larger species like the Osprey *Pandion haliaetus* (18–46 days, Bustamante 1995) or the Black Kite *Milvus migrans* (15–36 days, Bustamante & Hiraldo 1989). Juvenile Peregrine Falcons would reach independence in two or more months

(Cramp & Simmons 1980), a figure comparable to the 47 days (range: 27–84) of PFDP shown in our sample, and to the 50–82 days of juveniles tracked in Iowa (Powell *et al*. 2002). However, Dzialak *et al*. (2009) recorded a shorter period (15–36 days) during another tracking programme in USA, and observed that different rearing and habitat conditions significantly influenced the PFDP duration.

Environmental conditions experienced by juveniles within the natal area soon after fledging may play the ultimate role in determining the timing and orientation of dispersal (Hanson *et al*. 2003, Pasinelli *et al*. 2004, Walls *et al*. 2005), and might explain better than body-size and/or lifespan, and according to Dzialak *et al*. (2009), the PFDP patterns observed in Peregrine falcons and other raptors. As in the Osprey we found no relation between fledging date and PDFP duration (Bustamante 1995), in contrast to what was found in the Black Kite, in which migratory urgency seems to affect the timing of family break-up (Bustamante & Hiraldo 1989). Despite the overall PFDP pattern described so far, we should emphasise the role of individual behaviour during this phase, because only some individuals made temporary daily excursions of 40-50 km when still dependent on parents. In addition, all falcons scattered their flights from NNE to SSE, regardless from sex and sibling condition, and this resulted in a non-random bearing of PFDP flights headed on average toward 95° East.

Wandering is another particularly important period, because juvenile raptors both explore new areas potentially suitable for future settlement, and start to hunt exclusively by themselves for the rest of their life. The start of wandering in Sicilian Peregrines occurs on average in early July and lasts until 30 November according to the conventional deadline we used to distinguish wandering from the wintering phase. In most avian species, with the remarkable exception of migratory birds which disperse much farther than resident species (e.g. Kassara *et al*. 2017), dispersers move relatively short distances, and long-distance dispersal is uncommon (Sutherland *et al*. 2000). Many raptor species, from small kestrels to large vultures, have been reported to exhibit great individual variation in the timing of dispersal (e.g. Bustamante & Hiraldo 1989, Bustamante & Negro 1994, Walls & Kenward 1998, López-López *et al*. 2014). In our study, Peregrine Falcons travelled relatively short median distances of some 25 km, but showed large individual variation. Strictly speaking, one third of the 18 individuals in which we measured this phase did not disperse, showing median movements less than 10 km far from the natal cliff, but with temporary excursions in the range of 50–250 km. The presence of non-dispersers has already been noted in raptor populations (e.g. Walls & Kenward 1998). The other Sicilian individuals moved a maximum median distance of 200 km, with independent trajectories and being apparently limited only by the size of the island. We documented only occasional trips taken outside the island borders, most of them directed to the well visible Aeolian Island. Vice versa the juvenile tagged in Salina moved to Sicily. Females dispersed farther than males, as occurs in many bird species, including raptors and Peregrine Falcons (Greenwood 1980, Sutherland *et al*. 2000, Zuberogoitia *et al*. 2009, Katzner *et al*. 2012, Faccio *et al*. 2014).

Excluding the group of poorly dispersing individuals, and considering the insular context, the distances travelled by the Sicilian juveniles are comparable to those of continental populations. Female Peregrine Falcons from Northern Spain dispersed on average 80 km, and males 52 km during their pre-breeding movements (Zuberogoitia *et al*. 2009). In the New England (USA) population (Faccio *et al*. 2014), 75% of encounters occurred within the study area, with female dispersing greater distances (153 km) than males (88 km). However, the range of the remaining 25% of individuals extended until to Cuba and Nicaragua. Both Tordoff and Reding (1997) and Katzner *et al*. (2012) reported greater and much more variable dispersal distances, again with significant sex differences and with similar means (337 and 320 km for females, 161 and 176 km for males, respectively). As in the case of PFDPs, the first dispersal flights of Peregrine Falcons had a non-random bearing, on average toward 102° East. The main heading during PFDP did not influence the heading of the first dispersal flights. Juveniles, without sex differences, scattered mostly across the NNE and S quadrants, and only one individual did a westerly first dispersal flight. Non-random east-west bearing during dispersal has been already noted in Common Buzzard *Buteo buteo* (Walls & Kenward 1998), although with significant easterly directions only during the second wintering year. Such a non-random bearing in both PFDPs and first dispersal flights is probably related to the island geography, as already noted by Walls and Kenward (1998), who suggested that dispersing individuals cannot head south in their UK study area, due to the coasts, which act as barriers.

The seven individuals providing complete wintering data had independent home ranges scattered across Sicily and varying in size, the largest (234 km^2) was 4 times larger than the smallest one (51 km^2). We recorded a single case of spatial overlap of two falcons overwintering in the same area but in different years, and one individual had a double home-range and moved between the areas during the entire winter. Seven land-use classes were present in these wintering areas, however, falcons spent the majority of their time in cereal steppes, followed by arboreal crops, agri-mosaics and by the other land-use types. Habitat use indicates that juveniles choose open habitats, particularly human-managed and cultivated areas with both extensive non-irrigated cereal steppes and intensive (e.g. vineyards) crops. Nonetheless, land-use classes were not used proportionally to their availability, as the selection ratio (i.e. probability of use) specified, likely ranking the winter habitats according to the abundance of preferred prey flocks (feral and wood pigeons, starlings, jackdaws, magpies, etc.). Urban, arboreal crops, agri-mosaics and cereal steppes had a selection ratio higher than semi-natural habitats (shrubland, grazeland and woodland). This preference was consistent with the significant individual differences between the frequency of locations among the assortment of land-use classes. A similar use of open cultivated habitats during dispersal has been observed in the Bonelli's Eagle *Aquila fasciata* (Cadahía *et al*. 2010).

No data are currently available in the literature on roost use during the nights of the dispersal period. Overall, the frequency of chosen roost types was consistent between wandering and wintering with falcons roosting mostly on trees, rocks and pylons. Only three individuals had significantly different use of roost sites, roosting significantly more on pylons or rocks.

Concluding remarks

Judging from the onset of dispersal and genetic (see Mengoni *et al.* 2018) data available, the Peregrine Falcons living in Sicily and the surroundings island should be connected to a single and resident population, with still undetected but presumably poor connections to continental Italy. The progressing of investigation on natal dispersal will inform on the floater ecology of this population and will improve our understanding on the population dynamic of the Peregrine Falcons living in Mediterranean island.

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Migratory movements of Peregrine Falcons *Falco peregrinus*, breeding on the Yamal Peninsula, Russia

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Abstract We describe the migration pathways of 12 Peregrine Falcons *Falco peregrinus calidus* breeding on the Yamal Peninsula, Russia. Overall, we tracked 30 complete (17 autumn and 13 spring) and 5 incomplete seasonal migration routes. Winter ranges extended from the Atlantic coast of southern Portugal in the west to Kish Island in the Arabian Gulf in the east, and from Krasnodar in southern Russia in the north to South Sudan. Eight birds were tracked to their wintering sites, with migration pathways ranging from 3,557 km to 8,114 km, taking 14 to 61 days to complete. Birds spent an average of 190 days in their winter ranges (range 136 to 212 days, N = 14), and departure on spring migration took place in April. The home ranges used by wintering Peregrines were varied including coastal habitats, agricultural landscapes, savannah, desert and an urban city. Departure from breeding areas took place in September with birds returning in May. Peregrines exhibited a high degree of fidelity to their winter ranges, with four birds tracked over three successive migrations until the 2012 breeding season.

Keywords: migration pathway, birds of prey, range fidelity

Összefoglalás Oroszországban, a Jamal-félszigeten költő vándorsólymok *Falco peregrinus calidus* közül 12 egyed vonulási útvonalát írtuk le. Összesen 30 teljes (17 őszi és 13 tavaszi) és 5 részleges vonulási útvonalat követtünk. A telelőterületek nyugaton Portugália atlanti partjaitól, keleten a Perzsa-öbölben található Kish-szigetig, valamint északon az oroszországi Krasznodarszktól, délen Dél-Szudánig terjedtek ki. Nyolc madarat követtünk a telelőterületéig, ezek vonulási útvonala 3557–8114 km között változott, amit 14–61 nap alatt tettek meg. A madarak átlagosan 190 napot töltöttek telelőterületükön (136–212 nap, n = 14), majd a tavaszi vonulást áprilisban kezdték meg. A telelő vándorsólymok költőterülete változó volt, beleértve tengerparti, mezőgazdasági, sivatagos és szavannás élőhelyeket, valamint egy várost. A költőterületet a madarak szeptemberben hagyták el, és májusban tértek vissza. A vándorsólymok jelentős hűséget mutattak a telelőterületük iránt, amit 4 – a 2012-es költési időszakig 3 vonulási szezonon keresztül követett – madár bizonyít.

Kulcsszavak: vonulási útvonal, ragadozómadár, területhűség

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Introduction

Holarctic Peregrines *Falco peregrinus* breeding at northern latitudes are migratory, including *F. p. tundrius* and northern populations of *F. p. anatum* in the Nearctic, and *F. p. calidus* along with northern populations of *F. p. peregrinus* and *F. p. japonensis* in the Palearctic (White *et al.* 2002, 2013, 2018). In contrast to the Nearctic, little is known about the northern distribution limits of wintering Peregrines across the Palearctic. The Eurasian breeding range of the *F. p. calidus* subspecies extends from the Kanin Peninsula eastwards through Russia to Arctic Yakutia, where they intergrade with *F. p. japonensis*/*harterti* (White *et al.* 2013).

It has long been known that migratory Peregrines from Northern Eurasia can spend the winter in Europe and North Africa (Cramp & Simmons 1980), sub-Saharan Africa to the Eastern Cape (S33.73, E26.42 (Hd.dd); Jenkins & Stephenson 1999), the Middle East (Jennings 2010), Central Asia (Dementiev & Gladkov 1952), the Indian subcontinent (Naoroji 2006) and South-East Asia (White & Bruce 1986), reaching as far south as Christmas Island (S10.5, E105.66) (Carter & Silcocks 2010). However, relatively little data exists on the connection between breeding and wintering areas for migratory Peregrines in Eurasia. Ganusevich *et al.* (2004) successfully tracked two adult females from their breeding ranges on the Kola Peninsula, Russia to wintering areas in Western Europe, while Peregrines from the Taimyr Peninsula wintered in Central Asia (Eastham *et al.* 2000). More recently, systematic tracking of Arctic Eurasian Peregrines has shed further light on migratory connectivity, with birds wintering in SE Asia originating from breeding regions in northern Yakutia (Dixon *et al.* 2012), those wintering in the Indian Sub-continent originating from the Khatanga Gulf region (Dixon *et al.* 2017), while those reaching the Middle East and Arabia came primarily from the Yamal, Gydan and western Taimyr Peninsulas (Sokolov *et al.* 2016).

In this study, we describe the multi-annual migration movements and wintering locations of *F. p. calidus* Peregrines deployed with satellite-received transmitters at their nest sites on the Yamal Peninsula, Russia.

Methods

This study is based on data received from Peregrines breeding in the low-shrub tundra zone of the Yamal Peninsula, Russia (N 68.22, E 69.15), in an area of maritime valleys, low hills and tundra marshes with patches of willow thickets within a network of lakes, rivers and streams. Peregrines used river or lake sand cliffs up to 40 m high as nesting sites (see details in Sokolov *et al.* 2014).

In June 2009, we fitted 18g solar PTTs (Microwave Telemetry Inc., MD, USA) to 10 adult Peregrines (9 females and 1 male; including a breeding pair) at nine breeding territories within a 78 km^2 polygon. In August 2010, we fitted similar PTTs to two juvenile males prior to fledging; these were the offspring of two females deployed with PTTs in the previous year. All PTTs were attached to the birds by a Teflon ribbon backpack harness. The Teflon ribbon strand was attached at its midpoint to the anterior anchor of the PTT and the two ends were tied with a flat-knot to crossover the sternum, with the trailing ends attached to the posterior anchor points of the PTT. The PTT was mounted high along the dorsal midline with space to fit two fingers under the PTT unit (see Dixon *et al.* 2016).

We received telemetry data from the Argos satellite tracking system (CLS, France). We used the Douglas Argos Filter Algorithm ('DAR' filter) designed to retains points, which correspond to a realistic rate of movement and which do not form tight angles (Douglas *et al*. 2012, Wikelski & Kays 2017). We only included Argos data of ≥ LC1, removing duplicate timestamps, and set a maximum realistic movement speed between locations as 100 km/h, while the internal angle between successive locations was set at 15°.

We defined the start of migration as the first day the bird began continuous movement towards the north or south. In two cases, birds moved to a staging area prior to initiation of long-distance migration. Arrival at winter and breeding ranges was defined as the first day the Peregrines movements became localized. Average speed of migration was calculated as the whole distance from start to end divided by duration, while average flight speed during migration was calculated as the distance between successive location points divided by time between such locations. We did not calculate migration speeds for birds which stopped transmitting during migration. We identified stopover sites when birds travelled less than 50 km between two subsequent locations.

Results

Overall, we tracked 30 complete (17 autumn and 13 spring) and 5 incomplete seasonal migrations by 12 (9 adult females, 1 adult male and 2 juvenile males) Peregrines from breeding sites within 200 km^2 on the Yamal Peninsula of the Russian Arctic *(Figure 1)*. Four birds were followed over 3 years covering three complete autumn and spring migrations.

Typically, Peregrines departed on autumn migration during September, taking from two weeks to two months (mean = 25 days) to cover distances from 3,000 km to 8,500 km to reach their wintering areas *(Table 1)*. Spring migration from the wintering areas started in April and birds arrived at their breeding sites in May. On average, Peregrines spent 190 days in the wintering area and 117 days in the breeding area. The autumn departure dates of four

Table 1. Dates of the migration events for the Peregrine Falcons in 2009–2012
1. táblázat A vándorsólymok vonulásának dátumai 2009–2012 között

Seasonal event	N	Mean	Median	SD	Range
Autumn departure	20	14 of Sept	13 of Sept	9	28 Aug – 28 Sep
Arrival at winter range	17	11 of Oct	11 of Oct	18	17 Sept – 26 Nov
Spring departure	14	19 of Apr	23 of Apr	8	4 – 29 Apr
Arrival at breeding range	13	16 of May	15 of May	5	10 – 28 May
Duration of autumn migration (days)	17	26.8	24.5	11.7	14 – 61
Duration of spring migration (days)	13	25.8	23	8.4	14 – 47
Speed of autumn migration (km/day)	17	222.6	215.43	57.5	0.4–1072.6
Speed of spring migration (km/day)	13	239.6	214.6	77.8	0.6–1205.2

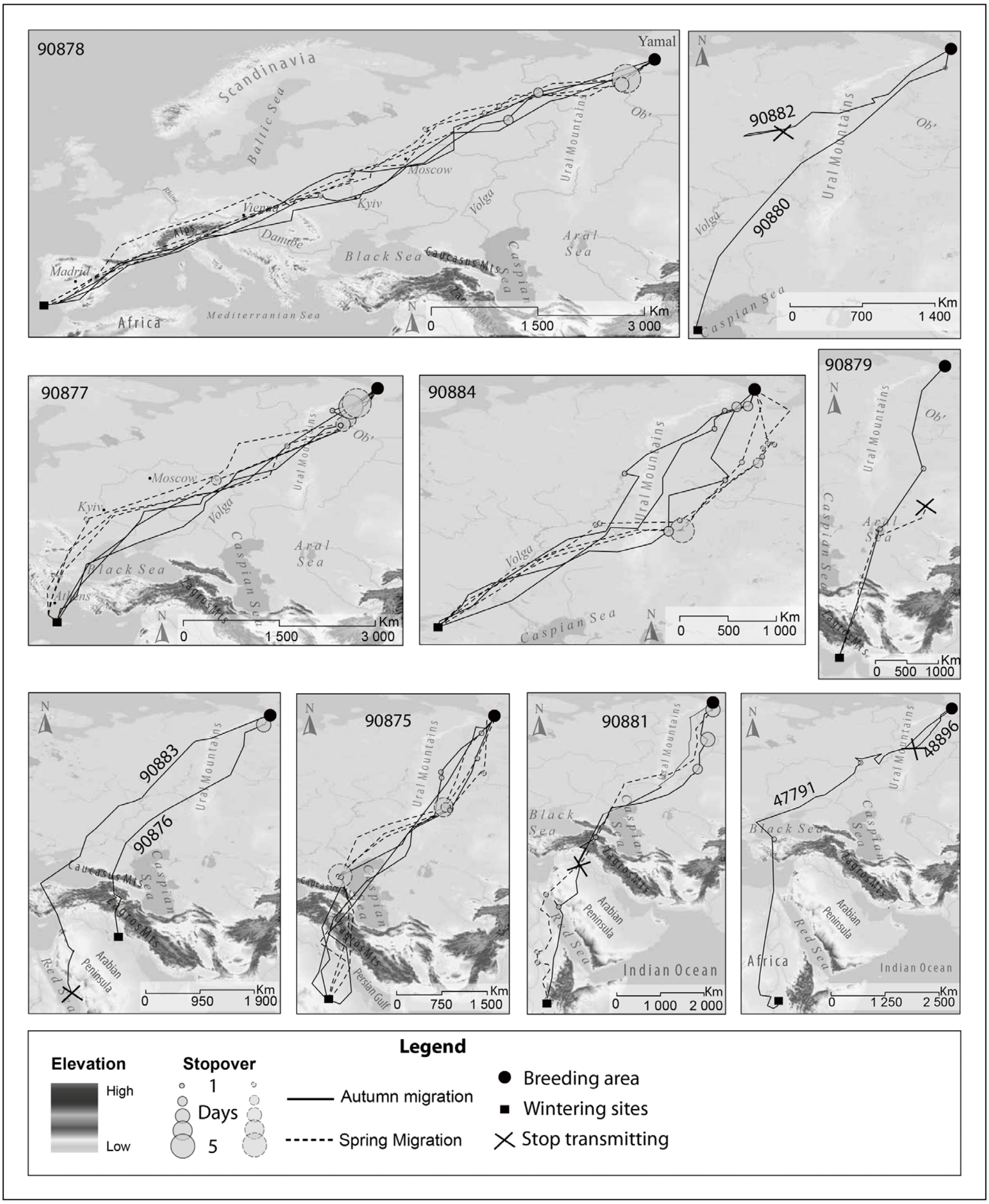

Figure 1. Migration of Peregrine Falcons breeding on the Yamal Peninsula. Number is ID of different birds. 90876 and 90883 are male and female respectively from a breeding pair. Juvenile male (47791) is a fledgling of 90884, whilst juvenile male (48896) is a fledgling of 90878

1. ábra A Jamal-félszigeten költő vándorsólymok vonulási útvonalai. A számok a különböző egyedek azonosítói: 90876 és 90883 egy párt alkotó hím és tojó. A 47791-es fiatal hím a 90884-es fiókája, illetve a 48896-os hím a 90878-as fiókája individual birds differed across three consecutive years by an average of 6.9 days (median = 6 days, range 1–14 days), while the corresponding difference for departure on spring migration was 3.3 days (median = 3.5, range 0–7).

The average daily distances travelled were 223 km and 240 km during autumn and spring migrations, respectively. The maximum travel distance detecting during one day (24 hours) was 1,072 km on autumn migration and 1,205 km during spring. The lower Ob River basin, 180 km south of the breeding area, was a regularly used utilized stopover area during both autumn and spring migrations *(Figure 1)*. We also identified stopover sites in the Ural Mountains for two birds (90884, 90875) and the western coast of the Caspian Sea for another (90880). All autumn migration routes exhibited longitudinal displacement to the west by 20° to 95°, and all distances travelled were longer than the Great Circle distance *(Table 2)*.

We localized 9 wintering ranges of Peregrines, extending from 8˚ W (Faro, Portugal) to 54˚ E (Kish Island, Arabian Gulf) in longitude and from 46˚ N (Krasnodar, Russia) to 6˚ N (Junqali, Sudan) in latitude *(Figure 1)*. All the winter ranges were situated SW of the breeding area, with a mean bearing of 225° and a mean great circle distance of 4,987 km *(Table 2)*. Three of the wintering ranges were on the Atlantic, Mediterranean and Arabian Gulf coasts, whilst a fourth was within 20 km of the Caspian Sea coast. The five others were situated in inland territories at least 100 km from the coast *(Figure 1)*.

Peregrines wintering at inland sites in Krasnodar, Russia (N 46.08, E 39.46), Dagestan, Russia (N 43.98, E 47.09) and Saudi Arabia (N 25.9, E 45.01) occupied ranges that encompassed mainly agricultural land, the wintering ranges of an adult and juvenile in South Sudan encompassed savannah (N 6.09, E 34.36; N 7.64, E 32.76), whilst a male wintering in Baghdad, Iraq (N 33.31, E 44.35) occupied a wholly urban range. The three coastal wintering ranges differed in character; in Portugal (N 37.09, E 8.38) the coast comprised urban areas, Mediterranean scrub and a saline lagoon, in Crete (N 35.50, E 24.17) the range encompassed islets and a rocky coastline backing on to Mediterranean scrub, agricultural land and an airport, whilst in the Arabian Gulf the Peregrine range encompassed urban areas, an airport and plantations on Kish Island (N 26.57, E 53.93), as well as rocky hillside of the adjacent mainland.

Table 2. Migration metrics for tracked Peregrines
2. táblázat A nyomonkövetett vándorsólymok vonulási adatai

Bird ID	Number of full migrations	Great Circle distance (km)	Mean migration path in autumn / spring (km)	Bearing
47791	1	7447	8554	220
90875	6	4983	5247 / 5330	212
90876	1	4190	4485	215
90877	6	4556	5048 / 5037	241
90878	6	5698	6366 / 6470	275
90879	1	4742	4978	200
90880	1	2967	3082	216
90881	2	7342	8114 / 8073	218
90884	6	2954	3557 / 3600	229

The breeding pair that we tracked would have occupied widely separated winter ranges; the male established a winter range in Baghdad, Iraq, whilst his mate stopped transmitting during her autumn migration 1,185 km to the SW on the Red Sea coast of Saudi Arabia. Individual Peregrines showed fidelity to their winter ranges and all four females that still had functioning PTTs were tracked back to the same winter locality in Saudi Arabia, Crete, Portugal, and Krasnodar in successive years.

Losses during autumn migration

All Peregrines deployed with PTTs in 2009 departed their breeding sites on the Yamal Peninsula, but two PTTs stopped transmission during autumn migration. One female (90882) started migration on 28 September, covering about 1,100 km in a SW direction over 11 days, but then location signals were received for a further 3 weeks from a localized area, probably stationary, on the border of the Perm and Komi regions ca. 190 km SE of Syktyvkar, Komi, Russia (N 61.34, E 54.35) before transmission ceased. The second female (90883) departed on 21 September and covered around 5,600 km before transmission ceased on 20 October close to Yanbu, Saudi Arabia on the Red Sea Coast (N 24.37, E 37.92); this being a well-known falcon trapping area (see also Dixon *et al.* 2011, Sokolov *et al.* 2016).

The PTT on one female (90881) stopped transmission during autumn migration in 2010; after departing from the breeding area on 22 September the last signal was received on 18 October around 4,200 km south ca. 30 km southwest of Al Qa'im, Syria (N 34.1, E 40.81).

A juvenile male (48896) departed its natal area in August 2010, this being the offspring of female 90878. After travelling ca. 1,000 km in a week, the bird reached an area close to Serov, Sverdlovsk Region, Russia (N 59.5, E 60.81). Signals were received from a localized area until early October, and briefly resumed again in spring 2011 indicating that the PTT was stationary.

Losses in wintering ranges

The PTTs on two birds, a male (90876) and a female (90880) stopped transmitting when they were in their winter ranges. The male wintering range was located in Baghdad, Iraq (see also Dixon *et al.* 2013) and after arrival on 20 September 2009 transmissions were received until 02 January 2010. The female occupied a winter range in an agricultural landscape on the Caspian coast in Dagestan, Russia, arriving on 22 September 2009 and transmitting location data until 07 January 2010.

A juvenile male (47791), the offspring of female 90884, reached its wintering area in South Sudan in early November 2010, having travelled ca. 8,500 km, but the PTT stopped transmitting signals within a week.

Losses on spring migration

One PTT stopped transmitting during spring migration in 2010. Female (90879), that wintered on Kish Island, Iran started spring migration 04 April, returning along a broadly similar pathway as the autumn migration to reach the coast of the Aral Sea, from where it deviated course, moving SE and then NE to reach an area ca. 80 km northwest Karsakbay, Kazakhstan (N 48.18, E 65.93) when signals came from a localized area ca. 2,600 km from the winter range, probably stationary, until the end of May 2010.

Losses in the breeding area

One PTT (90877) stopped transmitting in the breeding area in late June 2012 and when the nesting territory was checked on 20 June we did not find any Peregrines breeding and there was no sign of the female with the transmitter.

In summer 2012, we re-trapped the remaining three birds at their nesting sites and removed the PTTs (90875, 90878, 90884).

Discussion

Timing, duration and speed of migration

Our data confirm previous observations about the timing of autumn migration of Peregrines breeding in Arctic Russia. Prior to our study, it was known that Peregrines (ssp. *calidus*) disappeared from their breeding ranges on the Yamal Peninsula in September to early October (Paskhalny & Golovatin 2009), while five females, one adult and four juveniles, deployed with PTTs at nest sites on the western Taimyr Peninsula departed during September (Eastham *et al*. 2000). On the Kola Peninsula of Russian Lapland, four female Peregrines (ssp. *peregrinus*) were tracked via satellite and departed their breeding areas in September but only two were tracked to their wintering ranges, both arriving in October after migrations that lasted 15 and 26 days (Ganusevich *et al*. 2004). The timing of autumn and spring migration

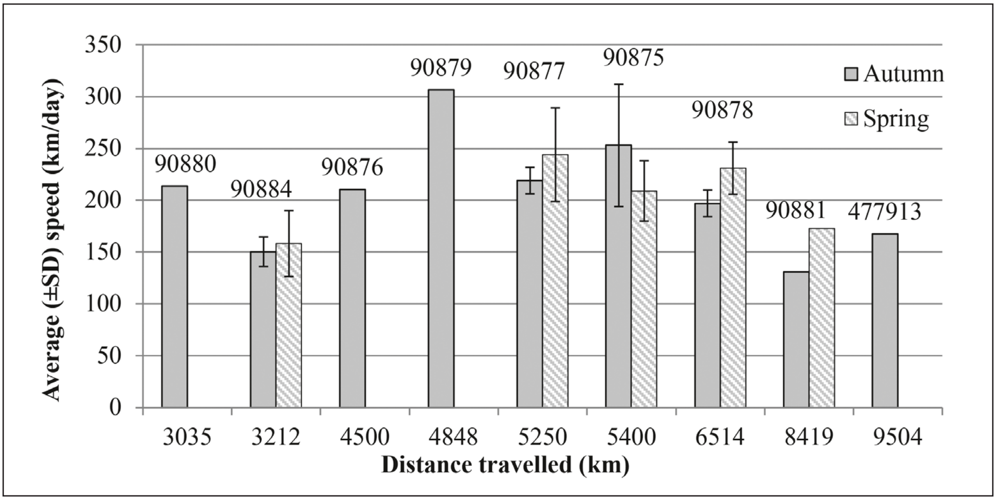

Figure 2. Average speed (±SD) of migration for individual Peregrine Falcons
2. ábra A vándorsólyom egyedek átlagos vonulási sebessége (±szórás)

of satellite-tracked Peregrines breeding in the eastern Taimyr region was also similar to that recorded in the present study, as was the separate migration pathways taken by breeding pairs (Dixon *et al.* 2017).

There was individual variation in speed between autumn and spring migration, but no general differences were apparent in terms of migration distance *(Figure 2)*.

Migration routes

Peregrines breeding on the Yamal Peninsula migrate over a broad front with a westerly displacement, and the birds tracked via satellite reached southerly wintering areas in Western Europe, Africa and the Middle East. Major geographical migration barriers along the migration routes comprised the Mediterranean Sea, Black Sea, Caspian Sea, Red Sea and Persian Gulf, the mountain range of the Caucasus and deserts of the Arabian Peninsula and Central Asia. It was notable that Peregrines whose winter range lay beyond the major sea barriers avoided long sea crossings or took routes that circumvented them. The migration routes taken by Peregrines in North America also appeared to be influenced by coastlines, indicating that long-distance sea crossings can be a barrier to migration (Fuller *et al.* 1998). In contrast, as previously described for the Himalaya (Dixon *et al*. 2017), the mountain chain of the Caucasus was not a barrier to Peregrine migration, and three birds travelling west around the Caspian Sea crossed these mountains to reach more southerly wintering destinations.

In contrast to the adults, which were likely to be returning to winter ranges occupied at least one year previously, juveniles were making their first migrations to unknown winter quarters. Juveniles departed the breeding region around the same time as adults, approximately 20 days after fledging, but not at the same time or along the same migration path as their satellite-tagged parent. One juvenile male (47791) was tracked to its wintering area in South Sudan *(Figure 1)*. This bird migrated independently of its female parent, which wintered in Krasnodar, Russia, on a bearing with a difference of 9° and travelling 4,500 km further. The other juvenile male (48896) initiated migration two days after its female parent (90878), which wintered in Portugal, but although we were only able to track this young bird for a distance of *ca*. 1,000 km, the direction of migration differed by 68°.

The main stopover site for birds departing from and arriving to the Yamal Peninsula was the Lower Ob River, a site where large numbers of waterfowl and waders can congregate during the autumn and spring migration periods (Krivenko & Vinogradov 2008). There was one instance on spring migration when a bird (90877) in 2010 flew from the stopover area on the Lower Ob River 180 km to its breeding area on 15 May, only to return after 7 days, presumably because of unfavorable conditions in the breeding area. Another stopover site was an area with many lakes in the Chelyabisk and Kurgan region in the southern Ural Mountains, a region known to hold large numbers of waterfowl and waders during seasonal migration (Tarasov & Lyakhov 2016). A third stopover location identified on the western coast of Caspian sea has previously been recorded as a stopover or wintering site for Peregrines (Lipsberg 1982), where they can hunt waterfowl wintering here (Dementyev & Gladkov 1952).

Wintering locations

Peregrines occupied discrete ranges in their wintering areas, spending more time there (*ca*. 6 months) than in their breeding ranges (*ca*. 4 months) and those tracked over multiple migrations returned to the same winter range in successive years. Fidelity to winter ranges contrasts with the observation of breeding dispersal in the same birds, where 33% of females dispersed to new breeding ranges up to 40 km away (Sokolov *et al.* 2014). All winter ranges were within the breeding distribution of resident Peregrine populations, encompassing the subspecies *brookei* in the Mediterranean, *peregrinus* in Russia, *pelegrinoides* in the Middle East and *minor* in Africa. When establishing wintering ranges, birds may face intraspecific competition from local resident Peregrines as well as other migrants, although we do not know the extent to which these ranges are occupied exclusively by individuals nor if they are defended against conspecifics.

The wide diversity of habitats used by wintering Peregrines in this study is notable, reflecting the adaptability of the species. This plasticity in habitat selection, together with the broad front migration to widespread winter locations across at least two continents, means that migratory Peregrines from our study population are not particularly susceptible to geographically localized threats outside the breeding area.

Acknowledgements

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Extreme territorial aggression by urban Peregrine Falcons toward Common Buzzards in South-West England

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Abstract Peregrine Falcons *(Falco peregrinus)* breeding on a city centre church in Exeter, in the south-west of England, have been studied in detail since first occupation in 1997. During this period, changes in both male and female falcons have been recorded. Following the arrival of a new female Peregrine in 2009, a dramatic change in behaviour towards Common Buzzards *(Buteo buteo)* on passage over the city was noted. Buzzards flying over Exeter are attacked by the falcons, especially so when in proximity to the church. We have attempted to document these attacks through our own observations, with additional information from local residents and wildlife organisations. Further records have come from veterinary surgeries and wildlife rehabilitators regarding injured buzzards found in the city. This paper documents the extreme levels of territorial aggression as demonstrated by the pair of Peregrines during cooperative attacks on Buzzards. We reveal this unique interspecific behaviour by summarising the number, frequency, timing and outcome of attacks undertaken over an eight-year period. We describe and illustrate the strategy employed by the Peregrines during a typical attack, plus consider implications on breeding productivity and the future scenarios should one of the current pair be replaced.

Keywords: Peregrine Falcon, *Falco peregrinus*, urban nesting, territorial behaviour, Common Buzzard, *Buteo buteo*, co-operative attack strategy

Összefoglalás A délnyugat-angliai Exeter belvárosában álló templomon fészkelő vándorsólymok *(Falco peregrinus)* már 1997 óta rendszeresen megfigyelt és vizsgált madarak. Az azóta eltelt időszakban a költőpárt érintő minden egyedi változás, mind hímeket, mind tojókat ideértve, feljegyzésre került. A 2009-ben érkező tojó óta jelentős változás figyelhető meg a város fölött átrepülő egerészölyvekkel *(Buteo buteo)* szemben tanúsított viselkedésben. Az Exeter fölött megfigyelhető egerészölyveket – különösképpen akkor, ha a templom irányába haladnak – gyakran megtámadják a vándorsólymok. Elhatároztuk, hogy lejegyezzük ezeket a támadásokat, saját megfigyeléseinket a helybeliek és vadvédelmi szervezetek információival kiegészítve. További adatok álltak rendelkezésre a városban megsérült egerészölyvekről, amelyeket állatorvosok és vadvédelmi szakemberek szolgáltattak. Jelen tanulmány célja a vándorsólymok egerészölyvekkel szemben mutatott közös támadásainak, agresszív territórium védelmének leírása. Ezt az egyedi, fajok közötti kölcsönhatást az elmúlt nyolc évben megfigyelt támadások számának, gyakoriságának, időzítésének és végkimenetelének közzétételével mutatjuk be. Továbbá részletesen foglalkozunk a vándorsólymok támadási stratégiájának ismertetésével, kitérve a költési siker és a lehetséges jövőbeli változások értékelésére.

Kulcsszavak: vándorsólyom, városi fészkelés, territoriális viselkedés, egerészölyv, együttműködésen alapuló támadási stratégia

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Introduction

The most recent census to determine the breeding population of the Peregrine in the UK, Isle of Man and the Channel Islands was undertaken in 2014, and estimated at 1,769 pairs, a 22% increase on the previous survey in 2002 (Wilson *et al.* 2018). Local populations in some traditional upland regions have declined, but much of the increase is due to increased lowland occupation and breeding in quarries and on a variety of built structures, with the majority being in urban environments.

The first church in the UK to be occupied by Peregrines, following their recovery from the population crash in the 1950's was in Devon, in the south-west of the UK. Peregrines were first recorded at St Michael and All Angels Church in Mount Dinham, Exeter in 1988 with a male holding territory, and with a pair resident in 1989. A nest box was erected in early 1990 but it was not used, and there was only sporadic occupation by a variety of single falcons for the following three years.

An adult pair was observed on the church in April of 1997, and first breeding occurred, with the falcons using a nest constructed earlier in the year on a flat ledge on the north face of the tower by Common Ravens *(Corvus corax)*. This site was used for successful breeding until 2007, when a new female found the original nest box (installed in 1990), and it has been used every year since. Whilst there have been changes of both adult falcons at this site, breeding has occurred every year, fledging 57 young between 1997 and 2017 (mean 2.7 chicks per year). The Peregrines' tolerance of human activity at street level just 30m below them allows weekly collections of fallen prey remains with no disturbance to the falcons.

Data from this study, together with detailed observations of behaviour, have provided a valuable opportunity for a long-term study of prey selection and diet, as well as a variety of other aspects of breeding biology and behaviour (Drewitt & Dixon 2008, Dixon & Drewitt 2012, Dixon 2017).

During this period, there have been recorded changes in the resident adults, and it is our belief that the current male arrived in March of 2005, and the female took occupancy in March of 2009.

Neither of the resident Peregrines are ringed, and we therefore cannot prove that the same individuals have been paired since 2009, although we strongly believe that this is so. This is due to almost daily observations of familiar behaviour of both birds at the church, by a variety of experienced watchers. There have been no gaps in occupation by either bird, and since they hold territory all year they can both be seen daily on regular perches.

Territorial interactions with Common Buzzards

In May of 2012, we heard that the Peregrines had attacked and knocked down a Common Buzzard near the church, and then attacked another one a few days later. This was new behaviour for the Exeter Peregrines, as Buzzards were often to be seen passing high over the city, but there had never been any interaction between the species.

The first confirmed record of this territorial aggression occurred a month later, on the 9th of June, 2012, during the weekend that the juveniles fledged, when A. Gibbs saw both adult

Peregrines attacking a Buzzard. The Peregrines repeatedly stooped onto the Buzzard high over the city, hitting it and causing it to fall. A. Gibbs was able to pinpoint its location and found it dead, 480 m to the east of the church. Later that day, we learnt that another attack had been witnessed during the morning, and the dead Buzzard also retrieved. Both Buzzards were easily found due to the loud and persistent alarm calling by corvids and gulls, which were surrounding and noisily mobbing the dead bird on the ground. Further attacks by the Peregrines were witnessed over the next few weeks, and A. Gibbs found another dead Buzzard which had fallen into the nearby river Exe, 150 m from the church. Ten attacks were observed or reported with four Buzzards seen knocked down over the city during 2012.

Many of these observed attacks on Buzzards involved both falcons working together in what appeared to be co-operative behaviour.

These events were later published in 'Devon Birds' to raise awareness of this behaviour, as such extreme levels of aggression by one pair of Peregrines appear not have been recorded before in the UK (Dixon 2013).

Following the attacks on Buzzards witnessed in 2012, we reviewed the recorded observations from previous yearly visits to the church during N. Dixon's weekly collections to retrieve prey items as part of a study into the diet and prey selection of the Exeter Peregrines. This confirmed that the first record of territorial aggression occurred in 2009, shortly after the arrival of the current female, when she repeatedly stooped onto a Buzzard near the church and drove it away. N. Dixon also recorded the first sighting of both Peregrines chasing a Buzzard the following year in 2010, but the outcome was unseen due to losing sight of the birds behind tall buildings. We also learnt of three attacks involving both falcons in 2011, seen by a photographer during the fledging period in early June.

It became apparent that the attacks on Buzzards began with the arrival of the new female in 2009 and although it had taken some time to understand what was happening, we were keen to see whether this level of aggression was maintained by the current pair of Peregrines in subsequent years.

Methods

During the following breeding seasons 2013 to 2017, where time allowed, we increased the frequency of our visits to the church to observe the territorial behaviour of the pair. A. Gibbs was often able to visit on most days during May and June, the months when previous attacks were most prevalent. These specific watches were undertaken from the top deck of a public car park, 250 m from the church, with panoramic views of the sky above Exeter. N. Dixon continued with weekly visits to the church to collect fallen prey remains, plus undertook occasional extended watches during May and June.

Both morning and afternoon watches were undertaken whenever possible, between two and four hours in duration during favourable weather conditions. Binoculars proved to be more useful than a telescope, offering a wide field of view and enabling the watcher to keep up with fast-moving events more easily, with many attacks easily observed by the naked eye.

The following details of each attack were recorded, whenever possible: a) initial location of Buzzard when first attacked, b) escape/attempted escape direction of Buzzard, c) final outcome of attack, d) location of any Buzzard brought down by the attack, e) nature of attack (by one or both members of the pair), f) number of stoops made during attack, g) time and duration of attack.

In addition to our actual observations, and reported sightings from members of the public, we informed local wildlife groups and bird watching organisations to increase awareness and asked them to record any interactions seen. Local veterinary surgeries, wildlife hospitals and rehabilitators were also contacted to make them aware of this behaviour and report any Buzzards found dead or injured in Exeter.

Attack strategy

The first indication that a Buzzard is present will be alarm-calling by one of the falcons, whether they are on their regular perches on the church or soaring high over the city. At this stage, the passing Buzzard may be almost invisible to the human eye due to its height over the city or its distance from the church.

The falcons will undertake a determined flight towards the Buzzard, whilst still alarm calling, either from the church, or from a high soaring position elsewhere in the sky. If one or both falcons begin their flight from the church, then considerable time and effort are required to get to a position above the Buzzard before an attack starts. Once they have gained sufficient height above the Buzzard, the attack will involve repeated individual vertical stoops down onto it, with immediately looping back up again to repeat the action. During a co-operative attack, the male Peregrine will stoop first, passing close enough to cause the Buzzard to 'flip' upside down to present its talons in defence. The female Peregrine will follow almost immediately aiming to hit the Buzzard on its head, wing or back as soon as it has righted itself, and before it has time to present its talons again.

The falcons will both continually loop back up again to a position above the Buzzard to begin repeated attacks. These synchronised 'stoop cycles' continue until the Buzzard reaches a territory boundary and the attacks are given up, or until the Buzzard is hit and knocked down.

All attack stoops made by the Peregrines are vertical or near-vertical, from an elevated position directly above the Buzzard. Sometimes an attack begins as a 'solo attack', usually when the adults are patrolling in different parts of the territory, or one is on the church. Alarm calls by the solo attacker alert the second adult and the described pattern of stoop cycles is usually initiated quickly.

When synchronicity is lost during 'stoop cycles', it is not uncommon to see either Peregrine 'waiting on' briefly above the Buzzard for its partner, to 'reset' the timing of attack.

The Buzzard's attempts to fly away are slowed by the repeated talon-presenting 'flips' in defence of an attack, but many Buzzards will escape if their flight direction takes them further away from the church. Once they reach a territorial boundary some distance from the church, the Peregrines will give up on the chase. It is unfortunate that a Buzzard under attack from repeated stoops is unaware that if its intended direction of escape takes it closer to the church, the more likely it will be subjected to increased attacks with greater ferocity.

If a Buzzard has been hit and fallen to the ground, gulls and corvids immediately take to the air and mob the Buzzard, especially if it has fallen onto a roof top or the ground but away from passers-by. After a successful attack, the Peregrines will either fly back to the church or return to soaring over the city. Occasionally, they appear unsettled and will give 'low intensity' alarm calls for up to two hours, while keeping watch, especially if a Buzzard has been injured and fallen but taken refuge in trees. In this case, behaviour during this period includes brief periods of alarm calling while making short return flights out from regular perches or from the entrance to the nest box. If the weather conditions are calm, one of the adult falcons, invariably the male, will often perch on the metal cross on the very top of the spire (72 m above ground level).

Annual frequency of attacks on Common Buzzards

Attacks on Buzzards by the Peregrines fall into two main categories: those by the pair and those by a single bird. *Table 1* shows all observed attacks on Buzzards from 2009 to 2017, with a total of 455 observed attacks, with 52 downed Buzzards. When adding the 18 injured or dead Buzzards found within 700m of the church in Exeter over this period where no attack was observed, the totals increase to 70 downed Buzzards from 473 attacks.

What is of interest, is that of the 455 observed attacks, 275 (60.4%) involved both falcons working together in highly effective co-operative behaviour, that often results in the Buzzard being hit and knocked down. The female alone has undertaken 118 observed attacks (25.93%) compared to the male at just 41 (9.01%).

The territorial attacks on Buzzards in 2012 were all recorded on days of good weather, often with blue skies, sun and some wind, and so from 2013, we tried to increase our observations of

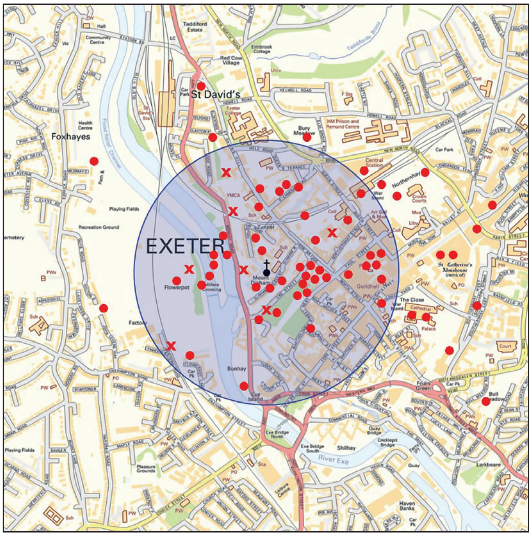

Figure 1. Map of Exeter city centre showing the locations of the 70 downed Common Buzzards described in the text. The map is a 2 km × 2 km square centred on St. Michaels and All Angels church, and the inner circle shows a radius of 500 m from the church. This map contains public sector information licensed under the Open Government Licence v3.0. This map has been updated, having first being featured in British Birds. Image by Fluke Art

1. ábra Exeter belvárosának térképe feltüntetve a szövegben részletezett 70 egerészölyv pusztulás helyét. A térkép egy 4 km^2 nagyságú területet mutat a St. Michaels and All Angels templomot középre igazítva, egy 500 m sugarú körlappal lefedve a templom környékét. A térkép az Open Government Licence v3.0 által meghatározott nyilvános adatokat tartalmaz. A térkép a British Birds lapban történő megjelenése óta frissítve. Készítette: Fluke Art

Table 1. Yearly totals of observed attacks by Peregrine Falcons on Common Buzzards in Exeter (2009–2017) NB. Outcome of Observed attacks. Buzzards seen hit and knocked down are recorded as 'Downed'. If the Buzzard was seen to fly off following an attack, it was 'Driven off', and 'Unseen' refers to attacks where the outcome was obscured by buildings or trees in the foreground.

1. táblázat A vándorsólyom egerészölyvek ellen indított támadásainak összesített értékei éves bontásban Exeter városában (2009–2017)

Year	No. of Attacks	By Pair	By Female	By Male	Reported attack, details unknown	Downed Buzzards	Outcome unseen/ Driven off
2009	1		1				1
2010	1	1					1
2011	3	3					3
2012	10	7		3		4 (1)	6
2013	45	38	1	4	2	10 (7)	33
2014	43	32	7	3	1	3 (1)	40
2015	217	121	59	26	11	26	191
2016	92	40	44	4	4	6 (6)	86
2017	43	33	6	1	3	3 (3)	40
Totals	**455**	**275**	**118**	**41**	**21**	**52 (18)**	**401**

the falcons during May and June. It is at the point when the young no longer require brooding, around 12–14 days after hatching, that the behaviour of the adult Peregrines appears to change, and they become far more aggressive towards Buzzards. At this stage, both adults spend much more time perching out of sight of the young but return to feed them regularly. In the three weeks prior to fledging, when absent from regular perches on the church, the adults were often to be found soaring high over the city. Initially, we assumed that this was hunting behaviour, but after many hours of observation we now believe that the main purpose of this behaviour is to patrol the territory. Our increased interest and monitoring of this behaviour resulted in 45 observed attacks and 17 Buzzards downed throughout the year.

2014 was an interesting year with 43 attacks observed, but with only 4 downed Buzzards. During our intentional watches, we attempted to record the number of stoop-cycles during each co-operative attack. We recorded between one and 12 stoop-cycles (i.e. 2 to 24 individual stoops) per attack, with a mean of five cycles. It was apparent that, depending on the initial location of the Buzzard, a single cycle is often sufficient to drive away a Buzzard if the attack starts close to the territory boundary.

Our increased watches plus additional records from local observers in 2015 resulted in figures that were totally unexpected in comparison to previous years. We recorded 217 attacks with 26 Buzzards knocked down, but this huge increase was due to a variety of factors. There were far higher numbers of Buzzards seen over Exeter than in previous years and A. Gibbs was able to spend many hours on watch during the spring and early summer months, and also enlisted the help of Exeter University Zoology undergraduates as additional observers.

Table 2 shows the monthly counts of attacks observed over Exeter through 2015, with attacks recorded in January and February. Egg laying began on 22nd March, with a clutch of four eggs laid by the 30th March. Incubation occurred throughout the month of April, but only two eggs hatched on the 30th April and the 2nd of May. Prior to hatching, most attacks on Buzzards were by the male as the female undertook most of the incubating.

The juvenile Peregrines no longer needed constant brooding from the 12th May, but we had already recorded dual attacks during this month, when the adult Peregrine, invariably the female would leave the juveniles and join its partner to attack Buzzards. It was during May and June (when the pair are at their most aggressive) that 145 attacks were carried out by the pair working cooperatively, resulting in 21 Buzzards being knocked down.

Two separate Buzzards were attacked and knocked down in May 2015 by the female Peregrine acting on her own, something we had never recorded before. During the first of these attacks, she descended in a high velocity stoop from a very high altitude down over the city at an angle of approximately 35 degrees in what we perceived as a 'hunting style' stoop, taking approximately seven seconds to reach the Buzzard which was soaring at a much lower altitude. This caught the Buzzard completely by surprise and it had no time to defend itself. The female struck the Buzzard then looped up to stoop down again, but the Buzzard was already falling with what appeared to be one wing trailing. This style of attack by the female has now been observed on four further occasions (Dixon & Gibbs 2015a, 2015b).

The second event occurred when she flew straight out from the church and North-eastwards toward the University, and then having gained height, she undertook a single stoop before striking a Buzzard which was gaining altitude having flown out from trees in the University grounds.

Table 2. Attacks by Peregrine Falcons on Common Buzzards in Exeter during 2015
2. táblázat Vándorsólyom támadások egerészölyvek ellen Exeterben 2015-ben

Month	No. of attacks	By the pair	By Female	By Male	Reported attack, full details unknown	No. of Buzzards downed
January	2	1	–	1	–	–
February	3	3	–	–	–	–
March	14	8	–	5	1	–
April	26	3	6	14	3	–
May	60	41	13	3	3	12
June	85	50	32	1	2	9
July	9	4	4	1	–	1
August	4	3	–	–	1	1
September	11	7	3	1	–	3
October	3	1	1	–	1	–
November	–	–	–	–	–	–
December	–	–	–	–	–	–
Total	**217**	**121**	**59**	**26**	**11**	**26**

In 2016, 92 attacks were observed, again with the additional help of watches by the Exeter University students, with six Buzzards seen knocked down and a further six found dead or injured in the city (Dixon & Gibbs 2016).

Unfortunately, work and other commitments reduced the time that we and other observers could spend on intentional watches in 2017, and only 43 attacks were observed, with three Buzzards seen knocked down and a further three recovered in the city.

Having spent considerable time observing this behaviour, it is apparent that Buzzards can be seen passing over the city at a range of altitudes from about 60 m above ground level to such a height that they are barely visible to the human eye and can be moving in any direction across the city. It is apparent that an extraordinary amount of effort is put into attacking any Buzzard encroaching into the Peregrines territory, by both adult falcons, and especially by the female. It is not unusual to observe the pair 'ringing up' to gain height for several minutes, in order to reach a Buzzard flying across the city at high altitude, and then launch an attack with multiple stoops. The longest flight we have observed to attain height above a passing Buzzard, prior to then mounting an attack, was on the 16th of June, 2015. The female took just under 10 minutes from the first alarm calling and leaving the church, to get to a position above a very high soaring Buzzard. This involved alternate direct fast wing flapping flights into the head wind combined with circular 'ringing up' flights before gaining height above the Buzzard and then making a number of direct solo stoops, which then drove it to the north. The previous week, on another intentional watch day on the 7th June, along with several members of the Gloucester Raptor Monitoring Group, 13 Buzzards overflying the city were attacked, with one downed and a total of 200 stoops counted.

The longest attack over the city to date has been timed at nine minutes, when a Buzzard was repeatedly stooped on over the city and driven east, almost to the territory boundary in 2014. In attempting to escape, the Buzzard then turned and flew back towards the city centre, under constant attack, before we lost sight of the birds as they headed north. A more typical attack, captured by a BBC film crew on 26th June 2013, showed the adults making 21 stoops in total on a Buzzard during an attack period of 1 minute 52 seconds.

Seasonal and diurnal timing of attacks from DB

Attacks observed between 2009 and 2017 have been recorded in all months of the year except December, with most from April through to August but with a dramatic increase in May and June, during the pre- and post-fledge period. This is due to a combination of factors: the juvenile Peregrines in the nest no longer need brooding, so both adult Peregrines are often to be found soaring over the city during periods of good weather, and the warmer conditions increase the likelihood of Buzzards moving across the region.

Attacks on Buzzards over the city mainly occur between 10.00 and 16.00 BST, which corresponds with the period of most Buzzard soaring activity during spring and summer (Dare 2015).

All the Buzzards that we have recovered after an attack by the falcons, either alive, injured or dead have been sub-adults, showing streaked plumage on the breast and a variety of wing and tail moult stages, indicating they are all between one and three years old. Eleven Common Buzzards have now been sent to the Predatory Bird Monitoring Scheme (P.B.M.S) at the

Centre for Ecology and Hydrology (C.E.H) Lancaster for tissue and organ sampling, and analysis. Full details have not yet been received on all the carcasses sent but initial findings show both male and female Buzzards in the sample. This would confirm our observations that any Buzzard over the city in the Peregrines territory is likely to be attacked, suggesting there is no bias towards the smaller males, and that the larger females are just as likely to be knocked down. Ongoing information from vets and the Royal Society for the Prevention of Cruelty to Animals (RSPCA) indicate that Buzzards recovered alive following an attack by the falcons are often underweight, confirming what we have found when weighing dead Buzzards.

Territorial interaction with other species

The Exeter Peregrines only exhibit this extreme territorial aggression towards Common Buzzards and show little interest in the many other species that pass through their territory or high over the city. No attention is paid to (Great) Cormorant *(Phalacrocorax carbo)* or Little Egret *(Egretta garzetta)* that regularly fly up the river Exe, passing in very close proximity to the spire of the church. There are very occasional and brief skirmishes with Common Ravens *(Corvus corax)*, Carrion Crows *(Corvus corone)* and the larger gull species involving little more than a single short stoop or fly-by, but with none of the intensity or aggression as that shown to any Buzzard within a kilometre of the church. Passing Red Kites *(Milvus milvus)* have been subject to varying degrees of behaviour, ranging from brief attention to occasional attacks by single falcons or the pair, but again these attacks have lacked intensity and have not involved synchronised the recognised 'stoop cycles'. Eurasian Sparrowhawk *(Accipiter nisus)* has been occasionally recorded as prey (Dixon & Drewitt 2012), and are often seen flying around the spire and above the nearby rooftops while the Peregrines are perching on the stone pinnacles at the same height, and they instigate no interest whatsoever.

Discussion

Peregrines and Buzzards are often found in the same traditional habitats, such as sea cliffs and upland crags, and increasingly across lowland regions as both species increase their ranges. Aerial encounters, mobbing and skirmishes can be frequent, or the two species may totally ignore the other. There are historical records of Peregrines killing Buzzards in the UK, and their remains have been recovered at Peregrine eyries, although this is very rare (Tubbs 1974, Ratcliffe 1993).

There can be no doubt that the extreme territorial aggression exhibited by the Exeter Peregrines towards Buzzards is unique, as this behaviour is not currently recorded anywhere else in the UK.

Since the arrival of the current female in 2009, they have knocked down 70 Buzzards from over 470 attacks over the city, up to the end of 2017. We strongly believe these figures to be the tip of the iceberg, and that many attacks are neither seen nor reported to us.

We started undertaking intentional watches from the car park roof in 2013, and whether it is a short watch of two hours or a day watch of six to eight hours, invariably the attacks that we observe are not subsequently reported to us by other local observers. This would indicate that in our absence, and on days of favourable weather when Buzzards are likely to be passing over Exeter, many interactions will be missed.

It is on these intentional watches, and when we are joined by other interested raptor workers, that the conversation often turns to why do this pair, or specifically the female, show such extreme levels of aggression towards Buzzards and why they, or specifically the female who appears to have instigated this, invest so much time and energy into this behaviour.

These are interesting questions especially given that attacking a Buzzard carries a high risk of incurring an injury to the Peregrine, and that Buzzards moving at high altitude over the city pose no threat to the falcons or their young. We will never know the cause of this behaviour and can only speculate that something must have happened in the past to trigger the current levels of aggression.

We have considered what the effects of this behaviour may have on breeding productivity as the female has demonstrated that she will leave eggs and newly hatched young in the nest to chase and attack buzzards.

The juvenile Peregrines have been observed joining in with attacks every year since 2013, often from late July and into September. These incidents are occasional rather than regular but raises the question as to whether they will take this learned behaviour into new territories and continue as adults. We began ringing and colour banding in 2012 and are currently only aware of one of the juveniles that fledged from the church (a male in 2015) which has established its own territory. This is on a church in a town approximately 30 miles away, which it first occupied in 2017, and bred successfully in 2018. There have been no territorial incidents with Buzzards there to date.

On a final note, we are watching with interest as to when we get a change of partner at the church, and what will happen next. If we are correct as to the dates of both falcons first occupation, it is likely the current male that will be replaced first, with a younger and fitter Peregrine.

If this should occur, will a new male learn and indulge in the current and highly effective co-operative behaviour towards Buzzards or leave it to the female? And if the female were to disappear or be replaced, it would be fascinating to see whether the male Peregrine would continue with attacks on Buzzards over Exeter.

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Influence of the Eagle Owl *(Bubo bubo)* on the Peregrine Falcon *(Falco peregrinus)* population in Germany

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Abstract In Germany, the Eagle Owl is the only animal species that has a massive impact on the distribution and breeding success of the Peregrine Falcon. Both species compete for the same breeding sites on rocks. In addition, the Peregrine Falcon belongs to the prey spectrum of the Eagle Owl. The Eagle Owl always dominates at places where the two species meet. Since the 1980s, the Eagle Owl has taken over many of the rock face breeding sites of the Peregrine Falcon in Germany. This trend towards the taking-over of Peregrine Falcon nesting sites is ongoing in areas with rocks, as not all regions of Germany have yet been completely colonized by Eagle Owls. Since 1975, the Eagle Owl initially nested on buildings in rural areas, but it is now also colonizing urban areas. Eagle Owls are more and more frequently taking over Peregrine Falcon nest boxes on buildings. The currently growing Peregrine Falcon breeding population on buildings is expected to decline in coming years due to predation by the Eagle Owl, even though these owls do not breed very successfully on buildings and many old and young owls are killed. These statements apply to large parts of Germany. In other areas of Europe, the future usage of buildings as Eagle Owl breeding sites can be expected to have an impact on the Peregrine Falcon populations there. At least eight other Peregrine Falcon breeding sites on buildings and rocks have been taken over by Egyptian Geese *(Alopochen aegyptiaca)*.

Keywords: breeding on buildings, Eagle Owl, Egyptian Goose, Peregrine Falcon, predation

Összefoglalás Németországban az uhu az egyetlen faj, amely jelentős hatással van a vándorsólyom elterjedésére és költési sikerére. A két faj ugyanazon sziklai fészkelőhelyekért van versenyben. Emellett, a vándorsólyom szerepel az uhu zsákmánylistáján. Az uhu minden esetben dominál, amikor a két faj együtt fordul elő. Az 1980-as évek óta az uhu számos sziklai élőhelyről szorította ki a vándorsólymot Németországban. Ez a folyamat jelenleg is zajlik, mivel nem minden németországi régiót kolonizálta még az uhu. 1975-től kezdődően az uhu elkezdett fészkelni vidéki épületeken és napjainkban már a városokat is elkezdte meghódítani. Az uhuk egyre gyakrabban foglalják el a vándorsólymok számára, épületekre kihelyezett fészkelőládákat. A jelenleg növekvő, városokban, épületen fészkelő vándorsólyom-állomány várhatóan csökkeni fog az uhu-predáció hatására, annak ellenére, hogy ezek a baglyok nem túl sikeresen költenek épületen, sok öreg és fiatal madár elpusztul. A folyamat Németország nagy részére igaz. Európa más részein is várható, hogy az uhu épületeken fog fészkelni, ami hatással lesz az érintett vándorsólyom állományokra. Legalább nyolc vándorsólyom fészkelőhelyet épületen és sziklán nílusi lúd *(Alopochen aegyptiaca)* foglalt el.

Kulcsszavak: fészkelés épületen, uhu, nílusi lúd, vándorsólyom, predáció

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Introduction

Everywhere in Europe where there is a rather dense Eagle Owl population, the species has an influence on the population of Peregrine Falcons. It has long been known that the Peregrine Falcon can fall prey to the Eagle Owl (Uttendörfer 1939). Peregrine Falcons and Eagle Owls can compete for the same rock face, and indeed for the same breeding niche. The Eagle Owl is capable of taking both adult and juvenile Peregrine Falcons. Although the predation by the Eagle Owl and the competition for breeding sites were briefly mentioned in various publications on the Peregrine Falcon, statements regarding the scope and importance of these aspects have been lacking (Hickey 1969, Glutz von Blotzheim *et al.* 1971, Fischer 1977). For example, in 1993 Ratcliffe only wrote "there are a good many records of falcons being killed by them." The exact influence of the Eagle Owl on the Peregrine Falcon population was not noticed for a long time because the Eagle Owl had become extinct due to persecution in many parts of Europe, or else its surviving populations were very small. In 1965, only about 100 Eagle Owl breeding pairs existed in Germany. By contrast, in 1950 there were about 1000 pairs of Peregrine Falcons in the country (Rockenbauch 1998). The few Eagle Owls simply did not come into contact with the Peregrine Falcon population. Since the 1970s, the populations of Eagle Owl and Peregrine Falcon have again increased strongly in Germany thanks to protective measures and reintroductions, and according to Wegner (in correspondence) the population numbered 1,300 to 1,400 pairs in 2016. Information sources differ regarding the Eagle Owl population size in Germany. Territory mapping carried out from 2005 to 2014 for a distribution atlas indicated 2,100 to 2,500 territories (Gedeon *et al.* 2014). However, this was almost certainly an underestimate, as the mapping was not specifically aimed at owls such as Eagle Owls. Another estimate is that 4,000 to 5,000 breeding territories are occupied in Germany (Mikkola 2013). Today, Eagle Owls have displaced Peregrine Falcons from many former rock-face territories. The relationship between the two species has meanwhile become even more explosive, as the Eagle Owl is increasingly colonizing buildings and urban areas where the majority of Germany's Peregrine Falcons today breed. In the German federal state of Baden-Wuerttemberg, it was already well documented in 1985 that the Eagle Owl is the only species in Europe which has a massive influence on the distribution and breeding success of the Peregrine Falcon. In 1984, about 10% of the potential falcon fledglings were lost due to the presence of Eagle Owls in the breeding territories (Schilling & Rockenbauch 1985).

Behaviour of the Peregrine Falcon in the presence of Eagle Owls

If Eagle Owls are present in the vicinity of a Peregrine Falcon breeding site, the falcons show a general nervous behaviour. If an Eagle Owl is visible near the Peregrine Falcon nest, the falcons utter persistent alarm calls. If this occurs at the beginning of the breeding season, they constantly fly around the breeding site calling all the time. The direct vicinity of the former breeding site is avoided. Often, there is a change of partner or a partner disappears. Also, the breeding attempt often commences later than normal. It is striking that if an Eagle Owl is present, the female falcon often only lays two eggs. Clutches of two eggs are rare in

Peregrine Falcons and usually only occur if the breeding site is disturbed in some way. The Eagle Owl is evidently a cause of considerable stress for the Peregrine Falcons and causes smaller clutch sizes. If the falcons achieve any breeding success at all, only one or two young birds usually fledge. Young falcons often disappear before or after fledging (Schilling & Rockenbauch 1985, Hepp *et al.* 1995, Lindner & Fruhen 1999). In East Germany, young falcons were killed in about 100 cases before and only in five cases after fledging. Adult falcons are apparently only killed directly at the breeding niche (Kleinstäuber pers. com.). Presumably, however, the number is likely to be larger, since controls by ornithologists are usually less intensive after the young birds fledge. Peregrine breeding success remains well below the average of the overall population if Eagle Owls are present. Due to the inconspicuous behaviour of the Eagle Owls, observers often do not register that they are responsible unless they directly take over the Peregrine Falcon breeding site. Therefore the losses of Peregrine Falcons due to Eagle Owls are mostly underestimated. Even observers involved in intensive nest monitoring often report that the site was abandoned for unknown reasons or because of disturbance, or that the clutch simply failed to hatch. Only with high observation intensity and intensive control of the fledged young falcons can the extent of Eagle Owl influence be accurately determined. Loss of the female falcon can often only be detected by a difference in the rings, as a substitute female may already move in on the second day after the original female Peregrine has disappeared (Kleinstäuber pers. com.). Young falcons very often disappear without a trace. Occasionally, the plucked feathers of missing falcons are discovered, or their remnants are found in Eagle Owl pellets at the nearest owl nest site. At a rock face site in Thuringia, Eagle Owls have killed Peregrine Falcons 25 times in 28 years. The victim was often the female falcon brooding eggs or sheltering the young. Finally, the breeding niche was closed off to prevent further use. The falcons moved to another site and subsequently had breeding success in 50% of the following years because they no longer nest directly in the vicinity of the Eagle Owl site (Kleinstäuber pers. com.).

If the Eagle Owl breeds at a Peregrine Falcon site, either on a rock face or on a building, sometimes even in the same niche or nesting box, Peregrine Falcon pairs respond in different ways. The majority of pairs simply do not breed. However, they generally remain at the breeding site or in its vicinity. They may still breed even very late in the year if the Eagle Owls have left in the meantime. Otherwise, they will breed only in years when the Eagle Owls do not breed.

The smallest distance between a breeding pair of Peregrine Falcons and a pair of Eagle Owls in Germany was 6 m in 2006 at the castle ruins of Niederhaus in Bavaria. As was to be expected, the falcons were unsuccessful (Mebs 2010). Under such circumstances the falcons are nervous and sometimes fly mock attacks. During such mock attacks the wildly calling falcon flies as close as 3 m to the female Eagle Owl. The owl generally shows no reaction other than looking at the flying falcon. In one case, mock attacks were flown for 40 minutes. In the end, the female Eagle Owl simply closed its eyes. The non-brooding bird of the Peregrine Falcon pair often sits in a place from which it can observe the Eagle Owl nest (Lindner & Fruhen 1999). In most such cases, breeding is almost always unsuccessful. This is generally true for Peregrine Falcon nests located at a distance of 400 m or less from Eagle Owl sites. Many breeding sites are abandoned by the Peregrine Falcon after only a few years.

Influence on peregrine breeding in Baden-Württemberg

In Baden-Württemberg (BW) with its area of 35,751 km^2, there were 239 Peregrine territories and 224 occupied Eagle Owl territories in 2017 (Rau *et al.* 2017). The Peregrine Falcon never died out in BW and had its lowest point in 1972 with 26 territorial pairs. The population subsequently increased to 294 pairs in 2003, after which a decline set in. The Eagle Owl, however, had its last breeding success for many years in 1937. Only since 1963 has the Eagle Owl again colonized BW, and since then its population has been steadily increasing. However, the number of broods slumps in some years, probably due to adverse weather (Rau 2015).

For BW the most extensive published data in Germany are available for the influence of the Eagle Owl on breeding Peregrines. For the period 1969 to 1997 documentation proved 147 x breeding prevented, 103 x clutch abandoned, 59 x young bird disappeared or killed, 11 x number of young reduced due to massive disturbance, 30 x adult birds or at least independent falcons (after August) killed (Rockenbauch 1998). The data quoted above relate exclusively to Peregrines breeding on rock faces, because from 1970 to 1988, the species only bred on natural rocks and quarries in BW. From 1987 to 2015, the proportion of rock face nests fell from 100% to 62%. From 1988 to 2015, the proportion of nests on buildings or man-made structures increased from 0% to 31.8%. In addition, 6.2% of nests were located on high voltage pylons. In 2015, Peregrine nests on structures and high-voltage masts made up 38% of the overall number of nests and 46% of the successful pairs, thus contributing significantly to breeding success in BW. Nests located on anthropogenic breeding sites are therefore overproportionally successful. In BW, this is mainly due to competition with the Eagle Owl. From 1965 to 2015, 4.5% of Eagle Owl nests were on man-made structures. In recent years, this proportion has continued to rise, as has the proportion of clutches laid on the ground and on nests built by other bird species on trees, since most suitable rock-face sites are already occupied (Rau 2015).

Influence on peregrine breeding in North Rhine-Westphalia

In North Rhine-Westphalia (NRW) with its area of 34,110 km^2, there were 228 Peregrine pairs in 2016 (Arbeitgemeinschaft Wanderfalkenschutz Nordrhein-Westfalen 2016) and 525 to 570 occupied Eagle Owl territories (Jöbges 2016). The Peregrine Falcon did not breed in NRW from 1971 to 1986 and the Eagle Owl was absent from the early 1960s until 1975 (Lindner 2014). Only three of the 228 Peregrine Falcon pairs in NRW still breed on rocks or in quarries. In fact, over the past few decades there have never been more than three to five breeding pairs of Peregrine Falcon in such sites per year. There is only one recorded case of a Peregrine pair moving into a quarry that was already occupied by breeding Eagle Owls. All other cases involved Eagle Owls moving into Peregrine territories. Virtually all the larger rocks and quarries have been populated by the Eagle Owl. Even at the few rock sites with Peregrine Falcon nests, there are cases of predation by Eagle Owls breeding at the same site or in the vicinity. Thus, practically the entire NRW population of the Peregrine

Falcon breeds on buildings. Peregrine populations that almost exclusively nest on buildings are otherwise only found in a few other lowland areas of Europe and parts of the USA (Cade & Burnham 2003).

In only a few cases where both species occupied neighbouring territories was the Peregrine Falcon successful, and this only if the Eagle Owl did not breed that year. In 1999, however, there was the exceptional occurrence where two Peregrine Falcon pairs succeeded in very close proximity to active Eagle Owl nests. One of these was at the Bornstein, part of the Bruchhauser Steine rock formation, where the Eagle Owl bred for the first time in more than 100 years. Both species successfully fledged one young. The Peregrines bred on the north side of the rock and the Eagle Owls on the south side, with a distance of 50 to 60 m between the nests. At the second site in a quarry at Burg, one Peregrine Falcon fledged, while the three young Eagle Owls in a nest 40 m distant disappeared without trace (Lindner & Fruhen 1999). These two broods in 1999 have remained extreme exceptions for Germany. The breeding site at the Bruchhauser Steinen can be considered as typical for a site where Peregrine Falcons bred without and with the presence of Eagle Owls. In a 5-year period between 1989 and 1994, without presence of Eagle Owls, 17 young falcons fledged and the number of young averaged 2.83. In the 22 years of 1995 to 2017, with presence of Eagle Owls, 20 young falcons fledged and the number of young averaged 1.10. In some years young Peregrines were predated after fledging, as in 2000 (3 young).

Up to the year 2000, Eagle Owls bred in NRW almost exclusively in quarries and rock faces. Since 2000, the species has been increasingly breeding on buildings, on the ground and on other large birds' nests, as all the suitable rock face sites are occupied. From 2011 onwards, Eagle Owls appeared at Peregrine breeding sites on buildings in NRW.

At Oettinger Brewery in Mönchengladbach, the Peregrine has been breeding since 2011. Eagle Owls appeared in 2016. A second nesting box, only 10 m from the old Peregrine box, was installed in an attempt to allow both species to breed. The persons taking care of the site thought that the two species would breed peacefully next to each other if they both had nest boxes. Both species in fact bred, but the male Eagle Owl killed the young falcons. The predation was recorded by cameras that had been installed in both nest boxes. At the end of 2016 the Eagle Owl nesting box was removed. In 2017, only a single Eagle Owl was seen.

At the Asdonkshof Waste incineration plant an Eagle Owl pair took over a Peregrine nesting basket at a height of 100 m on the chimney and laid an egg. After a disturbance, the Eagle Owl pair abandoned the nest. Around the 22nd of April the Peregrine Falcons laid three eggs. The three young Peregrines fledged successfully (Kladny 2017). This site is likely to be the highest Eagle Owl nest on a building anywhere in the world.

In 2017, a pair of Peregrines Falcons bred in a small niche without a landing board on the south side of the south tower of Xanten Cathedral while Eagle Owls bred in the Peregrine nesting box on the east side of the north tower about 15 to 20 metres distant. The only young falcon to hatch, a female, landed on the ground before it could fly properly. To prevent it being killed by the Eagle Owls, this bird was added to a clutch of young falcons at another breeding site (Kladny pers. com.).

At the tower of St. Mary's Basilica (aka St. Mary's Church) in Kevelaer, lay 2017 an eagle owl clutch in the nesting box and two metres away a peregrine clutch in the gutter. Probably the female eagle owl first laid a clutch there and later gave up. After abandoning the eagle owl clutch, the peregrine falcon females laid its clutch. Further details are not known (Kladny pers. com.).

In the administrative districts of Arnsberg and Münster (sub-regions of NRW), 15% of the Peregrine Falcon territories on buildings and structures had been taken over by Eagle Owls by 2014 (Lindner 2014).

Eagle Owls nesting on buildings in Germany

Eagle Owls use of buildings as nest sites had been widely known in the former German empire since the 16th century (Gessner 1555). Gessner wrote in 1555 that the Eagle Owl readily bred in ruins and churches. Breeding on buildings was by no means peculiar to Germany in former times, but occurred in many countries. In 1622, for example, Giovanni Pietro Olina wrote that in Italy the Eagle Owl inhabited dilapidated ruins, holes in walls and the roofs of deserted houses (Olina, & Macdonald 2018). Until the end of the 19th century, almost all German literature about the Eagle Owl mentioned breeding on buildings. The last three proven breeding occurrences on buildings took place in the 1880s. After that, there was a gap in documented cases until one in 1929 and then a further gap until 1975 (Lindner 2014).

By contrast, Peregrine Falcon nests on buildings in Germany have surprisingly been found only from 1809 onwards. Since nesting on buildings was never mentioned in previous literature, they must, if they existed at all, have been very rare. Until 1970, Peregrine Falcons' nests on buildings used to be found mostly in ruins and churches, just as in the case of the Eagle Owl in earlier times (Kuhk 1969, Mebs1969). Since Peregrines again started nesting on buildings in 1978, they have usually been found on modern structures such as power stations, bridges, industrial plants and pylons. However, some older buildings, such as churches, castles, etc., including historical breeding sites, are also occupied or re-occupied by the species. The Peregrine Falcon shows a far greater tolerance of disturbance than the Eagle Owl.

In various parts of Germany, Eagle Owls took over Peregrine nest sites on buildings from 1990 onwards. This trend accelerated from 2010 onwards. Increasingly, the Eagle Owl is also breeding in Peregrine nesting boxes (Lindner 2016). From 1975 to 2016 at least 170 buildings in Germany were known to be Eagle Owl breeding sites. These comprised 45 castles, castle ruins or similar, 50 industrial buildings and commercial buildings, 20 buildings in quarries and sand and gravel pits, 27 churches, 8 road and railway bridges, 4 telecommunications towers, 4 detached houses, 2 multi-storey buildings and 10 other structures. Extreme cases were nests on a funerary monument, an ammunition bunker, a submarine bunker and a bullet trap of a firing range. Prior to 1975, only ruins, castles, fortifications and churches had been known as breeding places (Lindner 2016). In 2016, at least 60 buildings were occupied by Eagle Owls Pairs, but breeding could not always be proved. At least 30 other buildings were occupied by single Eagle Owls, although in some of these cases it is possible that a pair was present but the second owl was overlooked. All these figures from recent decades are minimum numbers, as there are data gaps.

On the Neverstaven telecommunications tower in Schleswig-Holstein, situated on the 78 m high hill called Klingberg in an otherwise flat landscape, an Eagle Owl pair bred in 2008 and 2009 in a Peregrine nesting box at a height of 50 m. In 2010, a second Peregrine Falcon nesting box was installed at a height of 97 m (Robitzky 2010). In 2013, both species simultaneously attempted to breed for the first time, although the Peregrine Falcons were unsuccessful (Lindner 2016). Until 2017, there were other attempts at simultaneous breeding of both species, and at least in some years both Eagle Owl and Peregrine Falcons fledged. One interesting fact is that Eagle Owl droppings and pellets were also found on the platform with the Peregrine Falcon nest at 97 m (Robitzky pers. com.).

The period that individual buildings were occupied by Eagle Owls varied from 1 to 25 years. Only eight buildings were occupied for more than ten years. However, many nesting sites on buildings were occupied for only one or two years. On several occasions, breeding took place on buildings at heights of 50 to 70 meters. Clutches of eggs have been abandoned on a number of occasions after disturbance at the nest, and the Eagle Owls usually gave up such disturbed sites permanently. Eagle Owl fledglings move away from the nest site from the age of 45 days and explore the surrounding area (Penteriani *et al.* 2004). During this phase, they often jump from the building if there is no other way of leaving the direct vicinity of the nest successfully (Harbeck 1995). The higher the jump and the harder the landing place, the greater is the risk that the young owl will injure itself or crash to its death. Hard edges, fences and other sharp objects as well as shafts in the landing area increase the risk of injury to the young birds. In 2009, a fledgling survived the jump from a height of 50 m at the Neverstaven telecommunications tower in Schleswig-Holstein (Robitzky 2010). In 2017, one of two fledglings that jumped from a height of 65 m at the Luther Church in Kassel was killed (Löver 2018). There have been repeated cases of young Eagle Owls being picked up and brought to care stations after jumping to the ground in inner cities. These were then reared in the care stations and later returned to the wild (Lindner 2016). In some cases, after young birds had jumped from the nest the areas where they were located were closed off to humans, or else the birds were moved to safe areas from which they could eventually fly off (Harms 2016, Löver 2018). Presumably, the dangers due to road and rail traffic, impact against power lines, etc. are also larger in towns and cities and in the nearby feeding areas of urban Eagle Owls.

Eagle Owl nests on buildings have also been found in the last two decades in Spain, Sweden, Belarus, Austria, Italy, Finland, France and Russia. Today, in many parts of Europe more and more Eagle Owls are to be found on buildings, even in large cities. The cities where Eagle Owls have been recorded nesting on buildings include Stockholm, Helsinki, Madrid, Córdoba, Jerez de la Frontera, Trento, Budapest, Lyon and Marseille (Lindner 2016). This list of the countries and cities with Eagle Owl nests on buildings is very probably incomplete. While Peregrine Falcon nest boxes have been attached to structures in many countries of the world since the 1980s, probably the first Eagle Owl nest boxes were installed on buildings in Helsinki in 2007, (Lindner 2014). However, Eagle Owl nest boxes are probably still extreme exceptions in Europe.

Protective grating to prevent Eagle Owls from using Peregrine breeding sites

In eastern Germany and Baden-Württemberg, protective grating has sometimes been installed to prevent Eagle Owls from accessing Peregrine Falcon breeding sites in rock faces and on structures (Rauh and Kleinstäuber pers. com.). Experience shows that the bars should have a max. spacing of 17 cm because larger grid spacing has failed to stop Eagle Owls from using the nesting boxes or rock niches. The smaller the spacing the better, so that the Eagle Owl really has no chance to squeeze through. A determined Eagle Owl can force itself through grating bars spaced larger than 17 cm. Also, the distance of the grating from the nest hollow in the eyrie must be so large that the Eagle Owl with its amazingly long legs and claws cannot reach the falcons when it is pressing against the grating (Kleinstäuber pers. com.). All protective gratings installed so far have been at long-standing Peregrine Falcon nest sites. In spite of the protective grating, Eagle Owls can still take the young falcons during the begging phase, when they roost outside the protective grating. Even if protective grating is installed, the Eagle Owl can still disrupt the breeding by its pure presence. As the Eagle Owl is much more flexible in its choice of nest site, it can easily find a place in the immediate vicinity and still continuously bother the Peregrines. It is not possible to install protective grating on many rock-face breeding sites in Germany, as almost all of them have been designated as protected areas. In Peregrine Falcon protection societies in Germany, the installation of protective grating is a controversial subject.

Egyptian goose as a competitor for Peregrine Falcon nesting boxes

In recent years, Egyptian Geese have taken possession of some rock face breeding niches and nesting boxes of Peregrine Falcons in various regions of western Germany. In most cases, the Peregrine does not manage to defend its breeding site against Egyptian Geese. Egyptian Geese taking over nesting sites of Peregrine Falcons is a new phenomenon. Mostly, this concerns nesting boxes.

Since the late 18th century, Egyptian Geese derived from captive stock have been breeding in the UK. This population was long restricted to southeast England. However, since the 1970s the species has spread via the Netherlands to Belgium, France and Germany (Venema 1997). In the meantime, it has also colonized Switzerland, Austria and Poland. Egyptian Geese first bred in Germany in 1981. A census conducted from 2000 to 2009 already registered 5,000 to 7,500 territorial pairs (Gedeon *et al.* 2014).

According to incomplete data, Egyptian Geese took over Peregrine Falcon nest sites or disturbed the breeding falcons on at least 8 occasions in Germany up to 2017. At the Heiliggeist church in Heidelberg, a computer-controlled image recognition system was installed in a Peregrine nesting box in order to drive away Egyptian Geese. When Egyptian Geese entered the box, they were driven away by noise and flickering lights. When the PC registered a Peregrine Falcon image, no action was initiated. The Peregrine Falcons bred successfully (Gäng & Soergel 2016). If there are different nesting possibilities at one site, Peregrine Falcon and Egyptian Goose can also nest close to each other. In 2010, both species successfully bred in nests five metres apart on the keep of Burg Zwingenberg castle in Baden-Württemberg (Edelmann 2010). As a result of the current increase in size of Egyptian Goose populations all over Europe and their expansion into further areas, the Peregrine is likely to be driven out of even more breeding sites. Usually, however, the Egyptian Geese take over the Peregrine Falcon nest site for a few years only.

Conclusions

The ongoing increase in Eagle Owl populations in Germany, parts of Central Europe, Western Europe and Scandinavia will presumably continue to have a negative impact on the breeding success and distribution of Peregrine Falcons on rock faces, buildings and structures. Today, the food availability for Eagle Owls is likely to be better in cities than in many agricultural areas with their endless expanses of maize. In towns and cities there are plenty of prey animals of optimal size, such as pigeons, brown rats, rabbits and the waterfowl on city waters (Görner 2013, Lindner 2016). In the future, food availability for Eagle Owls is unlikely to deteriorate in Europe's towns and cities, which will therefore continue to be a magnet as the species' population levels grow. It can therefore be assumed that there will be a strong increase in the number of Eagle Owls nesting on buildings and structures over the next few years. In the course of this, it can be expected that a wide range of structures will be chosen as breeding sites. It is likely that the Eagle Owl will breed most successfully on buildings in rural areas. At or in the vicinity of buildings such as television towers, bridges and industrial buildings in the countryside there are usually significantly fewer flight obstacles than in urban areas and young Eagle Owls probably have better chances of survival in the branchling and post-fledging phases. There will be a growing competition between Peregrine Falcons and Eagle Owls for nest sites, both on buildings in cities and on buildings outside densely populated areas.

In the coming decades, the increase in Eagle Owls nesting on buildings will presumably lead to a decline in the number of breeding Peregrines in Germany. However, it is important to note that up to now Eagle Owl pairs have often nested on buildings in urban areas for periods of only 1 to 3 years, and only achieve a low fledging success rate. Often, adult and juvenile owls are found dead or injured because they have flown into obstacles or collided with road traffic. It is hardly possible to predict how great the negative impact of the Eagle Owl on the Peregrine population on buildings will actually be. The influence of the Eagle Owl on the Peregrine population is natural and cannot be influenced by nature conservationists. In Germany, many rock faces were populated by Peregrine Falcons as late as the 19th century or early 20th century only after the local Eagle Owls were eradicated by massive persecution. Presumably, in the 19th century and earlier the number of Peregrine Falcons was significantly smaller than today in many parts of Germany (Lindner 1998).

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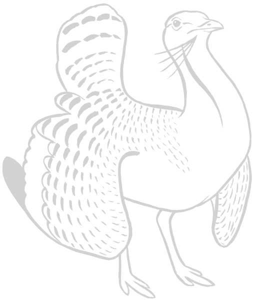

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Restoration of the tree-nesting Peregrine Falcon *(Falco peregrinus)* population in the Volga-Ural Region

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Abstract We have applied the method of a forming tree-nesting behavior pattern in the chicks of the cliff-nesting Peregrine Falcon. In June 2016 and 2017, in the Southern Ural Mountains and Bugulma-Belebey Upland, we discovered four nests of Peregrine Falcons, which were threatened by destruction due to various anthropogenic and biological factors. For preventing the death of the broods, the chicks were transferred from the occupied nesting niches in the rock cliffs to nesting platforms. On nesting platforms they spent from 3 to 12 days where they were fed by adults regularly. All four broods (9 young) flew out successfully and demonstrated typical behavior for the Peregrines of their age. Adults fed fledglings and taught them to hunt.

Keywords: Peregrine recolonization, Volga-Ural Region, nesting types, imprinting on tree-nesting

Összefoglalás A vándorsólymok fészkelési szokásai is változhatnak. Vizsgálatunkban sziklákon fészkelő párok viselkedését figyeltük meg fára helyezett fészkekbe átköltöztetett fiókáik nevelésével kapcsolatban. 2016 és 2017 júniusában négy pusztulással fenyegetett fészket találtunk a dél-uráli Bugulma-Belebey felföldön, amelyek emberi zavarásnak és más biotikus tényezőknek voltak kitéve. A fészekaljak megmentése érdekében a fiókákat az eredeti fészekrakó helyről mesterségesen létrehozott költőhelyekre szállítottuk át. A fiókák ezeken a mentőhelyeken 3–12 nap időtartamot töltöttek és a felnőttek rendszeresen etették őket. Mind a négy fészekalj, összesen 9 fióka sikeresen kirepült, és a koruknak megfelelő viselkedést mutatta. A felnőtt egyedek tovább etették, miközben vadászni is tanították őket.

Kulcsszavak: sólyom áttelepítés, Volga-Ural Régió, fészektípus, fészekhely-bevésődés

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Introduction

The habitat restoration and abundance of Peregrine Falcons is uneven for populations with the different nesting strategies in Europe during the 20th century after "pesticide" eco-catastrophe. As it is known, the population of the cliff-nesting Peregrine Falcon has demonstrated a considerably successful increase due to using of the ledge rocks and compound relief forms as nesting sites. At the same time, the Peregrine Falcons do not inhabit the vast plains of forest and stepper-forest zones from Western Europe to the Ural Mountains. Several dozens of breeding pairs of tree-nesting Peregrine Falcons were known in West and Central Europe, which were formed as a result of successful projects of Peregrine Falcon reintroduction in Germany, Poland and elsewhere in the EU (Langgemach *et al.* 1997, Kirmse 2001, Wegner *et al.* 2005, Mizera & Sielicki 2009, Cade 2013).

Since the end of the 20th century, the number of the cliff-nesting Peregrine Falcons in the mountains of the Southern Ural has been increasing, and nowadays, breeding pairs are distributing to the piedmont of the Ural Mountains and along the Volga River (Karyakin 1998, Karyakin & Pazhenkov 2009).

However, the cliff biotopes here are limited and subject to significant anthropogenic influence, and thus, nesting stereotype does not allow the Peregrine Falcon to occupy vast plains with rich trophic base. For these reasons, we carried out some field work for imprinting the tree-nesting stereotype among the cliff-nesting Peregrine Falcons in the Ural Mountains.

The successful imprinting of the tree-nesting stereotype in chicks of Peregrine Falcons was applied in Germany and Poland. The chicks from Peregrine Falcon hatcheries were transferred to the special cage on tall pine trees at the age of 30 days. The young Peregrine Falcons were fed (1-day chicks of quail) in the cages until 4–6 weeks after the Peregrine Falcon first flight. Thus, the young falcons have been formed tree-nesting stereotype. This approach demonstrated impressive results of the recolonization in the historic tree-nesting populations in Europe. Though, one of the most serious problems with artificial breeding of tree-nesting Peregrine Falcons (the hacking method) is the lack of parents who teach young birds to hunt and acquire social skills (Kleinstäuber *et al.* 2009, Sielicki & Sielicki 2010).

We have offered to apply somewhat different method of a forming tree-nesting behavior pattern at the wild chicks of the cliff-nesting Peregrine Falcon in the Volga-Ural Region in 2002. Recent observations have shown, that forming of the tree-nesting stereotype at cliff-nesting Peregrine Falcon chicks is possible in the case of the broods transferring at the age of 25–30 days from cliff nesting sites on the artificial nesting platforms in the trees. Besides, along with imprinting of the tree-nesting stereotype, chicks will be given parental care, hunting experience and all the rest natural social skills. Subsequent observations have shown a constant growth of number of the population of the cliff Peregrine Falcon in the Ural Mountains and possibility to use it as a donor for forming of the tree-nesting population. As we have seen, adults of the Peregrine Falcons demonstrate numerous cases of the care for the brood as well as the chicks bringing up despite of strong disturbance and human presence within nesting sites, and also bringing up of the chicks left their nests prematurely.

By the first step, it is necessary to confirm experimentally parental care of chicks while transferring them from the nesting niche on the tree platform.

Method

We have tested the technique of a forming tree-nesting behavior pattern in the chicks of the cliff-nesting Peregrine Falcon *(Falco peregrinus)*.

In June 2016 and 2017, in the Southern Ural Mountains and Bugulma-Belebey Upland, we discovered four nests of Peregrine Falcons, which were threatened by destruction due to various anthropogenic and biological factors. For preventing the death of the broods, the chicks were transferred from the occupied nesting niches in the rock cliffs to nesting platforms. These circumstances contributed to the decision to conduct the experiment.

Nesting platforms for simulating nests of large birds of prey *(Buteo buteo*, *Accipiter gentilis*, *Aquila chrysaetos)* were built in the upper third of the tree crown near the trunk. Nest platforms were arranged in such a way the trunk and crown of the tree would provide shading of the platform part and protection from the wind and rain. For these purposes, an additional canopy of branches was also created.

During the construction we took into account the need for a free approach to the nest platform, as well as a panoramic view of the adjacent valley.

We moved a small amount of food residues, feathers and stones, polluted with excrement, from the nest niches to attract adult Peregrine Falcons to nest platforms.

Near all the nested platforms were equipped with trail cameras. Chicks on the platforms were observed with telescopes. We did not visit platforms after the chicks were transferred. To avoid disturbance on the platforms No. 1–3, the trail cameras were installed at a distance of about 5–7 m from nesting platforms, for which some of the feedings were not recorded due to incorrect operation of trail cameras, while we were observing the adult Peregrine Falcons with prey with a telescope.

On nesting platform No. 4 the trail camera was installed 4 days after the chicks were transferred, as there was technically impossible to install trail camera for a distance of more than 1.5–2 m. Too close installation of the trail camera at the nest was considered to be an additional factor of disturbance that could slow the first arrival of the adult Peregrine Falcons. The first four days we recorded individual arrivals of the adults on the nest platform using a telescope.

Thus, we not able to spot some feedings and visits of the nesting platforms by adults and young birds.

Experiment

Nesting platform No. 1 was constructed on linden *(Tilia cordata)* at a height of 5 m from the ground. The tree was located at a distance of 17 m from the nesting niche. The cliff niche and the nesting tree were situated in the upper third of the steep forested slope with a total height difference about 150 m.

The brood consisted of three 33–39 days old chicks. The eldest chick could fly and left the nesting niche at the moment of carrying (15 June 2016). During the observation period he stayed close to the nesting niche and flew from one roost site to another.

The chicks spent three days on the nesting platform No. 1. During this period, the feeding was noted at least two times. On the third day, the chicks flew to the cliffs at a distance of 15 m from the nesting platform.

Nesting platform No. 2 was built on elm *(Ulmus glabra)* at a height of 4 m from the ground. The tree was located at a distance of 15 m from the cliff nesting niche. The cliff niche and the nesting tree were situated in the upper third of the steep forested slope with a total height difference about 50 m.

The brood consisted of two 28–30 days old chicks, which were transferred on the nesting platform on 16 June 2016. The chicks spent 11 days on the nesting platform, after that they started to fly to the nearest cliffs, located 5 m away from the nest. However, they were observed to return to the platform during the subsequent 8 days, where they were fed by adult bird. The adult fed the chicks at least 8 times in the period of their staying on the platform.

Nesting platform No. 3 was constructed on oak *(Quercus robur)* at a height of 7 m from the ground. The tree was located at a distance of 25 m from the cliff nesting niche. The cliff niche and the nesting tree were located in the upper third of the steep forested slope with a total height difference about 170 m.

The brood consisted of two 28–32 days old chicks, which were transferred on the nesting platform on 18 June 2016. The chicks spent on the nesting platform at least 10 days. During this period, the feeding was noted at least 32 times.

Nesting platform No. 4 was constructed on birch *(Betula pendula)* at a height of 12 m from the ground. The tree was located on the edge of a flat plateau at a distance of 100 m from the cliff nesting niche. The cliff niche was located at the top of the steppe slope with a total height difference about 100 m.

The brood consisted of three 26–31 days old chicks, which were transferred on the nesting platform on 19 June 2017. The chicks spent on the nesting platform at least 13 days. During this period, the feeding was noted at least 27 times.

Adult Peregrine Falcons fed chicks on nesting platforms on the day of transfer or the following day.

All four broods (9 young) fledged successfully and demonstrated behavior typical for Peregrine Falcons of their age. Adults fed fledglings and taught them to hunt. As they grow older, joint flights of adults and young Peregrine Falcons were carried out, followed by their return to the nesting site after a few hours of absence.

Summary

The care of adult Peregrine Falcons about their broods after transferring them on nesting platforms on a tree was justified by the experiment.

We consider the installation of the nesting platforms on trees near inhabited cliff nests and carrying of 26–30 days old chicks on them can become a promising method for reintroduction of the tree-nesting Peregrine Falcon populations in the Volga-Ural Region. At the same time, i strict observation of the methodical receptions directed to the preservation of the brood, minimization of disturbance and attracting of the adult Peregrine Falcons to nesting platform is necessary.

Of course, the most important factor that can ensure the success of this technique is the presence of a large cliff-nesting population of a Peregrine Falcon with a steadily growing number.

Moreover, the consequent interactions between cliff and tree-nesting Peregrine Falcon populations, which can have unique specific features in the Volga-Ural Region, will require a peculiar study in the future.

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Nesting habitat selection of Peregrine Falcons *(Falco p. peregrinus)* in Eastern Germany – the state of knowledge

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Abstract After the disappearance of the Peregrine Falcon during the DDT era, the re-colonization of Eastern Germany from 1981 was accompanied by colour-ringing of a high percentage of juveniles and systematic identification of these individuals on their later nest-sites. Before that period there were two geographically distinct subpopulations: tree-breeders in the north, and cliff-breeders in the south. We were able to restore the tree breeders' tradition by imprinting nestlings at stick nests in forests. Today, besides cliff- and tree-breeders there are also nest-sites on buildings and lattice structures. The population is increasing including all nest-site types. Here, we analyse nesting habitat choice with respect to the natal habitat of birds. The exchange between the four nest-site types is limited. Habitat fidelity was high in birds fledged on cliffs (95%) and on buildings (81%). The sample size for lattice structures is still too low for deeper analyses. The fixation towards trees was stable only in 56% of birds, and higher for males than for females. The influx from other habitat types is very limited and hardly supports the tree breeders' subpopulation. A growing number of tree-breeders go along with higher habitat fidelity which is stabilizing their sub-population.

Keywords: Peregrine Falcon, habitat selection, eastern Germany, tree-breeders' project

Összefoglalás A vándorsólyom DDT használat következtében történő eltűnése után 1981 óta ismét megjelent Németország keleti részén. Azóta nagy számban jelölik a fiatal egyedeket színes gyűrűvel, hogy a fészekelőhely-választásukat később meghatározhassák. Korábban két, földrajzilag jól elkülönülő alpopulációja volt ismert a fajnak: fán költők északon és sziklán költők délen. A visszatelepítési programoknak köszönhetően a fán fészkelő populáció újra megjelent a terület erdeiben. Napjainkban már nemcsak fákon vagy sziklákon, hanem emberi építményeken fészkelő párok is előfordulnak. Az állomány növekedésnek indult minden fészkelőhely típusnál. Jelen tanulmányban a vándorsólyom fészkelőhely-választását vizsgáljuk, különös tekintettel a fajra jellemző, eredeti élőhelyekre. A megkülönböztetett négy fészkelőhely típus közötti váltás korlátozott. A sziklaormokon és épületeken fészkelő egyedek fészektípushoz való hűsége magas (95% és 81%, ebben a sorrendben). A fán fészkelés iránti hűség is nagy, de az előzőkhöz képest alacsonyabb (56%), a hímek esetében magasabb, mint a tojóknál. Más típusokból való bevándorlás elég csekély, ami nem segíti a fán fészkelő populáció növekedését, azonban a fészkelőhelyek iránti hűségük stabilizálja azt.

Kulcsszavak: vándorsólyom, élőhelyválasztás, Kelet-Németország, „fán fészkelő“ program

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Introduction

In 1973, the Peregrine Falcon became extinct in eastern Germany, the former GDR area. Before the extinction in the context of the pesticide crash, there were exclusively two habitat types in the breeding area: 1) rock areas in the low mountain ranges with nest-sites in vertical cliffs including quarries, and 2) forests in the lowlands with stick nests of other large bird species on trees *(Figure 1)*. An area of about 50 to 100 km between tree breeders in the north and cliff breeders in the south was free of peregrine broods with the only exception of annually 1-2 cliff broods on the chalk coast of the island of Rügen. From the past, it is known that the two subpopulations differed not only from their nest type but also with regard to their nesting habitat as a whole, their breeding ecology, nest-site defence, hunting strategy etc. There is no evidence for genetic differences (Kirmse 1987).

Only a little number of Peregrine Falcons was ringed until then, and there was no colour ringing in order to get more insight into questions such as individual habitat choice and habitat fidelity. From today's point of view, we can only theoretically estimate the behaviour of the breeding birds in this respect.

The restoration of the population began in 1981 with the arrival of falcons released in West Germany and first breeding pairs in the Harz and Thuringia mountains near the inner German border. The recovering population was intensively monitored from the beginning and managed in order to optimize each nest-site. Just a few years later, released Peregrine falcons also occupied artificial buildings at industrial sites and in cities, first 1983 in Sangerhausen, and 1985 on a church in the centre of Berlin. An increasing number of broods like these stepwise covered both of the former habitat types and as well the area between.

However, there was no spontaneous repopulation of the forests in the North-east German lowlands. Before the extinction, the majority of the East German peregrine population lived here with several hundred pairs in earlier decades. "Each pine forest in Brandenburg has its Goshawk and its Peregrine", wrote Schuster (1932). Furthermore, the population covered the whole lowland range from the Netherlands in the West to the Ural Mountains in the East (Kirmse 2004). The lack

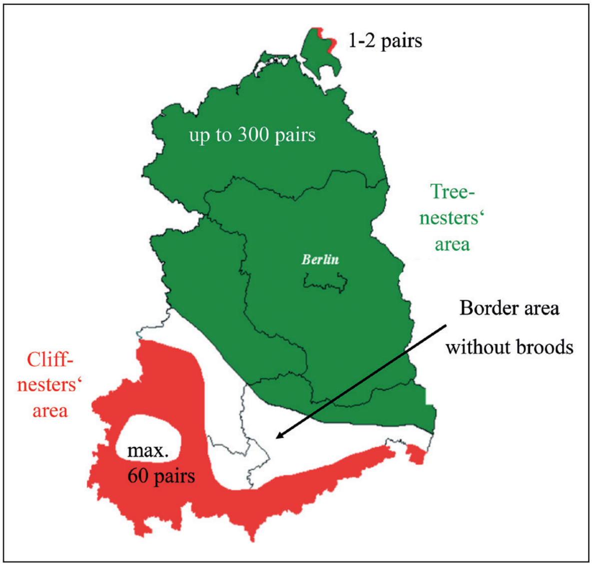

Figure 1. Historical ranges of tree-breeders and cliff-breeders in our study area in eastern Germany (Kleinstäuber *et al.* 2009)

1. ábra A fán, illetve sziklán fészkelő vándorsólyom populációk történelmi elterjedése a vizsgálati területe, Németország kelet részén (Kleinstäuber *et al.* 2009)

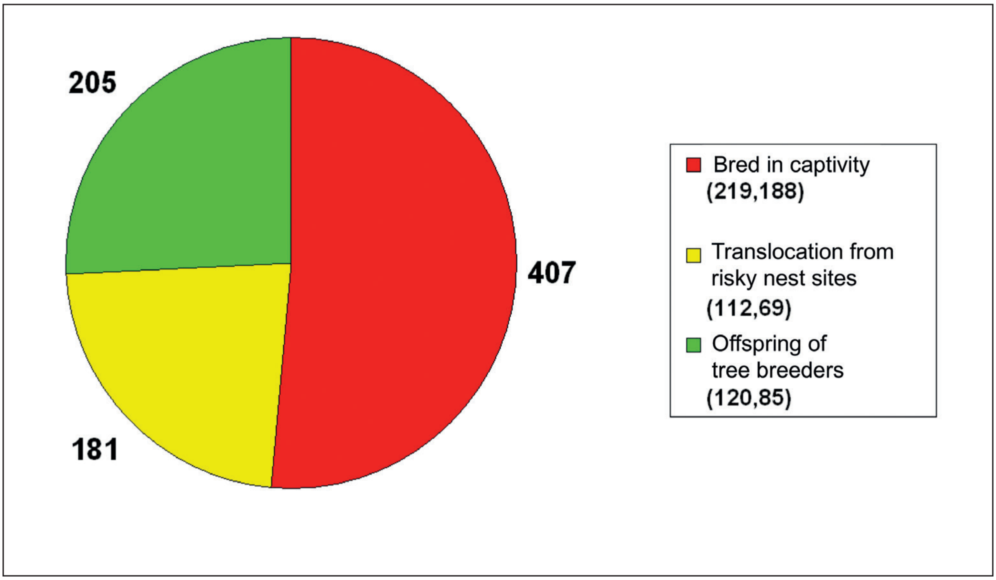

Figure 2. Origin from peregrines fledged in trees in eastern Germany 1990–2009 (Kleinstäuber 2013)
2. ábra Németország keleti részén, fáról kirepült vándorsólymok származási helye 1990–2009 (Kleinstäuber 2013)

of a spontaneous come back of the tree breeders was in accordance with our hypotheses: The recovery of the cliff nesters population will not automatically lead to a re-colonisation of the tree nesters' range as tree nesting needs imprinting on tree nests and the respective landscape in the juvenile period (Kirmse 1991, Kleinstäuber & Kirmse 2001). According to this assumption a reintroduction project for the tree-breeders' population was started in 1990, after pilot releases in the former West Berlin by C. Saar (overview Kleinstäuber 2013). Six years later, a first breeding pair established in northern Brandenburg with a successful brood in 1996 (Langgemach *et al*. 1997). From 1990 till 2009, 793 peregrines fledged in trees – 51.3% bred in captivity, 22.8% released after rescue translocation from risky nest-sites, mainly on buildings and industrial sites, and 25.9% as offspring of the growing tree-breeders' subpopulation *(Figure 2)*. After the successful end of the release project in 2011 the tree breeders' subpopulation comprised 37 breeding pairs and continued to increase up to 64 pairs in 2017.

After starting the reintroduction of tree-breeders, peregrine falcons spontaneously settled for the first time on steel lattice towers in nests of ravens and ospreys (cf. Kirmse 2001). These structures might resemble high dead trees and could be interpreted as a substitute nest-site for a tree brood – as buildings could be seen as artificial rocks. But is it actually the same? In this manuscript, we analyse individual nest choice and habitat fidelity of peregrines of the East German population with the four different nest-site types: cliff, tree, building, and lattice tower.

Material and methods

The re-colonisation after complete extinction provided a unique opportunity to quantify the emerging population and to document the life history of individuals by appropriate marking. Beginning in 1990, all released juveniles and the offspring from wild broods were individually marked, from 1992 onwards according to the so-called "Wachberg protocol" *(Figure 3)*: The left legs are fitted with a coloured ring of the ringing centre Hiddensee, the so-called "habitat ring", with red for rocks, yellow for buildings, and green for trees. From 2003 on different habitat rings have been fitted to birds from lattice structures, since 2015 black coloured rings. The right legs are fitted with the "identity ring" for remote identification with silver or aluminium, respectively, for juveniles from unmanaged wild broods and black for juveniles released via hacking or fostering.

Till 2010, nearly the whole East German population was ringed, and – even more important – the majority of the breeding birds were identified, at least their habitat colour. Only later, with growing population size, the percentage of birds not ringed and not identified increased, as the capacities of the essentially voluntarily working team are limited.

Identification of individuals took place by high-resolution spotting scopes with a magnification of 100 to over 200x. Individuals were recognized by their identity rings, but additional information was gained by birds which were merely identified by their colour rings, i. e. their

Figure 3. Ringing scheme in the eastern German Peregrine population since 1992. Black as an additional habitat ring colour has been used only from 2015 on – for birds fledged on lattice structures

3. ábra A keletnémet vándorsólyom állomány gyűrűzési sémája 1992 óta. A fekete szín 2015-től kezdve került a rendszerbe, a nagyfeszültségű távvezeték oszlopokról kirepülő példányok jelölésére

All individuals	4.684
Fledged juv. from 1982 on	3.783
Colour-ringed birds since 1990 according to Wachberg-Protocol	3.757
16 % of these later identified as breeding birds, i. e. known origin and habitat choice	**612**

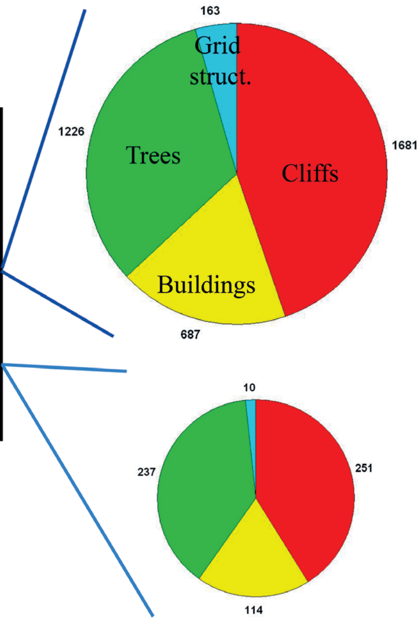

Figure 4. Database of the "Arbeitskreis Wanderfalkenschutz e. V." from 1981 to 2014
4. ábra Az „Arbeitskreis Wanderfalkenschutz e. V." (Vándorsólyom-védelmi Munkacsoport) adatbázisa 1981-től 2014-ig

Table 1. Database of the "Arbeitskreis Wanderfalkenschutz e. V." from 1981 to 2014, continued
1. táblázat Az „Arbeitskreis Wanderfalkenschutz e. V." adatbázis 1981 és 2014 között

Ringed birds identified as breeding birds since 1981 (since 1992 according to Wachberg-Protocol), corrected because of possible double-counting	600
From these 6% individuals of other origin (Western Germany, Poland, Czech Republic)	35
Individual code identified for habitat and individual analysis (59% from 600)	355
Colour ring identified for habitat analysis (41% from 600)	245

origin habitat. From 1992 to 2014, a database for 355 exactly identified individuals was built up, of which many were seen over several years. The origin and settlement of an additional 245 individuals was identified by recognising merely their colour ring but not their identity ring.

Figure 4 and *Table 1* give an overview about the database of the "Arbeitskreis Wanderfalkenschutz e. V." from 1982 to 2014.

Results

Population trend; trend and distribution of the four nest-site types

Figure 5 shows the development of the East German Peregrine population from 1981 to 2014 with respect to the four different nesting and habitat types. After spontaneous settling of released birds on rocks (1981) and buildings (1983, see above), the first tree brood was in 1996,

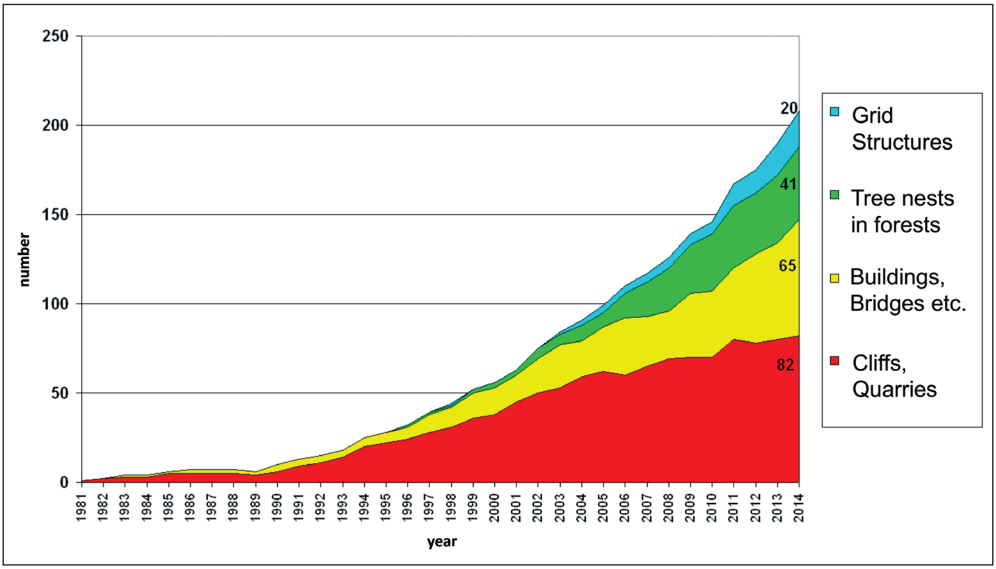

Figure 5. Trend of the Peregrine population in Eastern Germany with respect of the four different habitat types, 1981–2014

5. ábra A vándorsólyom-állomány változása Németország keleti részén a négy különböző élőhely-típusban, 1981 és 2014 között

followed by first broods on lattice masts: in 1998 near Rheinsberg by a pair imprinted on tree-nesting*, and 2003 (near Vockerode) by a male from a building and a tree-born female.

The regional distribution of the occupied territories 33 years after the start of the recovery in 1981 is shown in *Figure 6*. Compared to the historical situation (small map in the corner) several things are conspicuous:

- cliff breeders re-occupied most of their former range and even found the chalk cliff far away on the Baltic sea coast; and one single, isolated nest-site in a quarry north of the mountains;
- tree breeders are in the process of restoration of their former range with one large core area were the reintroduction project began, and more scattered sites mainly around the other release areas except the two south-westernmost;
- the former gap between the two sub-populations is now occupied by Peregrines breeding on buildings and lattice towers, but again not by tree breeders;
- as well, buildings and lattice towers are increasingly occupied in the two historical ranges but not in their core areas (mountains: Saxon Switzerland, Upper Harz, and Thuringian Forest, lowlands: South Mecklenburg and North Brandenburg);
- altogether, there is still the separation between tree breeders' and cliff breeders' range known from the past, but a regional co-existence of the new site types with both, except the core areas.

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* First (unsuccessful) brood of a newly established pair on a lattice mast in the core of an extended forest area; thereafter breeding exclusively in pine trees nearby – one of the very few exceptions of switch to another nest-type and come back to tree-nesting in the next year.

Habitat choice of Peregrines depending on their natal habitat

Earlier results showed that the decision for one of the different nest-site types is made with the first breeding attempt. This decision is for the whole life of a bird (Sömmer & Kirmse 2013), with very few exceptions, described by Kirmse & Sömmer (2015). This is important for the understanding of the following paragraphs on habitat choice.

According to *Figure 7*, habitat fidelity is highest on cliffs – the inherent nest-site type of Peregrines (95%). Only very few (3%) birds fledged on cliffs later chose buildings as nest-sites, whereas trees and lattice towers may be considered as exceptions.

Also on buildings ("artificial rocks") the habitat fidelity is rather high – 81% of the birds later came back to buildings to breed there, followed by 11% that changed towards cliffs pronouncing again rocks as the inherent nest site type. A slightly higher shift towards lattice structures (5%) and trees (3%) compared to birds from cliff nests may suggest that the bond to buildings is smaller than that to rocks.

The probability for Peregrines fledged on trees to breed on trees later is much lower (57%). There is a marked shift towards buildings which are regionally closest (26%), followed by cliffs and lattice structures (each 9%). The latter are abundant in proximity and offer plenty of nests from ravens and ospreys, however, the tradition to breed there is very young from evolutionary point of view. The growing tendency towards lattice towers in recent years is evident *(Figure 5)*, showing the attractiveness of this nest-site type. At least 9% changed from trees to rocks which are much more distant than other nest-site types.

The number of birds fledged on lattice structures is still too low for deeper analyses. Even though this nesting type started to establish in 2003, the increase was slow. Also the number of later re-sightings is lower than expected, which needs further investigations. Nevertheless, there is a markedly increasing number and percentage of respective broods in recent years.

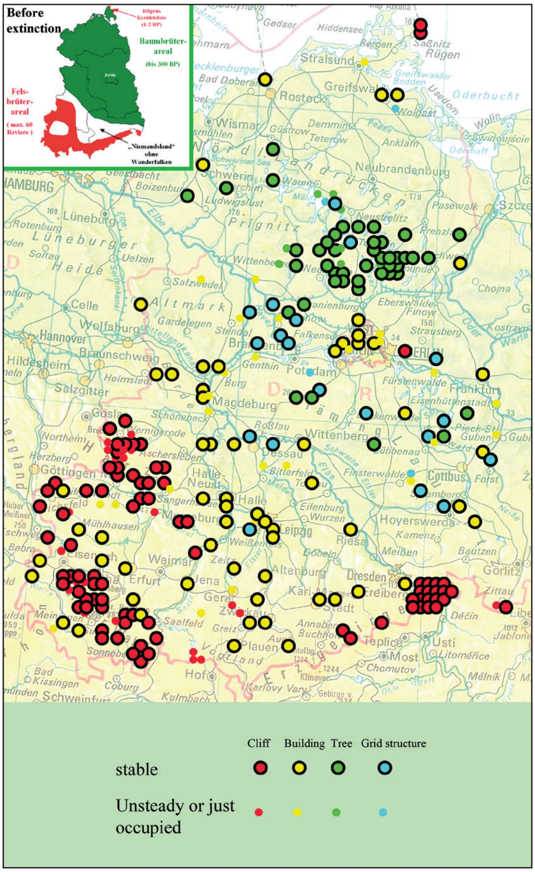
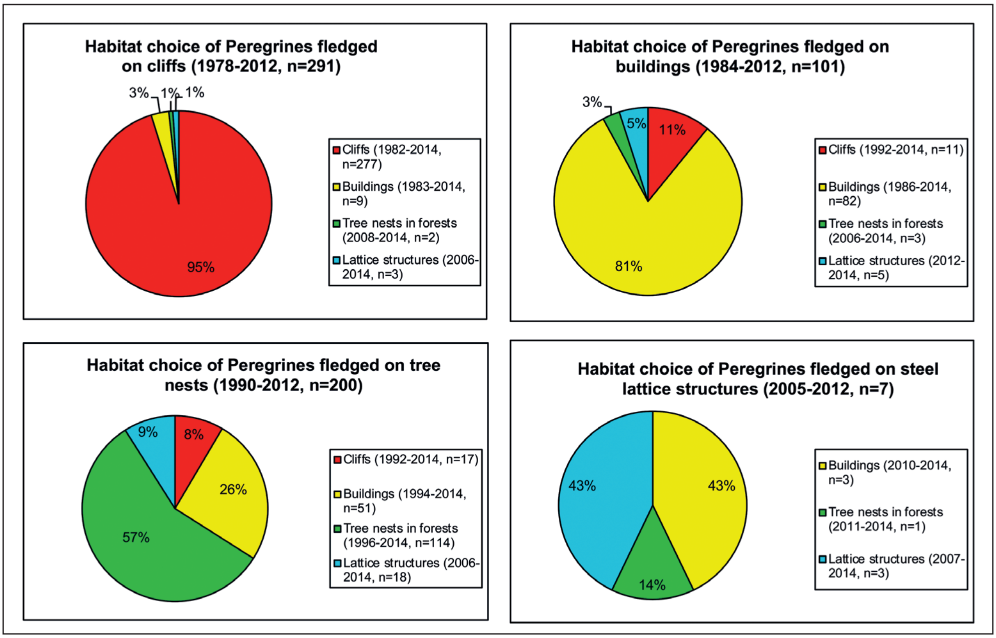


Figure 6. Regional distribution of the occupied Peregrine territories in 2014, 33 years after the start of the recovery in 1981; historical situation above left for comparison

6. ábra A foglalt vándorsólyom revírek regionális eloszlása 2014-ben, 33 évvel a visszatelepedés kezdete, 1981 után; a korábbi állapotot balra fent ábrázoltuk, az összehasonlítás kedvéért



Habitat choice of Peregrines fledged on cliffs (1978-2012, n=291)

Habitat choice of Peregrines fledged on buildings (1984-2012, n=101)

Habitat choice of Peregrines fledged on tree nests (1990-2012, n=200)

Habitat choice of Peregrines fledged on steel lattice structures (2005-2012, n=7)

Figure 7. Habitat choice of Peregrine Falcons in eastern Germany, depending on their natal habitat. Years in the boxes mean year of registered settlement, therefore differences to the time span of fledging years in the respective title. An additional bird (female) from a cliff settled as a ground-breeder on a North-Sea island

7. ábra A vándorsólymok élőhelyválasztása Németország keleti részén, a kikelési helyük függvényében. A szövegdobozban lévő évszámok a regisztrált megtelepedés évét jelentik, ettől eltér a kirepülési évek időintervalluma, ami a megfelelő címsorban található. Egy szikláról kirepült (tojó) példány egy északi-tengeri szigeten telepedett meg és a földön fészkelt

Origin of Peregrines breeding on cliffs, trees, buildings and lattice towers

More insight into the mechanisms behind may be gained by looking from the other side: Where do the birds that breed on cliffs, trees, buildings and lattice towers come from?

Most of the cliff breeders (91%) come from cliffs, only a smaller percentage from trees (5%) and buildings (4%), and so far none from lattice towers *(Figure 8)*.

There is a mixed figure in Peregrines breeding on buildings: 57% are of the same origin, but not less than 35% originally fledged on trees, and at least some on cliffs (6%) and lattice towers (2%). The shift from trees to buildings was highest in the first decade of the tree-breeders' project when the chance to meet a partner in the tree-breeders' range was still low.

The tree breeders recruit mainly by themselves (95%), and only single birds (altogether merely 5%) come from the other habitat types. In conjunction with the low habitat fidelity shown previously, that makes the tree-breeders the group which is most vulnerable to shift towards the other nest-site types – an additional indication for the lacking genetic fixation of the phenomenon.

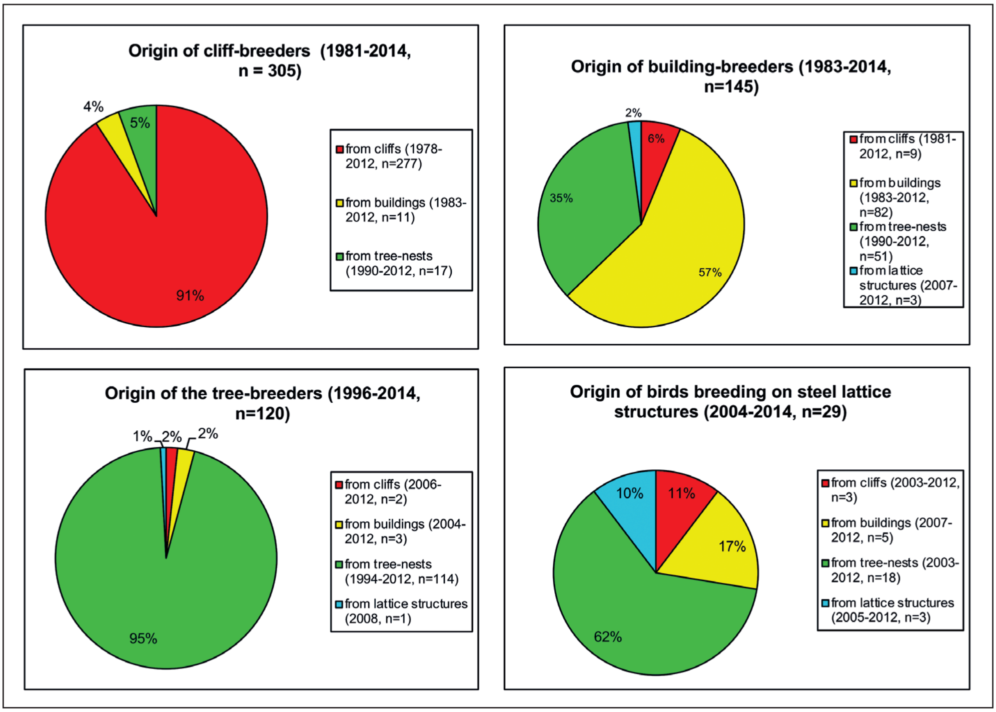


Figure 8. Natal habitat of East German Peregrines breeding on cliffs, trees, buildings and lattice towers
8. ábra Sziklán, fán, épületen és távvezeték oszlopon fészkelő kelet-németországi vándorsólymok származási élőhelytípusa

The number of 29 ringed birds breeding on lattice towers compared to 7 analysed above is a sign of the increasing tendency towards this nest-site type. The majority of them (62%) hatched and fledged on trees (see previous paragraph), but nests on lattice towers attract Peregrines from cliffs (11%) and buildings (17%) as well. The latter includes industrial sites many of which were abolished during the last years. Surprisingly, there is only a small recruitment from the same nest-site type (10%). Nevertheless, available nests on lattice structures seem to be a very attractive resource for Peregrines as shown by an updated analysis (Kleinstäuber unpubl.): The number of occupied territories increased from 20 in 2014 (cf. *Figure 5*) to 49 in 2017. Altogether 38 ringed breeding birds were identified meanwhile regarding their original habitat: Still, most birds (55%) came from trees, 8% from cliffs, and 29% from buildings. Compared to 2014 *(Figure 8)*, there was not a single additional bird coming from a lattice structure, resulting in merely 8% for these three identified birds.

Habitat fidelity towards trees depending on the release method / natural fledging

As the tree-breeders show the least habitat fidelity it is a question of conservation concern to compare the offspring of natural broods with juveniles which were brought by artificial management into the population (cross-fostering with other species as a method tested in Poland was not used in the German project). In the course of the tree-breeders' project we analysed this for the years 1996 (first tree brood) to 2009. The generally high juvenile mortality has to be kept in mind, and the fact that many birds got lost towards other habitat types. *Figure 9* shows that hacking as the starting method – the release of nearly fledged juveniles from captive breeding – has the lowest return rate: 7% of the released birds were identified later as birds breeding in tree nests. The results are slightly better (11%) with birds from translocations, i. e. juveniles from urban or industrial nest sites with known mortality risk that were taken from the nests and released in trees via hacking. Even better did the birds from captive breeding or translocation after fostering by wild pairs in trees: 15% were found later breeding in tree nests. It should be mentioned that translocations took place at an earlier age than the transfer of captive bred juveniles to the release site. Furthermore, translocations were preferably managed in the surroundings of the release sites. These aspects are considered to be relevant for the better success compared to the hacking method. Offspring of naturally breeding birds on tree nests are doing best – 18% were found later as tree breeders. Summarizing, it is unavoidable to start with methods of comparatively low prospect of success. However, as soon as possible the chance of improvement by switch to the fostering method should be used (as happened in our project). A growing number of tree breeders released an increasing number of juveniles with a higher return rate into the subpopulation. This is part of the explanation of the ongoing increase after the stop of the release in the end of 2011.

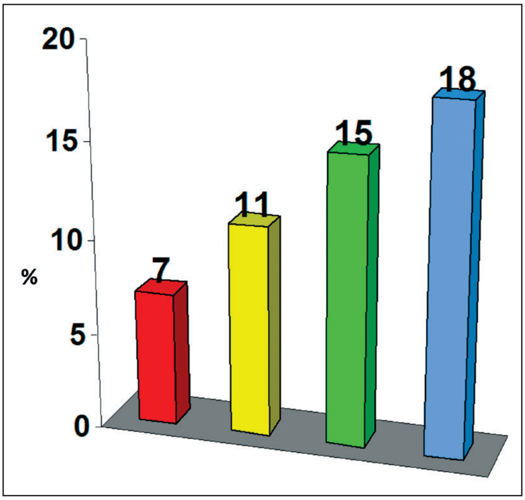


Figure 9. Percentage of habitat fidelity within the tree-breeders' project depending on the release method or natural fledging respectively, 1996–2009.
Red: Release of nearly fledged juv. from captive breeding via hacking (26 settled in forests from 378 released birds);
Yellow: Release of nestlings from translocations via hacking (14 settled in forests from 124 translocated birds);
Green: Release of small nestlings (captive bred or translocated) via adoption in wild broods (9 settled from 60 adopted birds);
Blue: Own offspring of wild breeding birds (23 settled from 124 fledged birds)

9. ábra Az élőhelyhűség százalékos bemutatása a fán fészkelő vándorsólymokkal foglalkozó project kapcsán, a visszatelepítési módszer vagy természetes szaporulat függvényében, 1996 és 2009 között
Piros: Tenyésztett, kirepülés előtt álló fiatal vadröpítése (26 telepedett meg erdőben a 378 elengedett madárból)
Sárga: Más fészekből áthelyezett fiókák vadröpítése (14 telepedett meg erdőben, a 124 áthelyezett példányból)
Zöld: (Tenyésztett, vagy természetes szaporulatból származó) kis fiókák adoptálása természetes fészekaljakba (9 telepedett meg a 60 madárból)
Kék: Természetes szaporulat (23 telepedett meg a 124 kirepült fiatalból)

Table 2. Comparison of the breeding performance of Peregrine Falcons of the four different nest-site types in Eastern Germany (2014 as an example)

2. táblázat A vándorsólymok költési sikerének összehasonlítása a négy fészkelőhely típusban, Németország keleti részén (az adatok 2014-ből származnak)

Habitat-Type	N breeding pairs (BP)	Successful BP	Fledged juv.	juv. per BP	juv. per successful pair
Cliffs	82	38 (46%)	105	1.3	2.8
Buildings	65	40 (62%)	109	1.7	2.7
Tree nests in forests	41	36 (88%)	96	2.3	2.7
Grid structures	20	14 (70%)	36	1.8	2.6
altogether	208	128 (62%)	346	1.7	2.7

Breeding performance of Peregrines depending on their nesting habitat

In *table 2* we show the markedly different breeding performance of Peregrines breeding on cliffs, buildings, trees, and lattice structures in the East German population. It is evident that the number of juveniles per successful pair is rather similar, with cliff nests ranking highest and nests on lattice towers lowest. However, the percentage of successful nests and consequently juveniles per territorial pair is by far the highest in tree nests and much higher than the lowest value among the habitat type. This results just from cliff broods which virtually are the inherent breeding strategy of Peregrines. The main reason for this low rate of successful pairs is predation and nest-site competition by eagle owls. For tree-breeding, on the other side, it is demonstrably that it cannot be seen as an "artefact" in the breeding ecology of Peregrine falcons, much more as a prospering alternative strategy to extend the range towards lowlands without rocks.

Discussion

This article refers to selected aspects of the colour ringing programme: the habitat choice depending on the original habitat, and in tree breeders depending on management methods vs. natural broods. Many more aspects comprise inter alia settlement distance from the place of birth, influence of the sex, duration of the occupation of territories, life reproduction, partner change, mortality etc. some of which are published in earlier papers (e. g. Kleinstäuber *et al.* 2009a,b, Kleinstäuber 2013).

Concerning the habitat choice depending on the habitat of origin, the results demonstrate convincingly that there is no free exchange of Peregrines between the different habitat types, as could be expected. Instead, we found strong habitat fidelity in birds resulting from cliff nest-sites, and – slightly reduced – in birds fledged on buildings, which form the nest type most similar to cliffs. This habitat fidelity may be related to the inborne nesting scheme of the Peregrine. In this respect, the tree-nesters differ much from cliff- and building-nesters in as far as their habitat choice depends fundamentally on the individual experience with that habitat type in the period of growing up and fledging. The relevant imprinting period for a nestling obviously is the time between first active orientation (ca. 14 days) and the first weeks after fledging (Kirmse & Sömmer 2015). That makes the imprinting effect most stable in natural tree broods compared to all kinds of management *(Figure 9)*.

This individual experience or imprinting competes with the inherent nesting scheme of the species and is able to overwhelm it at a rate of nearly 60% following our results with tree-nesters. This rate seems to be positively correlated with the size of the tree-nesters' subpopulation and the increasing chance to meet a partner for a tree brood – i.e. the higher the number of occupied territories in tree habitats, the bigger the probability for a bird to breed later in a tree nest. The males play a crucial role in this context as they are the sex that is responsible for the choice and occupation of a nest site. With 90%, their habitat fidelity is much higher than that of females. Additionally, males settle markedly closer to their place of origin than the females – after an earlier analysis 26 km (100 males) vs. 114 km (86 females) (Kleinstäuber 2013, Kleinstäuber *et al.* 2009a). That may be the reason why the core areas of the cliff-breeders in the mountains and the tree-breeders in the lowlands are still largely free of broods on buildings and pylons.

Our data could prove that tree-nesters recruit nearly exclusively from themselves, and they hardly benefit from the other nest site types (the very few cases are described by Sömmer & Kirmse 2013). That has important implications for management and conservation. Most relevant, with respect to the restoration of the tree-breeders' population in Central and Eastern Europe, is to avoid any support of broods on buildings, industrial sites, and lattice towers in the tree-breeders' range. Nest site management has exclusively to focus on tree nests in order to stabilize the tree-nesting tradition in this subpopulation. In cases of new potential tree-breeder pairs in suitable surroundings additional "guidance" may be taken in consideration, e. g. from a fire watchtower (blocking of suitable niches) to trees (nest basket in optimal position). Large forest areas free of cliffs and high buildings are most promising for the establishment of new tree-breeders' territories.

Outside the tree-breeders' range, single breeding attempts on trees or even successful broods have been reported during the last decades (e. g. Wegner 2013, Brauneis 2017). The respective territories usually sustain no longer than one or two years. Only exceptionally cases of longer existence of a tree-nest territory outside the tree-breeders' range have been reported in Central Europe (e. g. Preusch *et al.* 2018 in Southwest Germany), however never a starting increase of their numbers in the surroundings.

A new artificial nest-site type is steel lattice constructions such as pylons of high-voltage powerlines, big cranes, broadcast towers etc. They offer new nesting opportunities as there are plenty of stick nests available, mainly from ospreys, ravens, and carrion or hooded crows. Due to long-term cooperation with the electricity companies, natural osprey nests are usually stabilized after the first brood with artificial nest constructions making these nests even more stable and attractive to Peregrines. In our population, Peregrines started to use this nest type in 1998, and in spite of a very low rate of comeback in our database, this new tradition is spreading increasingly, mainly in farmland areas but also within forests, or mixed habitats. For the tradition of tree-nesting this is detrimental because of the evident shift of tree-born Peregrines towards lattice structures. The former hope pylon-breeders could be a source for the tree-breeders did not fulfil and had to be corrected. The opposite is true: the shift from trees towards lattice towers is increasing (compared to “stable” towards cliffs and buildings).

The re-colonisation of the tree-breeders’ range may be slowed down by the shift to lattice structures but it is not really threatened by that. The subpopulation of the tree-breeders is still growing, last but not least due to intensive nest site management in many of the existing territories – artificial nests, nest protection zones, and co-operation with the forestry – resulting in the best breeding results among the four nest-site types. In farmland areas in the lowlands were no Peregrines used to exist before the pesticide crash, today lattice structures with stick nests of ospreys, ravens and to some extent even crows, enable the spread of the species into these new habitats.

Finally, we want to stress the interesting fact that the first nest-site choice is very stable, and there are only few cases of a later change. After our experience changes of an established pair towards another nest-site type are usually triggered by an emergency situation, and in all known cases of our investigation the pair stayed in the near surroundings of the former nest-site. In fact, the birds keep up their habitat and merely change the nest-site.

We suppose that single tree-broods outside the tree-breeders’ range as described by Wegner (2013), Brauneis (2017) and others have a comparable background. This is confirmed by case studies from Wegner (2013). For that reason they are not stable and cannot be the foundation of a population of tree-breeders’ or even a mixed population of tree-breeders and cliff-breeders which in fact cannot and does not exist in Central Europe. Our assumption is that also reports about tree-broods in other countries refer more to single events than to the existence of “hidden” populations of tree-breeders.

Outlook

In total, we expect a further increase of the Peregrine population in East Germany. However, there will be differences between the four nest-site types due to different ecological conditions, resulting differences in breeding performance, and as well due to shifts between the four groups as described in the results.

Nest-sites on rocks increasingly reach the limits of their availability and have a low breeding success, mainly due to eagle owl predation and competition. There are limited opportunities for a marked increase of Peregrines breeding on rocks or quarries. Likewise, there is hardly any population pressure from the other nest-site types.

There is some potential for additional nest-sites on buildings and industrial sites, however, breeding performance and survival of the juveniles are limited there. Without nest-site management even former strongholds loose their importance, such as in Berlin after the decision to stop nest-site management on buildings there in favour of the tree-breeders in the surroundings of the city.

The subpopulation of the tree-breeders is still far from their historical size. The availability of stick nests from ravens, ospreys and white-tailed eagles today is much higher than before the extinction of Peregrines in the 1970s. Combined with a good breeding performance we expect a further increase over the next decade even if the tree-breeders continue to loose birds towards the other nest-site types. Gradually, this shift may decrease as a thriving tree-breeders' population *per se* is attractive to Peregrines in preparation of their first brood. If offspring of tree-breeders switches to other nest-site types, this will happen increasingly towards steel lattice structures, first of all electricity pylons.

With their huge supply of stick nests, steel lattice structures will more and more outpace buildings and industrial sites with respect to their attractiveness. Situated in the whole area of cliff-breeders, tree-breeders and the space between, the shift towards these structures is quite easy for Peregrines from other nest-site types. Therefore, broods on lattice structures are supposed to increase further, more due to shifts than due to own reproduction. The annual removal of corvid nests by the energy companies could slow that gradually down and lead to more spatial dynamics; on the other side that could be outbalanced by artificial nests provided routinely by the energy companies for Ospreys.

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