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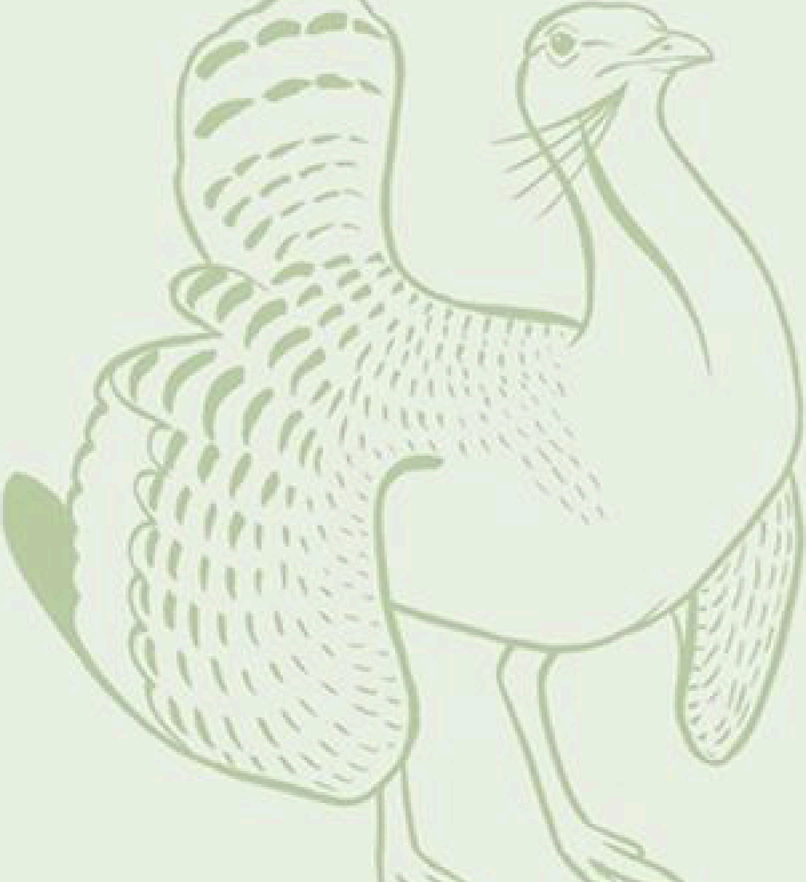

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Demography, breeding success and effects of nest type in artificial colonies of Red-footed Falcons and allies

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Abstract Shortage of breeding sites is an important limiting factor of bird populations. Artificial breeding platforms, nest-boxes or man-made twig nests often present solutions with remarkable results, however long-term sustainability of these populations remains to be resolved. Furthermore, the question whether the inference of results of studies conducted on birds breeding in artificial breeding sites can be generalized to other populations, still remains open. Here we present the history, and the results of a 20 year old (1995-2015) nest-box programme initiated to increase potential breeding possibilities of Red-footed Falcons in an area, where nest-site shortage was a severe limiting factor. We show how various other species (Jackdaws, Kestrels and Long-eared Owls) have utilized these resources, and present descriptive statistics on their reproductive performance. Analysing the data of a total of 1432 breeding attempts, we show that Red-footed Falcons have similar clutch sizes, and nesting success (i.e. ratio of nests with at least on fledgling), however fledging success (ratio of the number of eggs/fledged nestlings) was different in artificial nest-boxes. When we excluded closed box types from artificial nests, this difference was not apparent. In case of Kestrels (n=1626 breeding attempts) clutch size was significantly higher in artificial nests, while we found no difference in fledging or nesting success. When only comparing open boxes to natural nests, the difference in clutch size was no longer significant. We also analysed the effect of nest box design on reproductive parameters of the two species using regression trees. Inter annual effects were the most important in shaping clutch size and fledging rate of both falcon species, however we also found nest-box design effects, but only in Red-footed Falcons. In years when mean clutch size was high, these birds had lower clutch size in an older, darker nest-box type compared to an alternative design, and to open boxes. However, fledging rate in the same years was lower for both open boxes and older nest-boxes. We conclude that artificial colonies are an important and successful tool in Red-footed Falcon conservation, and that the breeding parameters measured in artificial colonies depend on nest-box design. We present correlative evidence that closed boxes have a significant positive species specific effect on reproduction, probably due to their protection against weather. We also show that birds may have a preference for a certain nest-box design, and that the breeding success in the less favoured box type may be similar to that in open nests. We recommend that future studies incorporate nest-type and nest-box design effects in all comparisons made on reproductive performance in case of Red-footed Falcons and Kestrels.

Keywords: *Falco vespertinus*, *Falco tinnunculus*, *Asio otus*, *Corvus monedula*, nest-box, fledging success, clutch size, population trend, colony

Összefoglalás A fészkelőhelyek hiánya fontos limitáló tényezője lehet egyes madárfajok előfordulásának. Mesterséges fészkekkel, fészekodúkkal, költőládákkal vagy műfészkek kihelyezésével ezt a hiányt lehet pótolni, de az állományok hosszú távú fennmaradása az ilyen, ember által kialakított fészkelőhelyeken erősen beavatkozás-függő, önmagában tartósan nem biztosított. További probléma, hogy nem tisztázott, mennyire lehet az ilyen rendszerekben végzett kutatások eredményeit általánosítani természetes fészkekben költő állományokra. Ebben a vizsgálatban bemutatjuk egy 20 éves (1995–2014) telepes költőláda program történetét és eredményeit, amit azzal a céllal kezdtünk el, hogy fészkelőhelyet teremtsünk a kék vércsék számára egy olyan területen, ahol a költőhelyek hiánya súlyos limitáló tényező volt. Bemutatjuk továbbá, hogy az általunk kihelyezett költőládákat hogyan hasznosítják más, nem feltétlenül koloniális madárfajok (vörös vércse, csóka és erdei fülesbagoly), és leíró statisztikákat közlünk a költési eredményeikről.

A kék vércsék esetében 1432 költési kísérletet elemezve azt találtuk, hogy sem a fészekaljméret, sem a költéssiker nem különbözik a természetes és a mesterséges fészkek között, azonban a kelési siker alacsonyabb a természetes fészkekben. Ha kihagyjuk a zárt ládákat az elemzésből, ez a különbség nem kimutatható. Vörös vércsék esetében 1626 költési kísérlet elemezve a fészekalj méret szignifikánsan magasabb a költőládákban, de a fészkelési sikeresség és a kirepülési siker nem tér el. Ha kihagyjuk a zárt ládákat az elemzésből, ez a különbség szintén eltűnik. A különböző költőláda típusokban a költési paramétereket döntési fákkal elemeztük. Mindkét vércse fajnál az év hatása a legmeghatározóbb a költési paraméterek formálásában, azonban a költőláda típusoknak szignifikáns hatása volt kék vércsék esetén. A magas átlagos fészekalj méretű években a madarak átlagosan kevesebb tojást raktak egy régebbi, zártabb és sötétebb költőláda típusban, mint a többi ládatípusba. A repítési siker ezekben a jó években mind a régebbi költőláda típusban, mind a nyitott műfészkekben alacsonyabb volt, mint az új kisebb és világosabb zárt ládákban. Korrelációs eredményeink szerint létezik fajspecifikus ládatípus preferencia. Kék vércséknél a zárt ládákban mért magasabb reprodukciós siker feltehetően a tetővel rendelkező ládák zord időjárási körülmények ellen való védelmét tükrözi. Javasoljuk, hogy a későbbi vizsgálatok ne csak a fészkek típusát (természetes, mesterséges), de a mesterséges fészkek esetében a láda típusát is vegyék figyelembe.

Kulcsszavak: *Falco vespertinus*, *Falco tinnunculus*, *Asio otus, Corvus monedula*, költőláda, költőodú, költési siker, fészekalj méret, kolónia

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Introduction

Preserving, managing and exploring the grasslands of the Pannon Biogeographic region is one of the top priorities of Hungarian nature conservation (Báldi *et al.* 2005). River management and the intensification of agricultural practices of the past 150 years all contributed to the drastic loss of grasslands in the region. Today, Hungary holds the third largest proportion of agricultural land in the EU (Donald *et al.* 2002). Conservation of grassland type habitats (or so called 'puszta') entails two general approaches, 1) management of landscape level habitat composition and quality through regulations and subsidies (Ángyán *et al.* 2002) and 2) active, often species or plant association specific conservation measures (e.g. Fehérvári *et al.* 2012). In the latter case, measures may include habitat reconstruction, eradication of invasive species and supplementing breeding possibilities like nesting islands, artificial twig nests or nest-boxes. For instance, two emblematic species, the Roller *(Coracias garrulus)* and the Red-footed Falcon *(Falco vespertinus)* typically suffer from shortage of nesting opportunities in Hungary (Bagyura & Palatitz 2004, Fehérvári *et al.* 2009, Palatitz *et al.* 2009, Kiss *et al.* 2014). The meticulous nest-box programs of the past decades had shifted the majority of breeding pairs of these two species to artificial nesting sites. Red-footed Falcons occupy naturally occurring breeding possibilities like nests built by other species. In Hungary, species that build adequate nests for the falcons are of the genus *Corvus*, typically Rooks *(Corvus frugilegus)*, Hooded Crows *(Corvus corone cornix)* and Magpies *(Pica pica)*. In the 1940s, the estimated 2000–2500 pairs of Red-footed Falcons predominantly used rookeries. However, due to a direct corvid specific poisoning protocol, and presumably due to large scale changes in land use, and the collapse of animal husbandry, approximately 90% of previously available rookeries were either demolished or have shifted location to unsuitable habitats for Red-footed Falcons (Fehérvári *et al.* 2009). By 2006 the estimated breeding population was a below 600 pairs (Palatitz *et al.* 2015). An international conservation program initiated in 2006 with the primary objective to halt this tendency succeeded in increasing the number of breeding pairs, primarily through provisioning over 3500 nest-boxes (LIFE05/NAT/HU/122, see www.falcoproject.eu). Today approx. two-thirds of Red-footed Falcon pairs breed in man-made structures in Hungary (Palatitz *et al.* 2015). Provisioning artificial breeding structures for these falcons has a long history in the Carpathian Basin, the first records of nest-baskets used date back to the first decade of the 20th century (Csörgey 1908). Since then a series of local and/or small scale programs built up valuable experience, that aided the success of the countrywide program (Bagyura & Palatitz 2004). For instance, in 1989 the Csongrád County local group of MME/BirdLife Hungary started an artificial nest program at three separate locations (Csanádi-puszták, Cserebökényi-puszták and Baksi-puszta). There was no considerable large breeding population of Red-footed Falcons in the County in the past 60–70 years (Keve & Szijj 1957, Sterbetz 1959, 1975), only a single larger colony (70 pairs) was reported from Baksi-puszta in the 1960s (Molnár & Tajti 2007). The neighbouring Békés County held a total of 550 pairs in 13 colonies in 1990, however this population decreased by 50% in the following five years (Tóth 1995). By the early 2000s, the majority of the remaining pairs also disappeared (Bagyura & Palatitz 2004). Despite the relative low number of breeding birds in the region, the occupancy rate of the artificial nests and open nest-boxes was surprisingly high (Vajda 1992, Molnár 2000). This program was followed in the Vásárhelyi-puszta in 1995 and still continuous to date, resulting in one of the densest Red-footed Falcon breeding site within the EU (Palatitz *et al.* 2009). Despite the deliberate aim of colonies to increase the number of Red-footed Falcon breeding pairs, various other species (e.g. Kestrel – *Falco tinnunculus*, Jackdaw – *Corvus monedula*, Long-eared Owls – *Asio otus*) are also taking advantage of the nesting sites (Kotymán 2001). The fact that territorial species like Kestrels use colonial nest-boxes, shows the extreme shortage of nests in a near tree-less landscape.

Although nest-boxes are installed for a wide range of species (Mainwaring 2015), and are especially successful in case of small predatory birds in Europe (Hamerstrom *et al.* 1973, Fargallo *et al.* 2001, Franco *et al.* 2005, Bux *et al.* 2008, Gottschalk *et al.* 2011, Catry *et al.* 2013) and in North America (Bortolotti 1994, Katzner *et al.* 2005), the effect they have on breeding is still poorly understood (Lambrechts *et al.* 2012). Particularly difficult is to establish whether the inference of studies carried out on birds breeding in structures deliberately erected for them can be generalized to populations breeding in naturally occurring nest sites. For instance, disentangling nest-type effects from that of the foraging habitats can be challenging, as breeding site provisioning is typically carried out as a conservation tool in areas, where they limit population growth of the focal species (Mainwaring 2015).

In this study we report the used box-types, the temporal patterns of colonization of the four most abundant species (i.e. Red-footed Falcon, Kestrel, Jackdaw and Long-eared Owl) and present descriptive statistics of breeding parameters based on large sample sizes from the Vásárhelyi-puszta nest-box

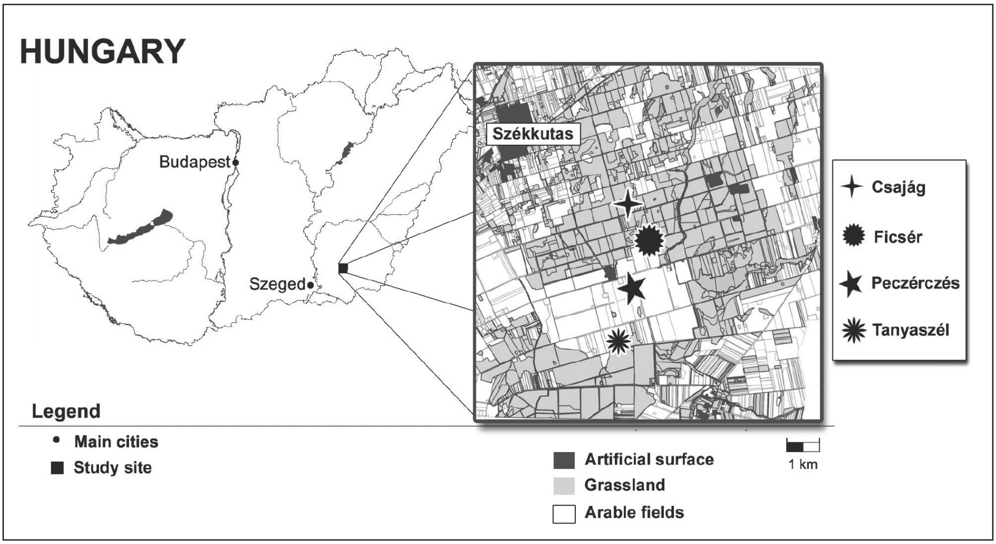

Figure 1. Location of the study site and 4 artificial colonies within. The fifth colony (Tótkutas, see *Table 1*) is approx. 6 kms southeast from the 10×10 km study area. The study area was defined primarily to assess habitat structure in previous studies (Palatitz *et al.* 2011). We also used this area to map solitary pairs breeding in natural nests in the vicinity of the artificial colonies. Recently, two rookeries were established within the loose colony Csajág (see *Table 1*), the other one is approx. 17 kilometers from this site (outside the study area)

1. ábra A vizsgálati terület és azon belül a 4 mesterséges fészektelep elhelyezkedése. Az ötödik telep (Tótkutas, lásd *1. táblázat*) mintegy 6 kilométerre található a kutatási területtől délkeletre. A 10×10 km-es kutatási terület lehatárolást elsősorban korábbi vizsgálatokban használtuk élőhely összetétel meghatározásra (Palatitz *et al.* 2011), de ebben a vizsgálatban ezt a területet használtuk a természetes fészkekben költő szoliter vércsék feltérképezéséhez. A közelmúltban két vetési varjú telep is létesült: egy a Csajág nevű mesterséges kolóniában (lásd *1. táblázat*), és egy másik, mintegy 17 kilométerre innen

program. We also exploit the rare possibility of assessing nest-type effects on breeding performance without marked habitat variability as our data derive from colonies located close to each other *(Figure 1)*.

Materials and Methods

Study site

The Vásárhelyi-puszta lies within the municipality borders of Hódmezővásárhely, Békéssámson, Székkutas, Orosháza and Kardoskút (N 46°28’25”, E 20°37’30”). A total of 8000 ha comprises the area, out of which 5629 ha are part of the Körös-Maros National Park since 1999. The protected area and its surroundings are also Natura 2000 sites and constitute the HUKM 10004 SPA. Approximately 60% of the area is grassland, of which the bulk is utilized as meadows. The composition of livestock grazing extensively in the area is made up of 250–800 cattle, 1800–2500 sheep, 10–60 horses. Mowing prior to grazing is carried out on circa 30% of the grazed areas. The natural type habitats are interspersed with arable fields of variable sizes (2–150 ha), where maize, sunflower, various cere-

Colony Name	First breeding season	Dominant tree species	Height (m)	Total area (ha)	Description
Ficsér	1995	*Fraxinus excelsior*	7-9	0.6	Dense, compact colony
Csajág	1996	*Quercus robur, Eleganus angustifolia, Gleditsia triacanthos*	4-10	10	1 dense and 2 loose group of nest-boxes and a rookery
Peczérczés	2005	*Ulmus minor*	11-13	0.44	Dense, compact colony
Tanyaszél	2009	*Robinia pseudoacacia*	8-15	0.2, 0.4	Dense, compact colony in two distinct group of trees
Tótkutas	2013	*Robinia pseudoacacia*	8-10	1.2	Dense, compact colony

Table 1. Description of the five studied artificial colonies
1. táblázat A vizsgált 5 mesterséges kolónia jellemzői

als, and alfalfa are cultivated typically with intensive agro-technologies. Large scale irrigation is absent from the area. Shallow, endorheic basins in between the arable fields, and grasslands retain temporary saline lakes or marshes. However, total water coverage on the grasslands is not uncommon from early spring to mid-summer. Dirt roads, channels and ditches create a relatively dense network of linear structures in the landscape. Five-six decades ago, the landscape had a sizeable human population with a total of 200 active farms in the area. Currently only 20 active homesteads and 2 livestock farms are present.

The area is plain flat, with an elevation of 86–88.5 m (a.s.l.). Typical soil types of the region are highly alkaline solonchaks, and solonetz. Mean annual sunlit hours are 2000–2050 while temperature 10.4–10.6 °C. Daily average maximum temperature in summer is high (34.6–34.8 °C), while annual cumulative precipitation is highly variable (280–850 mm). Highest average rainfall months are May and June. These two can provide 25% of the total annual precipitation. The original vegetation of the grassland remained around the saline lakes and marshes. Typical plant associations of the grasslands are short *(Achileo-Festucetum pseudovinae)* to medium *(Agrostio-Alopecuretum pratensis)* vegetation height (Molnár *et al.* 2012). The most treasured natural value of the area is the diverse bird life present throughout the year. The Kardoskúti Fehér-tó alkaline lake is a Ramsar site, as it is a migratory hotspot for Greater White-fronted Goose *(Anser albifrons)*, Common Crane *(Grus grus)*, and for various waders (Charadriiformes). Typical breeding species are Yellow Wagtail *(Motacilla flava)*, Skylark *(Alauda arvensis)*, Lesser Grey Shrike *(Lanius minor)*, Marsh Harrier *(Circus aeruginosus)*, Roller, Avocet *(Recurvirostra avosetta)*, Great White Egret *(Casmerodius alba)*, White-tailed Eagle *(Haliaeetus albicilla)* and Imperial Eagle *(Aquila heliaca)*. Most common mammals of the area are the periodically gradating Field Vole *(Microtus arvalis)*, the European Hamster *(Cricetus cricetus)*, Steppe Mouse *(Mus spicilegus)*, Common Hare *(Lepus lepus)*, Roe Deer *(Caprimulgus europeus)*. Typical predators are Red Fox *(Vulpes vulpes)*, Beech Marten

(Martes foina) and Weasel *(Mustella nivalis)* (Kotymán L. pers. obs.).

Location of artificial colonies

Trees that may support nest-boxes are typically present at the location of former farms, homesteads. Altogether we have created 4 larger colonies more or less aligned on the central north-south axis of the area. A total of 5 larger colonies *(Table 1)*, smaller nest-box groups and a handful of solitary nest-boxes were interspersed between the larger colonies. In 2014 we drastically increased the number of solitary nest-boxes, distributing them to various distant locations of the area. The number of breeding platforms was gradually increased at each colony, and currently a total of 250–255 artificial breeding sites are available for the birds. The boxes were placed below the canopy, at 3–8 meters typically on the trunk, or one of the larger branches of the trees. Positioning and exposure of the nest boxes varies, the governing rule of decisions was based on tree structure rather than favouring a chosen direction. Intriguingly, we noticed, that if a nest-box is placed in near perpendicular tree fork, the life expectancy of the nest-box grew considerably. Due to the shortage of trees capable of holding a nest-box we placed often placed 2–9 boxes on a single tree.

Nest-box types

We predominantly used 3 types of nest-boxes during the past 20 years, 1 open plastic box (1. O.B.), and 2 covered wooden boxes (1. C.B. and 2. C.B) (see *Figure 2* for detailed dimensions). The open platform was a 20 litre canister sawed in half, and perforated with 1 cm holes on the sides and the bottom to allow water to flow through. The useful area is 0.1 m^2 and the weight is 0.46 kg. Prior to installing these on the trees, we pressed a 5–8 cm turf block into the platform and formed a nest like cavity. This was the only box type used until 1999.

We started placing out 1.C.B. type boxes in 2000. This box comprised of 2 cm thick pine sideboards, the roof cut out from plywood and strengthened with a tin sheet, while the bottom was created from wattle boards. The total weight is a considerable 7.2 kgs, and the inner useful area is 0.11 m^2 of this box. We also used 1 cm wide and 12 cm long metal strips strengthened to the back of the box to help fixing the boxes in place.

Since 2005 we have been using a new closed box type (2.C.B.), which is smaller and lighter compared to the previous version. Here the sideboards and the roof are made from pine, the bottom from either oak (*Quercus* spp.), or locust-tree *(Robinia pseudo-acacia)*. All boards got fungicide soaking prior to assembly. Fixing the box on the trees is aided by a 50 cm long pine board screwed on the back of the box. We also glued a 5x10 cm mirror on the inner surface of the roof to allow assessing the content without having to climb up to the box. The weight of 2.C.B. is 5.3 kg while the useful inner area is 0.0625 m^2. As nest material, we used a 3–5 cm thick dry grass bedding. In case the nest material comprised from leftover pellets and remains from previous breeding attempts, in general we did not clean them but see (Fehérvári *et al.* 2015). All nests were numbered on the bottom, side and front, with either visible white oil paint or with chalk. In a few cases we found a couple of successful Red-footed Falcon nesting attempts in closed D-type boxes, Common Buzzard *(Buteo buteo)* nests and Wood Pigeon *(Columba palumbus)* nests, however the vast majority of all

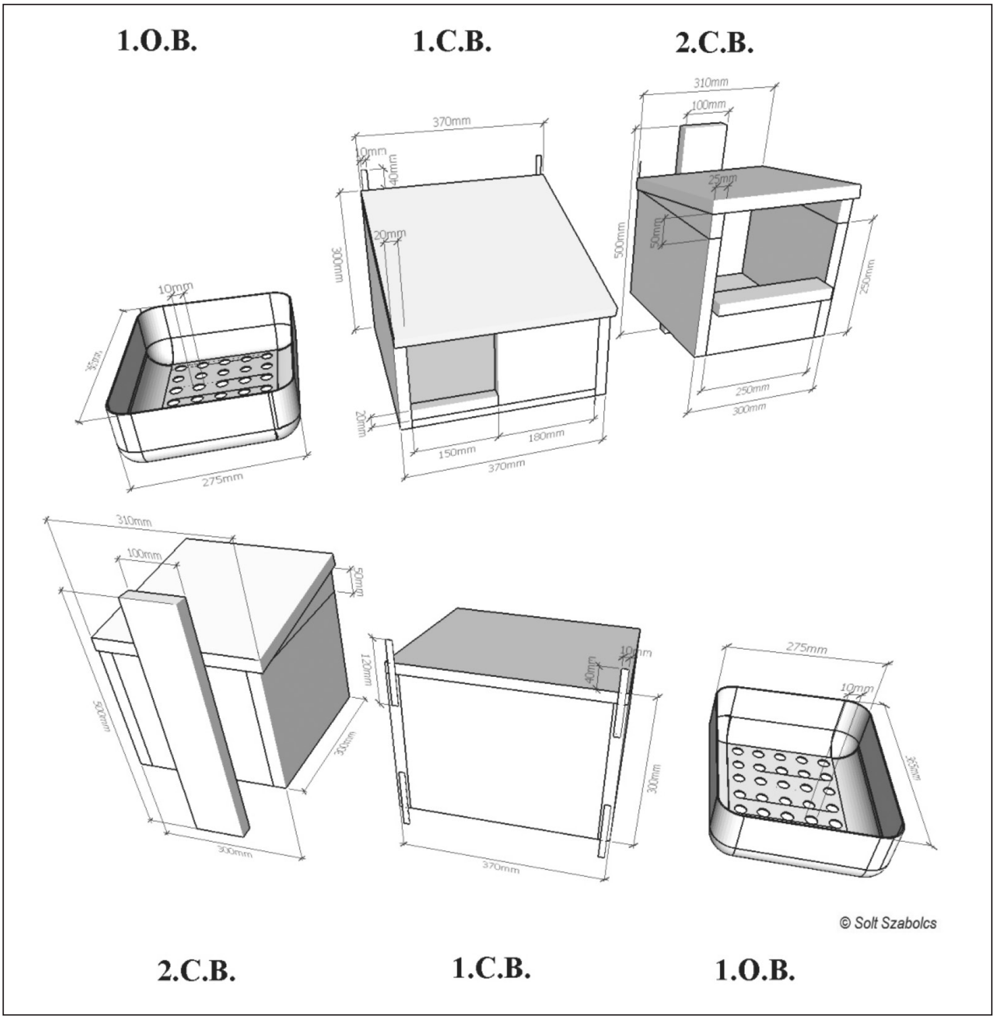

Figure 2. Schematic drawings of the three most commonly used nest-box designs. The open box 1.O.B. was created from 20 litre plastic canisters sawed in half, while the other two are made of wood. All boxes were erected to approx. the same height and with various orientations

2. ábra A három leggyakrabban használt ládatípus tervrajzai. A nyitott láda (1.O.B.) félbevágott 20 literes műanyag marmonkannából, míg a másik két típus fából készült. Az összes ládatípus közel hasonló magasságban és véletlenszerű orientációval került kihelyezésre

breeding attempts occurred in the three nest-box types.

Corvid nests

Prior to the mid ’90s only a dozen or so pairs of Magpies or Hooded Crows bred in the area. However, the local breeding population of both species increased somewhat during the past 20 years. Moreover, the previously completely absent Rooks have also started breeding in 2009 (Horváth *et al.* 2015). By 2014 over 500 breeding pairs were present in 2 rookeries.

To monitor Red-footed Falcons not only in artificial colonies, but also in solitary corvid nests, we created the Red-footed Falcon study area in the Vásárhelyi Plain, a 10×10 km study area centred on the oldest colony (Palatitz *et al.* 2011), where we mapped all possible breeding attempts.

Assessing breeding performance

Nest occupancy, clutch size, hatching success and fledging success were monitored throughout the study period by visiting each nest individually. In all cases we used ladders to climb up to the nest, even though from 2006 we had mirrors installed into 2.C.B. type boxes. These mirrors were only used for verification of observations, if deemed necessary. In most cases all nests were visited on the same day, or if conditions hindered this, we visited all nests within a couple of days. In the first two years 2-3 visiting rounds, from 1997–2005, 3–8 rounds, and from 2006, 6–12 rounds were made annually. Red-footed Falcon and Kestrel eggs are practically inseparable based on colour or morphology, therefore to assess the species we collected additional information with spotting-scopes and binoculars. The timing of visits was always adjusted to the individual year's conditions. In general, the first visiting round was made in mid-March and we also carried out necessary maintenance works like refilling nest lining, or refurbishing the boxes in the first round. In April we typically surveyed the boxes 1–2 times, in May at least twice. In June we switched to visiting protocol with 8–14 days in between, while in July the visits were made more frequent with a visit every 7–10 days. In August typically only a handful of late breeders had nestlings, however we followed through with their visits until the last of the fledglings left the boxes. This pattern made it possible to estimate the breeding performance of all species breeding in the boxes, but we were also able to collect data on egg laying date in case of the most common species. We avoided timing the visiting rounds on cold, rainy, or windy days especially during the incubation period. In spring we typically performed rounds around mid-day, while in summer we took advantage of early mornings and late afternoons.

In case of all nests we recorded the species and sex of the birds that left the box upon arrival, the content of the nest-box (species, eggs, nestlings) and all other information that pointed to future occupation of the nest-box (scrapings, missing nest-lining, pellets etc.). We also recorded the type and frequency of identifiable food remains, like carcasses, feathers, skulls. In case we found nestlings, we aged the whole clutch to days, and recorded all abnormalities, like obvious symptoms of illnesses, or general poor condition. Since 2006, 99% of all Red-footed Falcons were ringed with individually coded colour rings.

We also monitored all breeding attempts that occurred in natural nests within the artificial colonies, in rookeries or at solitary nests with similar intensity. In case of natural nests, however it is not always possible to climb up to the nests, therefore we used a large pole with a mirror attached to the end. The mirror was placed over the nest and the content was checked with binoculars. In this case mid-aged downy nestlings cannot be counted only their presence confirmed. However, once they start growing flight feathers this is easily achievable, thus causing no bias in later analyses. In case of rookeries, we labelled the nests on the trunk of trees to allow identification similar to that

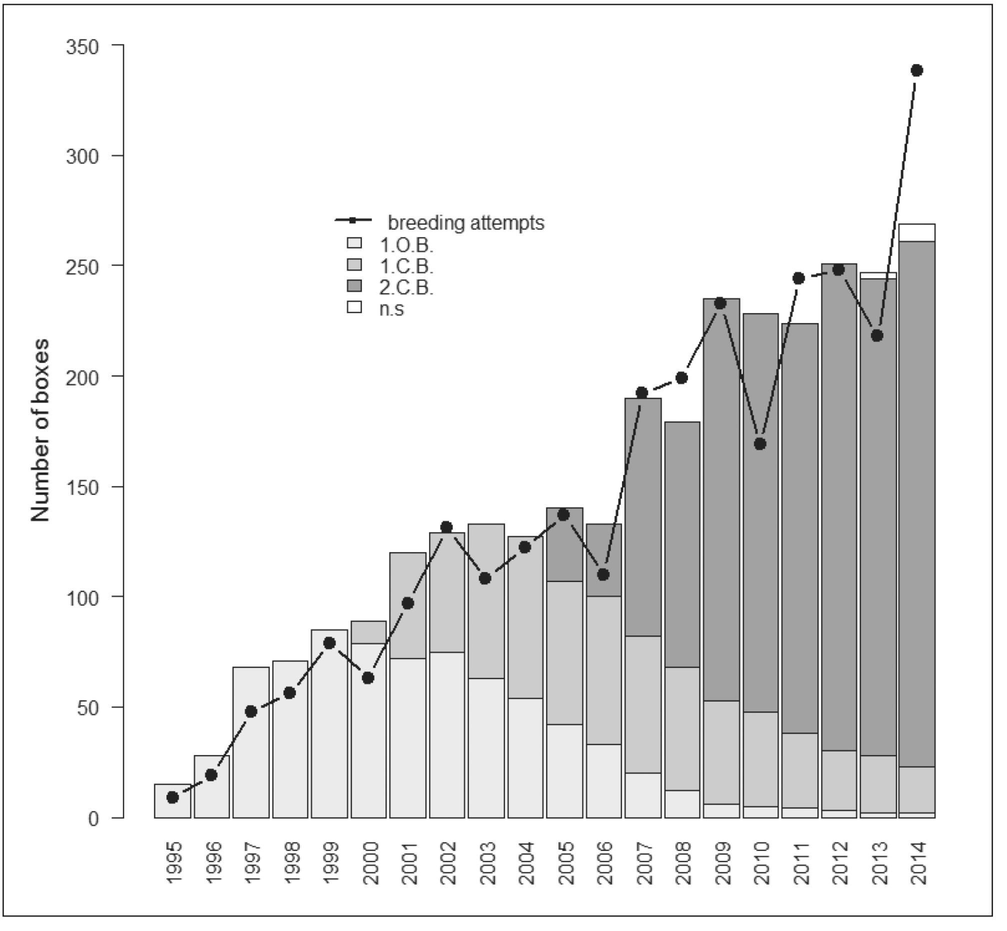

Figure 3. Cumulative number of nest-boxes, and the number of box designs available in each year of the study period. We have gradually shifted the proportions of nest-boxes to type 2.C.B: since 2006. Not specified (N.S.) are a small number of various other nest-box designs that have not been described in detail

3. ábra A kutatási területen található költőládák kumulatív száma a vizsgálati években, és az éveken belül elérhető különböző ládatípusok aránya. A nem definiált (N.S.) kategóriába olyan ládák tartoznak, amelyeket jelen cikkben nem részleteztünk

of artificial colonies. We also recorded the geographic coordinates of all solitary nesting attempts.

Statistics

To evaluate the potential differences in breeding success parameters between natural and artificial breeding sites, we only used the data of colonial pairs. Natural nest sites occurred in all studied artificial colonies, as a couple of hooded crows, or magpies built nests in the canopies of the trees holding the nest-box colonies. Since 2009, two rookeries were also established in the study area, that were used for breeding by Red-footed Falcons, thus we included the data deriving from these breeding attempts. To evaluate

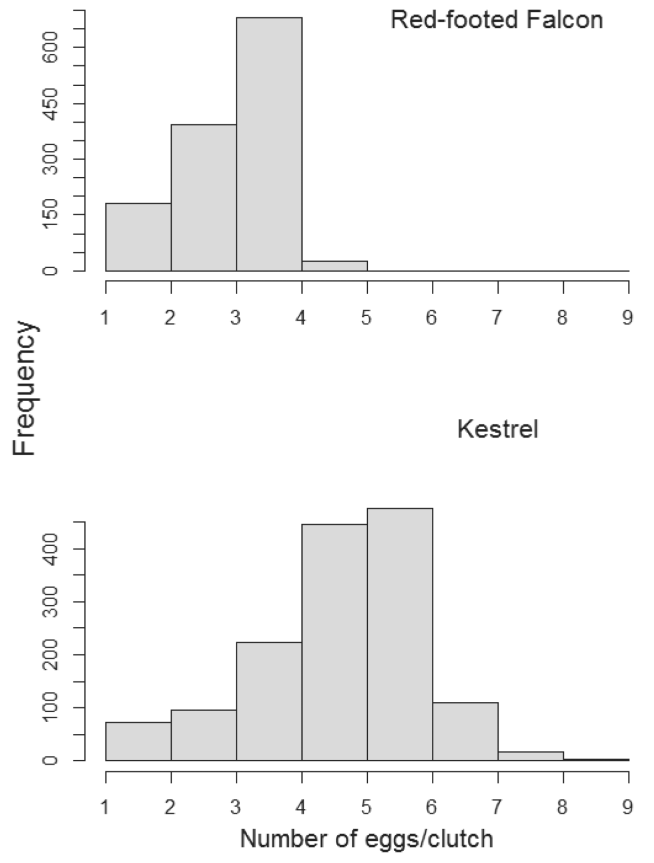

Figure 4. Clutch size histograms of Red-footed Falcons (n=1280 clutches) and Kestrels (n=1442 clutches) during the study period

4. ábra Fészekalj méret hisztogramok a kék vércsék (n=1280 fészekalj) és a vörös vércsék (n=1442 fészekalj) esetén

Species	Number of nesting attempts	Percentage of solitary attempts (%)	1.O.B.	1.C.B.	2.C.B.	Rook	Hooded crow	Mapgie	Other
Kestrel	1626	11.6	395	319	686	53	37	111	25
Red-footed Falcon	1432	9.1	224	148	654	206	31	145	24
Jackdaw	702	1.1	1	366	333	0	0	0	2
Long-eared Owl	217	15.7	53	13	59	18	7	65	2

Table 2. Number of breeding attempts of the four most common species according to different breeding platforms observed during the 20 year study period

2. táblázat A négy leggyakoribb faj 20 év során megfigyelt költési kísérleteinek száma a különböző fészektípusokban

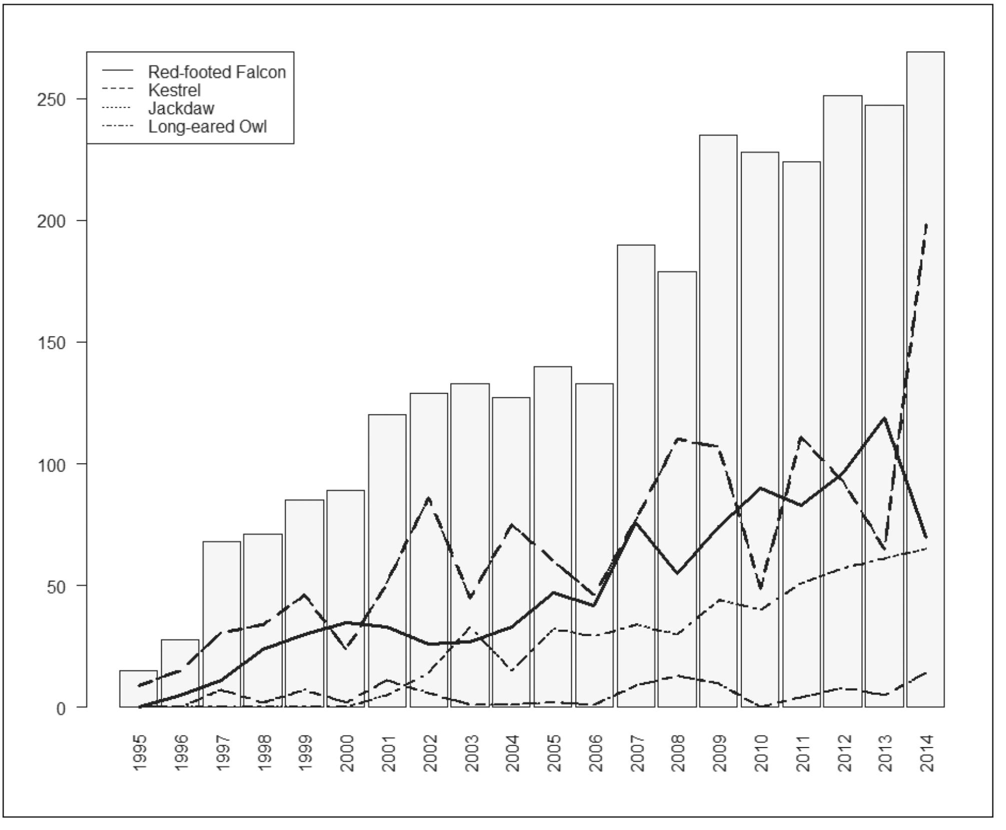

Figure 5. The cumulative number of nest-boxes (bars) and the number of breeding pairs (clutches with at least one egg) during the study period. Red-footed Falcons, Kestrels and Jackdaws show a significantly increasing trend (see *Table 3*), while Long-eared Owls remain relatively stable within the time framework presented. (The total number of breeding pairs may exceed the number of boxes available as the same boxes may be used by several species within a breeding season.) In 2014, the total number of Red-footed Falcons seemingly drops, however a relatively large proportion of the population used rookeries (natural nests, not depicted here), therefore the overall number of pairs increased within the study site

5. ábra Az összesen elérhető ládák száma (oszlopok) és a bennük költő különböző fajok párjainak (legalább egy tojást raktak a ládába) száma. Szignifikánsan nőtt (lásd. *3. táblázat*) a kék vércse, vörös vércse és a csóka párok száma, míg az erdei fülesbaglyoké kevéssé változott az elmúlt 20 évben. (Egy adott évben a párok száma összesen magasabb lehet, mint az elérhető ládák száma, mert egy adott fészket a különböző fajok, vagy akár azonos faj különböző egyedei egymást követve használhatják egy költési perióduson belül). A kék vércsék esetén az utolsó évben látható csökkenést elsősorban az okozza, hogy ebben az évben a párok jelentős része a területen található vetési varjú telepeken költött

nest-box design effects we only used the data deriving from years (since 2006), when all nest-box types were available for the birds *(Figure 3)*. As dependent variables we analysed clutch size (number of eggs/nest), fledging success (fledged nestlings/number of eggs) and nesting success (at least one fledged nestling/nest). We interpreted clutch size as a measure of the product of parental quality and investment and fledging success as the measure of parental quality and environmental effects.

In case of Kestrels, clutch size distribution and consequently other breeding performance parameters follow a relatively symmetrical distribution, however for Red-footed Falcons this is considerably different *(Figure 4)*. Here, the distribution has a considerable skew, with 53% of all observed clutches containing 4 eggs. Modelling such distributions can be challenging with conventional general linear models (Faraway 2005), therefore avoid inferring results based on non-fitting linear models we used non-parametric tests in case of simple comparisons and Classification and Regression Trees (CART) to assess nest-box design effects on breeding performance (Breiman *et al.* 1984, De'ath 2002). The advantage of CART models is that they are less sensitive to the distribution of the dependent variables, and that they allow to map out multi-level effect hierarchy of explanatory variables (De'ath & Fabricius 2000, Olden *et al.* 2008). To aid comparability, we applied these models for all species and we used nest-box type, year and type of breeding (colonial/solitary) as explanatory variables for all models. We used R 3.2.0 for all statistical analyses carried out (R Core Team 2015).

Results

We recorded a total of 3977 breeding attempts of the four focus species between 1995 and 2015 *(Table 2)*. Kestrels were the first to use the nest-boxes, a total of 9 pairs successfully fledged nestlings in the first year the artificial breeding sites were available *(Figure 5)*. The first Red-footed Falcon pairs appeared in 1996, 2 years after the program started, followed by the first Long-eared Owl pairs in 1997. The first Jackdaws only started breeding when 1.C.B. type boxes were first available in 2001 *(Figure 5)*. The two falcon species and Jackdaws showed a significant increase in number of breeding pairs throughout the study period, while the number of Long-eared Owl pairs remained constant *(Table 3)*. Descriptive statistics of breeding parameters of the four species are presented in *Table 4*. Albeit not apparent from the summary data, the two falcons have a considerable difference in the distribution of clutch size *(Figure 4)*. In case of Red-footed Falcons, we found no difference in mean clutch size (Mann-Whitney U test: U=71512, p=0.43) and nesting success rate (χ^2 test: χ^2=0.261, df=1, p-value=0.6) between colonial pairs breeding in artificial and natural nests. However, fledging success was significantly different (Mann-Whitney U test: U=48826, p=0.02), with higher fledging success in artificial nests. When we excluded closed box types from artificial nests (1.C.B. and 2.C.B.), and only compared 1.O.B. to natural nests, this difference was not apparent (Mann-Whitney U test: U=1457.5, p=0.77). In case of Kestrels clutch size was significantly higher in artificial nests (Mann-Whitney U test: U=30816, p<<0.001, median difference=1 egg), while we found no difference in fledging success (Mann-Whitney U test: U=10354, p=0.12) or nesting success (χ^2 test: χ^2=2.98, df=1, p-value=0.08). When only comparing 1.O.B. to natural nests, the difference in clutch size was no longer significant (Mann-Whitney U test: U=894, p=0.28).

In case when only artificial nests were considered, clutch size of Red-footed Falcons was grouped by nest-box type in the second level, with 1.O.B and 2.C.B. having significantly higher number of eggs/clutch compared to 1.C.B. in certain years *(Figure 6)* according to the CART analysis. However, clutch size was only influenced by

Species	Effect of year	SE	t-value	p-value	R^2
Red-footed Falcon	8.2	0.86	9.35	<0.0001	0.83
Kestrel	6.6	1.47	4.47	<0.0001	0.49
Jackdaw	4.05	0.41	9.83	<0.0001	0.88
Long-eared Owl	0.31	0.20	1.58	0.13	0.07

Table 3. Linear regression effect summaries of time (year) on the number of breeding pairs of the 4 most common species at the study site. The number of Red-footed Falcons, Kestrels and Jackdaws show a significant mean increase, however the number of Long-eared Owl pairs remains constant over time

3. táblázat Az év, költés, költési kísérletek száma összefüggésre illesztett lineáris regressziós modellek becsült együtthatói és tesztjei, valamint R-négyzet értékei a négy leggyakoribb faj esetén. Az erdei fülesbagoly kivételével mindegyik faj költőállománya szignifikáns növekedést mutat az elmúlt 20 évben

Clutch Size						
	Mean	SE	SD	Median	Range	n
Kestrel	5.05	0.03	1.35	5	1-9	1442
Red-footed Falcon	3.38	0.02	0.88	4	1-5	1280
Jackdaw	4.35	0.05	1.32	5	1-7	511
Long-eared Owl	4.72	0.16	1.78	5	1-10	132
Number of Fledged nestlings						
	Mean	SE	SD	Median	Range	n
Kestrel	4.01	0.05	1.54	4	1-8	1442
Red-footed Falcon	2.76	0.04	1.05	3	1-5	1280
Jackdaw	2.44	0.06	1.22	2	1-6	511
Long-eared Owl	3.09	0.20	1.51	3	1-7	132
Fledging rate (%)						
	Mean	SE	SD	Median	Range	n
Kestrel	51.87	1.12	39.43	66.66	0-100	1442
Red-footed Falcon	48.77	1.29	42.29	50	0-100	1280
Jackdaw	34.94	1.55	32.77	33.33	0-100	511
Long-eared Owl	30.25	1.55	36.05	0	0-100	132

Table 4. Descriptive statistics of clutch size (maximum number of eggs), number of fledged nestlings (i.e. reproductive success) and fledging rate (i.e. ratio of successfully fledged nestlings/maximum number of eggs layed), for the 4 most common breeding species at the study site

4. táblázat A fészekaljméret, a repített fiókák száma, illetve a repítési siker (fiókák száma/fészekaljméret) leíró statisztikái a négy leggyakoribb költő faj esetén inter-annual differences in case of Kestrels, with similar between year patterns as in case of Red-footed Falcons *(Figure 7)*. Fledging success of Red-footed Falcons was superior in 2.C.B. nest-boxes, regardless of seasonal effects *(Figure 8)*, while only large (8.5–77% mean fledging rate) annual differences were observed in case of Kestrels *(Figure 9)*.

Discussion

The colonization of the newly established artificial colonies by Kestrels, Long-eared Owls and Red-footed Falcons was rapid. Kestrels were the first to breed in the 1.O.B. type boxes in the first year, followed by Red-footed Falcons and Long-eared Owls in the next year. This immediate and large scale acceptance of the man-made platforms probably indicates that nest-site shortage was a severely limiting factor in an area of high quality. The fact that Kestrels were the first to colonize is not surprising, this species was present as a breeder in solitary natural nests prior to the first nest-boxes were in place, albeit in small numbers. However, Red-footed Falcons were absent from the

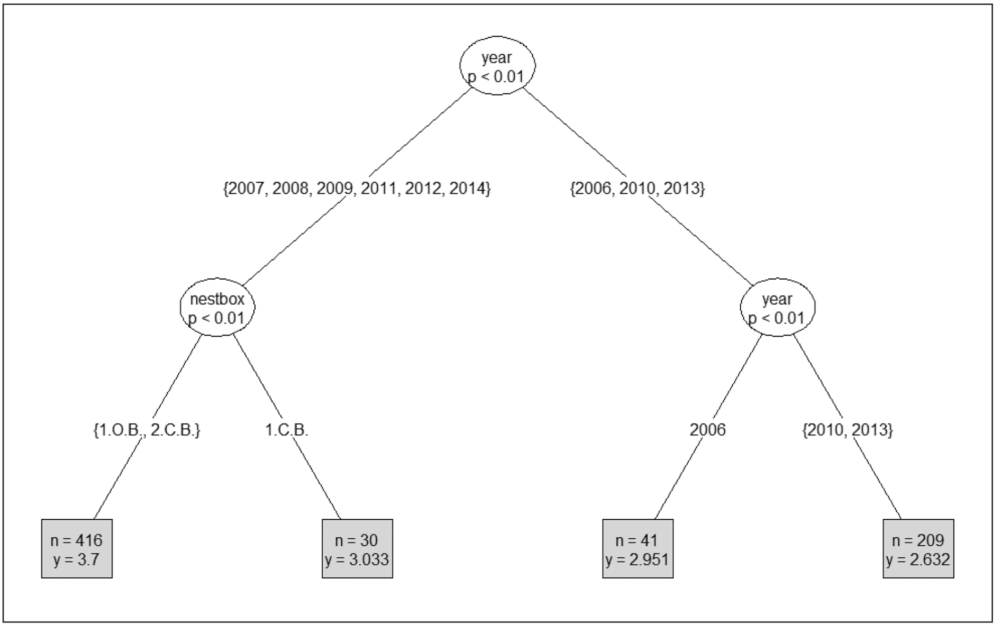

Figure 6. Regression tree on Red-footed Falcon clutch size grouped by years and nest-box type. Terminal nodes (grey boxes) show respective sample size (n) and mean clutch size (y). In years when mean clutch size is larger (2007–2009, 2011, 2012 and 2014) nest-box type has a significant effect, with clutches in 1.C.B. being nearly an egg smaller on average compared to the other two box types. However, in low clutch size years (2006, 2010 and 2013) there is no apparent effect of nest-boxes

6. ábra Regressziós fa a kék vércsék fészekalj méretére az évek és a költőláda típus függvényében. A leveleken (szürke dobozok) az adott leágazáshoz tartozó mintaszámot (n) és a csoportátlagot ábrázoltuk (y). Azokban az években, amikor az átlagos fészekalj méret magas (2007–2009, 2011, 2012 és 2014), az 1.C.B. ládatípusban átlagosan majdnem egy tojással kisebb fészekaljat raknak a madarak. Azonban azokban az években, amikor az átlagos tojásszám alacsonyabb (2006, 2010 és 2013), a ládatípusnak nincs hatása area and practically from the surrounding region as well. It still remains unresolved how individuals find these resources. Perhaps non-breeding individuals, dispersing juveniles or passage migrants memorize potential future breeding sites, and return in the following seasons. Due to the relatively treeless landscape, the created artificial colonies stand out and are probably easily detectable for birds from larger distances. Another possibility is that falcons located and decided to breed in the colonies through heterospecific habitat copying (Parejo *et al.* 2005, Kivelä *et al.* 2014), using the cues provided by Kestrels (Sumasgutner *et al.* 2014). Jackdaws first appeared as in 2001, coinciding with the first breeding season when 1.C.B. type boxes were made available. These boxes are darker due to the relatively small entrance located asymmetrically on the front. Presumably, this design resembles the natural cavities, cliffs and corners of abandoned houses/ church towers typically used for nesting by Jackdaws (Soler & Soler 1996, Henderson *et al.* 2000, Campobello *et al.* 2012). However, once a considerable number of pairs have established in the colonies, this species

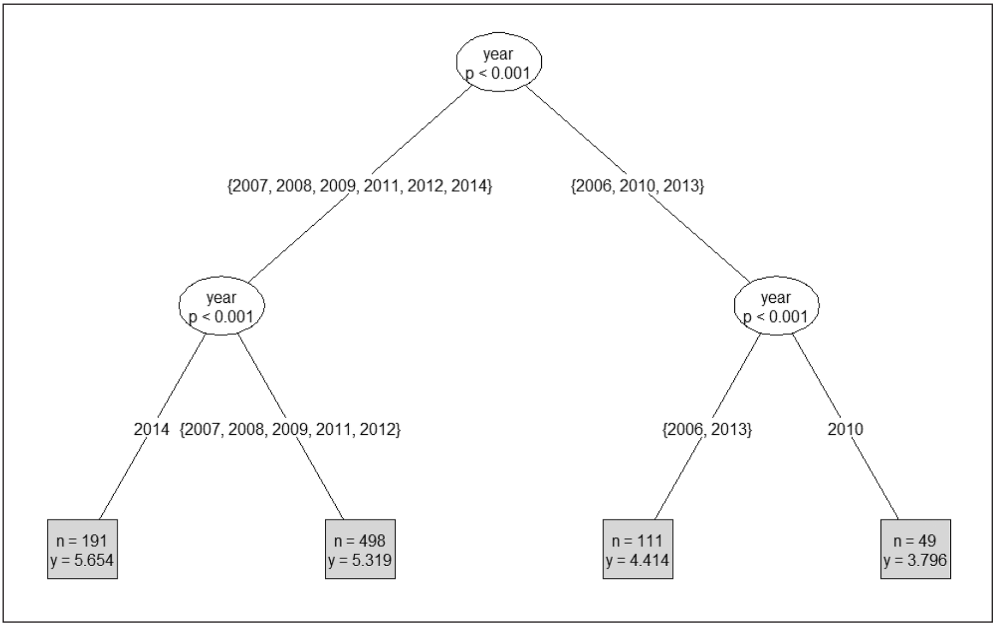

Figure 7. Regression tree on Kestrel clutch size grouped by years. Terminal nodes (grey boxes) show respective sample size (n) and mean clutch size (y). Nest-box type has no effect in neither years with high mean clutch sizes (2007–2009, 2011, 2012 and 2014) nor in low clutch size years (2006, 2010 and 2013). However, the inter-annual variation is remarkable, the differences in average clutch size can be up to nearly two eggs

7. ábra Regressziós fa a vörös vércsék fészekalj méretére az évek és a költőláda típus függvényében. A leveleken (szürke dobozok) az adott leágazáshoz tartozó mintaszámot (n) és a csoportátlagot ábrázoltuk (y). Sem azokban az években, amikor az átlagos fészekaljméret magas (2007–2009, 2011, 2012 és 2014), sem azokban, amikor alacsonyabb (2006, 2010 és 2013) nincs a láda típusának hatása. Azonban jelentős évek közötti eltérést lehet megfigyelni, majdnem két tojásnyi átlagos eltérés is lehet

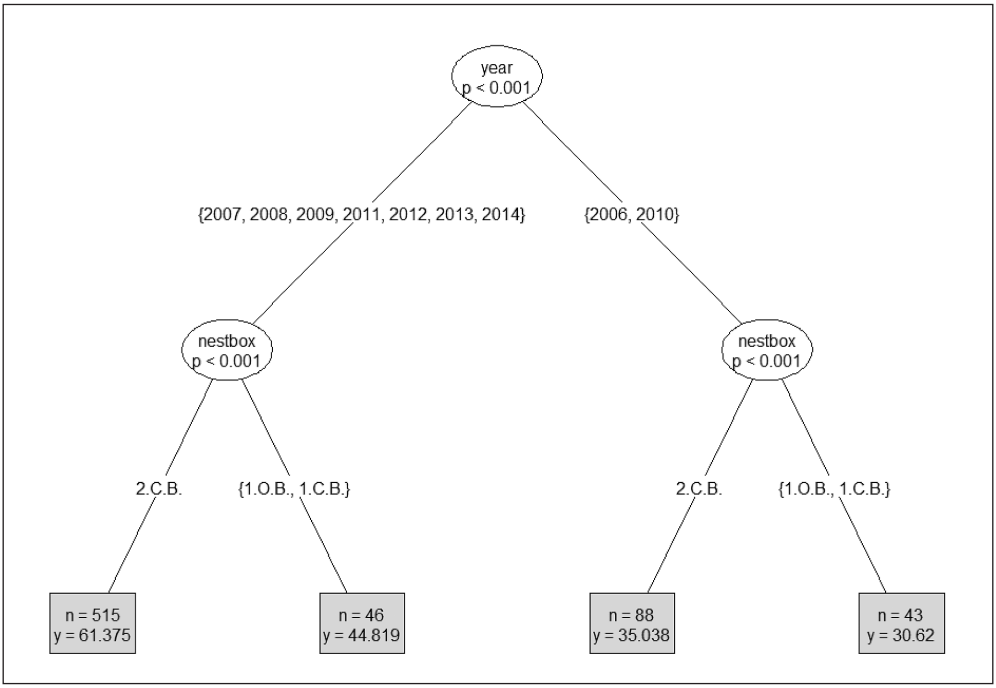

Figure 8. Regression tree on Red-footed Falcon fledging success (i.e. number of fledged nestling/ maximum number of eggs per clutch) grouped by years and nest-box type. Terminal nodes (grey boxes) show respective sample size (n) and mean clutch size (y). In years when fledging success is higher (2007–2009, 2011–2014) and in years when it is lower (2006 and 2010) nest-box type has a significant effect, with eggs in 2.C.B. having higher probability of becoming fledged nestlings

8. ábra Regressziós fa a kék vércse repítési sikerére az évek és a költőláda típus függvényében. A leveleken (szürke dobozok) az adott leágazáshoz tartozó mintaszámot (n) és a csoportátlagot ábrázoltuk (y). A repítési siker magasabb volt a 2.C.B. típusú ládában, mind azokban az években, amikor sikeresebbek voltak a madarak (2007–2009, 2011–2014), mind pedig azokban, amikor sikertelenebbek (2006 és 2010)

was able to switch to 2.C.B. nests in some occasions. Long-eared Owls appeared at the colonies together with Red-footed Falcons, however as opposed to the other three species, the number of breeding owl pairs remained near constant over the study period. This species is the most common nocturnal avian predator in the region, therefore it is unlikely that local population size is causing the observed pattern. Long-eared Owls are restricted territorial breeders, and may often breed in clusters (Rodriguez *et al.* 2006), thus intraspecific exclusion may have a smaller role in regulating breeding numbers at our colonies. Moreover, these birds are often the first to commence breeding at our study site (pers. obs.), thus the lack of empty potential platforms can be excluded. Owls are often mobbed by birds (Pavey & Smyth 1998), and we have also observed such behaviour at our study site. Owls were mobbed by both falcon species quite often when flushed during nest-inspections, regardless of the presence of humans. We have also observed Red-footed Falcons harass incubating owls to the extent that the owls de-

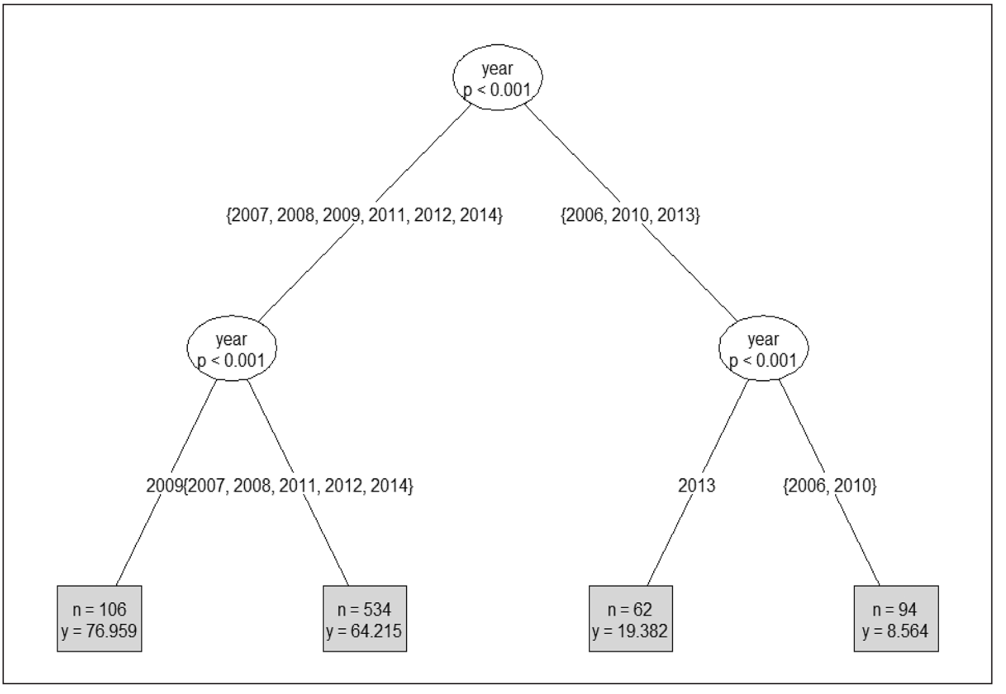

Figure 9. Regression tree on Kestrel fledging success (i.e. number of fledged nestling/maximum number of eggs per clutch) grouped by years. Terminal nodes (grey boxes) show respective sample size (n) and mean clutch size (y). Nest-box type had no significant effect here, however there is a considerable difference between years as in the most successful year (2009) 77% of eggs reached became nestlings on average while in the worst years only 8.6% did

9. ábra Regressziós fa a kék vércsék repítési sikerére az évek és a költőláda típus függvényében. A leveleken (szürke dobozok) az adott leágazáshoz tartozó mintaszámot (n) és a csoportátlagot ábrázoltuk (y). Szemben a kék vércsékkel, a láda típusnak nincs csoportosító hatása, csak az évhatás határozta meg a repítési sikert. Azonban jelentős eltérések mutathatók ki évek között, míg a legjobb évben (2009) átlagosan 77%-a a lerakott tojásoknak kikelt és kirepült, addig a legrosszabb években mindez csak 8,6%

serted their clutch, leaving the box to be used by the harassing falcon pair. It may be plausible that despite their early breeding and potential to cluster into a confined area, the number of adverse interspecific interactions creates a pressure, that only the most competitive and/or resilient pairs can cope with, and that this pressure limits the number of pairs breeding in the studied colonies.

Concerning the effect of nest-type in colonies, we found that Red-footed Falcons laid the similar sized clutches in both artificial and natural nests however median fledging success is lower in natural stick nests. The former parameter reflects parental quality and investment into reproduction, indicating that breeding pairs probably did not differentiate among boxes in general and twig nests. The fact that fledging success was significantly lower in artificial nests, but when only considering open boxes, this difference disappeared probably indicates how closed boxes protect the clutches. Stick nests in our area are predominantly open nests, with the exception of newly built Magpie nests. These are seldom used by the falcons, typically 2–3 year old nests are occupied where the roof like structure is often missing. Thus, natural nests predominantly constitute open, roofless nests, while artificial nests are dominated by boxes with complete cover. The lack of significant difference in open boxes versus artificial nests therefore probably indicates how cover over clutches protects them from either predators or more likely, from adverse weather conditions. Stochastic extreme weather conditions are known to have a direct and detrimental effect on avian populations by causing direct mortality (Newton 2007). Heavy rainfall and hail from thunderstorms are not uncommon at our study site, and we have observed mass mortality effects of these previously. However, Kestrels had significantly larger clutch size in artificial closed nests, but had similar median fledging and overall nesting rates in natural nests. One would expect that cover over the clutches would have similar and general effects causing similar patterns across species. It is possible that Red-footed Falcons have different physiological coping mechanisms to extreme weather, or that roof cover is just a confounding effect masking true cause of the observed pattern.

When concentrating on nest-box types, in general only Red-footed Falcons were affected to a certain degree by the box-design, but both species were sensitive to inter-annual effects. The predominant prey for both species is the Common Vole *(Microtus arvalis)*. Population density of this small mammal fluctuates multi-annually (Tkadlec & Stenseth 2001) and can produce mass outbreaks (Jacob *et al.* 2014) as has happened in 2014. In a previous study, we have showed that despite the low variability in clutch size, Red-footed Falcons adjust their reproductory investment to vole abundance (Fehérvári *et al.* 2011). Kestrels are small mammal specialists with various adaptive responses to fluctuating prey abundance that entail immigration to high prey density areas and adjusting clutch size (Korpimäki & Norrdahl 1991). Thus, the inter-annual effects in clutch size can be interpreted as adaptive responses to prey availability and to some degree to weather during the breeding period (Fehérvári *et al.* 2011). However, in years when mean clutch size was larger, Red-footed Falcons had significantly smaller clutches in 1.C.B., indicating that either parental quality and/or investment was different in case of pairs breeding in these boxes. These boxes may have different thermal regimes, light-levels within and a narrow view-point from the inside for incubating birds. Moreover, Jackdaws that predominantly prefer these boxes often build stick nests within, further decreasing light and visibility. It is possible that Red-footed Falcons generally avoid and thus, only less competitive pairs utilize these boxes, due to these factors. Fledging success was also lower here, together with 1.O.B., in both high and low success rate years compared to that in 2.C.B. nests. The lack of difference in clutch size between 1.O.B. and 2.C.B., while a significant deviation in mean fledging rate may indicate, that the falcons showed no avoidance to open boxes, but had lower success due to the lack of cover. On the other hand fledging success was also lower for 1.C.B. compared to 2.C.B. while both boxes provide cover. The indication of lower parental quality/investment in 1.C.B. boxes based on clutch size may also be reflected in fledging success. Therefore, the observed pattern in the two box types may derive from alternative processes resulting in similar reproductive output.

Our results demonstrate that multi-species nest-box colonies may be extremely successful in aiding the colonization of novel areas by several species. Seemingly, the falcon species breeding in these artificial colonies have somewhat different breeding success patterns compared to natural nests, however they are not inferior to these. Generalizing results obtained at these colonies is possible to birds breeding in natural nests, providing future statistical analyses incorporate nest-type effects. However, it is possible that individuals breeding at these sites experience factors not present at natural breeding sites. For instance, Red-footed Falcons have to cope with a dynamic within colony nest location pattern that changes each year in rookeries (Purger & Tepavčević 1999), while the location of nest-boxes remains constant over a long time period. Furthermore, closed boxes restrict field of view from the birds' perspective compared to open rook nests. These may alter social interaction patterns, and thus birds may have different adaptive responses to these as in rookeries. From a conservation perspective, as tool, nest-boxes in this environment are successful and have to be propagated. However, mid-to long term research and conservation efforts have to concentrate on preserving, managing and if possible further increasing the number of rookeries to ensure sustainability of the already existing population.

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Provisioning nest material for Rooks; a potential tool for conservation management

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Abstract Active conservation measures often entail supplementing scarce resources, such as food or nesting site to high conservation value species. We hypothesized that adequate nest material in reasonable distance is a scarce resource for Rooks breeding in open grassland habitats of Hungary. Here we show that Rooks willingly utilize large quantities of provided excess nesting material, and that this procedure may alter nest composition, and increase the number of successful pairs. Our results show that while nest height remains constant, twig diameter is significantly larger, the number of twigs used per nest is presumably smaller, and that the ratio of nests with fledglings is higher in a rookery where supplementary twigs were present. Providing twigs and branches in the vicinity of rookeries may serve as an active conservation measure to increase the number of nests in a rookery, and thus the potential number of nesting possibilities for Red-footed Falcons.

Keywords: scarce resource, *Corvus frugilegus*, nest composition, Red-footed Falcon, *Falco vespertinus*, colony

Összefoglalás Aktív természetvédelmi beavatkozások gyakran egy faj számára fontos, ritka források pótlására irányulnak, ilyen lehet például megfelelő táplálék kihelyezése vagy fészkelőhely biztosítása. Hipotézisünk szerint a pusztai élőhelyen költő vetési varjak számára fontos limitáló tényező lehet a megfelelő és könnyen elérhető fészekanyag. Vizsgálatunk megmutatja, hogy a varjak a számukra a telep közelében kihelyezett nagy mennyiségű gallyat beépítik a fészkeikbe. Eredményeink szerint, míg a fészek magassága hasonló, a fészekben található gallyak átmérője, és a fiókás fészkek aránya is nagyobb azon a telepen, ahova fészekanyagot helyeztünk ki. Véleményünk szerint fészekanyag kihelyezése jó módszer lehet a vetésivarjú-telepek fészekszámának növeléséhez, melyek így több fészkelési lehetőséget biztosítanak az ezeken a telepeken költő, fokozottan védett kék vércsék számára.

Kulcsszavak: ritka forrás, *Corvus frugilegus*, fészek összetétel, kék vércse, *Falco vespertinus*, kolónia

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Introduction

Species-specific conservation efforts often consider shortage of resources that threaten the viability of a focal avian population, and present solutions to these (Palatitz *et al.* 2009). For instance, decay in food supply due to the degradation of foraging habitats evoke responses that entail the restoration or improvement through habitat altering regimes ranging from local to landscape levels (Donald *et al.* 2002, 2006, Franco & Sutherland 2004). Improving complex systems is often time consuming, thus conservationists may choose temporary solutions of directly providing scarce resources (Robb *et al.* 2008, Cortés-Avizanda *et al.* 2010). Consider the example of the declining European vultures, where the change in habitat usage altered animal husbandry, consequently creating a large scale shortage in carcasses (Wallace & Temple 1987, Green *et al.* 2004, Bose & Sarrazin 2007, Deygout *et al.* 2009). However, in certain cases, a network of supplementary feeding stations coupled with the promotion of vulture-friendly livestock keeping proved to be effective in halting the decline (Houston 2005). In case of cavity nesting/ non-nest building species, one of the key factors influencing reproduction may be the lack of nesting sites. Supplementing artificial nesting platforms, nest-boxes or artificial twig nests often resolves these issues (Hamerstrom *et al.* 1973, Avilés *et al.* 2000, Libois *et al.* 2012), however these efforts may inherently result in a highly conservation dependent population. For instance, Red-footed Falcons *(Falco vespertinus)* typically use rookeries for breeding (Ferguson-Lees & Christie 2001). Rooks *(Corvus frugilegus)* were considered as agricultural pests (Solt 2008), and were heavily persecuted in the last century in Central Europe (Kalotás & Nikodémusz 1981, Orłowski & Czapulak 2007, Fehérvári *et al.* 2009, Palatitz *et al.* 2009). This, coupled with altered land use of the past decades resulted in a dramatic decline of the rook population (Solt 2008), leaving suitable foraging habitats without nesting sites for the Red-footed Falcons in the Carpathian Basin. An over decade long country-wide nest-box scheme has temporarily resolved this resource shortage, however, sustainability of these breeding sites remains to be improved (Palatitz *et al.* 2009, 2015, Kotymán *et al.* 2015). Rooks are generalist feeders and build their own nests, hence supplementing breeding facilities, or foraging stations are unlikely to have a substantial effect on local or regional demography where natural foraging areas are still available (Olea & Baglione 2008). However, considering the scarcity of mature forest patches in typical habitats of Central European Rooks, a potential resource may be adequate nest material. The scarcity of twigs and sticks that build up the body of a nest may be even more apparent if one considers the facts that a) up to several hundred nests are built at the same location, b) the weight of a branch may be sizeable considering an individual's body mass, hence birds are likely to minimize search radii for this resource. Rooks have been observed to willingly steal nest material from conspecifics in a rookery (Goodwin 1955). Our personal, sporadic observations also support the prevalence of robbing twigs from neighbouring nests, and that actively built nests are seldom left unattended prior to incubation. A previous study explored the possibility of provisioning nest material to nest-building colonial Egrets (Baxter *et al.* 1996). The birds in this case willingly accepted the supplementary sticks.

In this study we first explored the possibility of provisioning nest material at a given rook colony. We then assessed its potential effect on nest material characteristics, and whether provisioning has any repercussions on the number of nests built, or the ratio of successful rook nests in supplemented colonies.

Materials and Methods

Study site

The study was conducted at the Red-footed Falcon study area, Vásárhelyi Plain (SE Hungary, see Kotymán *et al.* 2015 for details). This site holds one of the largest artificial nest-box colony systems in Hungary, however rooks were absent from the area since the 1990s. In 2009, a rookery formed in the immediate vicinity of an artificial colony (Colony A) and another in similar habitat 17 kms from the previous site (Colony B). Both colonies are located in tree plantations, Colony A in narrow-leafed ash *(Fraxinus angustifolia)* interspersed with oleaster bushes *(Eleagnus angustifolia)* and black locust *(Robinia pseudo-acacia)* trees, while Colony B is located in a black locust plantation with a loose oleaster bush hedge surrounding the location. The average height of trees is similar at both colonies (8–10 metres).

Supplementing nest-material

Initially, we supplied small quantities (approximately 0.5 m^3/year) of twigs for colony A between 2008–2013. The primary objective in this period was to confirm whether rooks use the provisioned nest-material and to qualitatively assess that birds use these resource in multiple seasons. Meanwhile no nest material was presented in Colony B. In 2014 we provided larger, up to 6 m^3 twigs and sticks of various length (range: 20–60 cm) width (range: 0.1–2 cm) at colony A. The nest material green refuse deriving from park maintenance works of nearby municipalities, thus constituted a variety of species (ash, hackberry, oak, maple, various fruit trees, dog rose and grape vines). We used various colour combinations of canned paint spray to mark the twigs, and allow us to identify them later in the nests.

Monitoring nest occupancy

The number of nests changes dynamically in a rookery, as rooks tend to demolish and rebuild their nests throughout the breeding season. Therefore, we assessed the maximum number of nests prior to all monitoring activities (March). Our primary focus was to monitor the breeding performance of Red-footed Falcons at the rookeries, however these birds commence their breeding 30–45 days later than Rooks. Thus, to minimize the disturbance for Rooks, no nest visits were carried out starting from early June. Rooks typically build their nests in the top third of the canopy, making regular controls difficult using conventional techniques like ladders. As an alternative, we used a 10 metre telescopic fishing pole with a large concave mirror attached to the end. The mirror is positioned over the nest, while a second person uses binoculars to check the reflected image of the nest content. All nests were individually labelled during the breeding season on the tree trunk. Due to the timing of nest visits we do not have data on clutch size, hatching and fledging success for Rooks, only the number of nests where fledglings are present can be accurately assessed. We considered a nest successful, if at least one nestling had nearly fully developed feathers.

Assessing nest material usage

Initially, we collected complete nests at both colonies. These were either found on the ground, or were taken off from the canopy using poles. Rooks often remain in the vicinity of the rookery and use the forest patches as roost-sites well after the breeding season. Therefore, to minimize disturbance, we only collected the nests once the birds left the area (November-December). By that time considerable proportion of the nests are either demolished by birds or by weather erosion, leaving a relatively low sample size of 21 and 14 nests in Colony A and B, respectively.

For each collected nest we measured nest height (base to rim in cm) carefully dismantled the nests, counted the twigs and branches that build up the nest and identified the colour coded supplementary twigs used. We then randomly selected 20% of the twigs and measured their length and width to the nearest millimetre (n=2039 for Colony A and n=1545 for Colony B). All nest material that constituted the nest-lining was excluded from the analyses. The relatively long time period between the presentation of the supplementary nest material and the identification of marked twigs presumably allowed for the paint to dissolve or wear off from the marked twigs. Therefore, we only used the marked twigs to confirm the usage of the supplemented nest material, further quantitative analyses were not carried out.

Statistical analyses

We used Fisher's exact test to analyse the difference in the number of nests with fledged rook nestlings in relation to all nests in the year large scale nest-material provisioning was carried out (2014) and in the year preceding it. To understand potential effect of supplemented nest-material on twig composition of nests we used linear mixed effects models (Pinheiro & Bates 2000) to analyse mean differences in twig length and diameter between the two colonies. In case of both models we included colony as a fixed effect term. To avoid bias caused by individual preference for a certain twig size, we used nest identity as a random factor for both models. Dependent variables were log-transformed to meet model assumptions. All analyses were carried out using R.3.2.0 (R Core Team 2015).

Results

We found that all supplied nest material disappeared within days, in the initial phase of this study (2008–2013). In 2014, all presented supplementary nest material disappeared, despite the 12-fold increase in quantity. We found supplementary twigs in 100% of analysed nests.

The ratio of rook pairs with at least one fledged nestling in relation to all nests was similar in the year preceding the large scale supplementation of nest materials across colonies (Fisher's exact test; p-value=0.11). The number of total nests increased in both colonies *(Table 1)*, yet the ratio of successful nests was significantly higher for Colony A.

Nest height was similar (Welch two sample t-test; t-value: 0.03, p-value: 0.97) *(Figure 1)*, however, we found a near significant difference in the median number of twigs used/nest in the two colonies (Mann-Whitney-U test; U: 88.5, p-value=0.07, median difference=140 twigs) *(Figure 1)*. Mean twig length did not differ between colonies, however mean twig diameter was significantly higher for Colony A *(Table 2, Figure 2)*.

Discussion

This study is the first to show that nest building rooks willingly take supplementary nest materials presented close to the colony, and will incorporate it into their nests. Our observation, that regardless of the quantity of provisioned nest-material, birds utilized all sticks and twigs presented may indicate that suitable nest material is a scarce resource for Rooks in our study area.

We also found deviation of nest material composition and ratio of successfully

	Colony A		Colony B	
	2013	2014	2013	2014
Maximum number of nests in March	133	174	215	311
Rook pairs with fledged clutches	23	68	22	68
Other species	8	86	16	104
Empty nests in June	102	37	136	78
Nests demolished in March-June	0	0	41	61

Table 1. Monitoring results of the studied rookeries in 2013 and 2014. The maximum number of Rook nests was counted in March, however all other parameters were assessed starting from early June. Meanwhile, rooks may destroy/rebuild nests, and thus the total number of nests built, and the total number of nests monitored may deviate (Nests demolished in March-June). Other species predominantly entail Red-footed Falcons, but a small proportion of nests were used by Long-eared Owls and Kestrels

1. táblázat A vizsgált két vetési varjú telep monitoring eredményei 2013 és 2014-ben. A fészkek maximum számát márciusi számolással állapítottuk meg, de a fészkek foglalási mintázatát csak június elejével vizsgáltuk. A két időpont között a varjak tönkretehetnek fészkeket, melynek mértékét az utolsó sor jelzi. A többi faj elsősorban kék vércséket jelent, de kis számban mindkét kolóniában költött erdei fülesbagoly és vörös vércse is

fledged clutches/all nest in supplemented versus control rookery. However, our results remain tentative as our analyses may be confounded by several factors. Although the habitat composition of the two rookeries is largely similar, the tree species supporting the colonies are different. We hypothesize that the majority of nest material are collected in, or in close proximity of the colony, thus tree species composition considerably influences branch quality and availability. Increasing the sample size of treated and control colonies would also allow for more general inference of results.

However, if we entertain the possibility that our results were truly caused by the use of supplementary nest material, several intriguing hypotheses can be made on the mechanism of how it affects a rookery. If nest material is a scarce commodity, supplementing it may allow birds that would otherwise not breed to build nests, resulting in the increased number of pairs or increased number of unoccupied nests. In our case, the number of nests was larger in both colonies compared to a year before supplementing the nest material. Therefore, the observed pattern is probably reflecting an inter-annual difference in factors affecting both colonies, like weather or food availability. On the other hand we found that the number of successful clutches/all nests was higher where nest material was provided.

It has recently been proposed that woven or twig nests may serve as extended phenotype signals (Schaedelin & Taborsky 2009). For instance, Black Kites *(Milvus migrans)* use nest decorations to signal viability, nest quality and conflict dominance to conspecifics (Sergio *et al.* 2011). In passerines, nest building activity may be a post-mating, sexually selected signal for parental investment (Lens *et al.* 1994, Moreno *et al.* 1994, Soler *et al.* 2001), allowing sexes to adjust their reproductive behaviour to the quality of their mates. In case of Magpies *(Pica pica)*

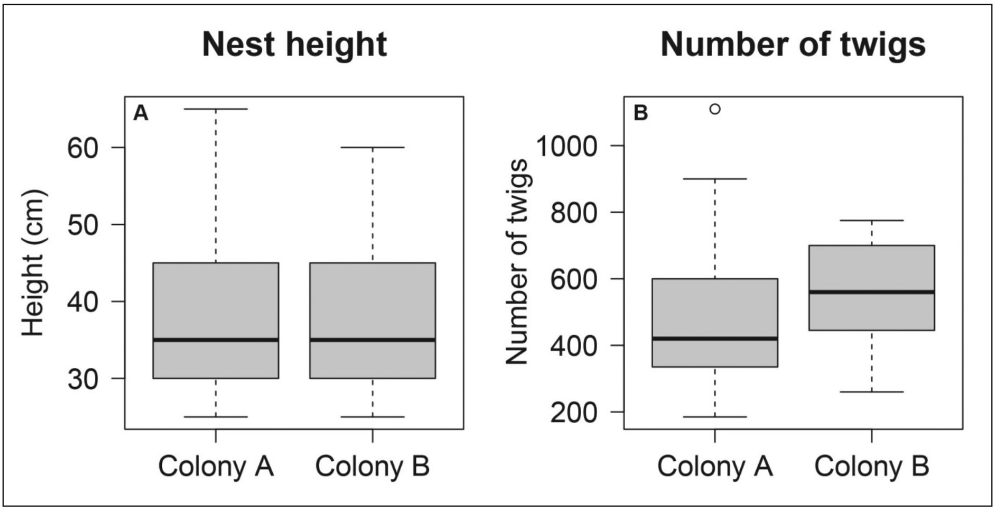

Figure 1. Boxplots on nest height and number of twigs found in nests collected at two rookeries. A total of 35 nests were analysed, 21 from colony A, and 14 from colony B. In case of colony A, we presented approx. 6 m^3 of supplementary twigs in the vicinity of the rookery prior to egg laying. Although median nest height was similar at both colonies we found a near significant (p=0.07) difference in median number of twigs used, with lower number of twigs/nest in colony A

1. ábra A fészkek magasságára és a fészkekben található gallyak számára illesztett boxplotok két vetési varjú telepen (A és B kolónia). Összesen 35 teljes fészek került elemzésre, 21 az A kolónia és 14 a B kolónia esetén. 2014-ben az A kolónia közvetlen környezetében mintegy 6 m^3 fészekanyag lett kihelyezve. Bár a két telepen található fészkek magasságában nem találtunk eltérést, a fészkeket alkotó gallyak száma közel szignifikánsan (p=0,07) eltért

Twig length	**Estimate (mm)**	**Standard Error**	**p-value**
Colony A	299.58	1.03	<0.001
Colony A – Colony B	0.92	1.05	0.117

Twig diameter	**Estimate (mm)**	**Standard Error**	**p-value**
Colony A	5.38	1.02	<0.001
Colony A – Colony B	0.88	1.05	0.008

Table 2. Fixed effect parameter estimates of the LME fitted on length and width of twigs found in nests of the two studied rookeries. We found no significant difference in mean length, however mean twig diameter was larger for colony A, where supplementary nest material was presented to the Rooks

2. táblázat Gally hosszra és gally vastagságra illesztett lineáris kevert modellek paraméter becslései a kolóniák függvényében. A gally hosszban nem találtunk szignifikáns eltérést a két telep fészkei között, azonban az átlagos gally vastagság szignifikánsan nagyobb volt ott, ahol fészekanyag kihelyezést végeztünk

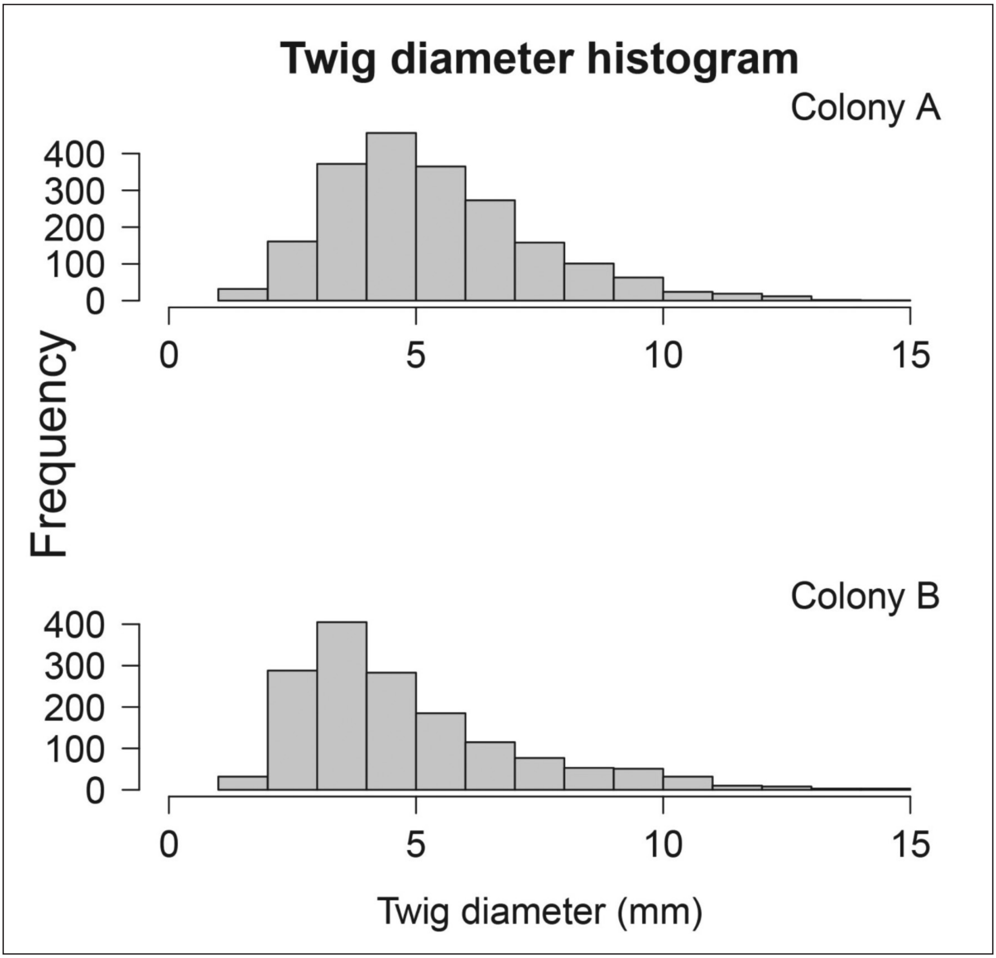

Figure 2. Histogram of twig diameters measured used as building material for nests in two rookeries. Rooks in colony A used sticks with significantly larger diameters compared to colony B (see also *Table 2*)

2. ábra Két vetési varjú-telepen talált fészkeket alkotó gallyak átmérőjének hisztogramja. Az A kolóniában a fészkeket szignifikánsan vastagabb gallyak alkották (lásd *2. táblázat*-ot is)

experimental studies show convincing relationships between reproductive decisions of females and nest-size (Soler *et al.* 2001, de Neve & Soler 2002). The close evolutionary relationship with Magpies may allow to hypothesize that nest size or nest building activity is also associated with courtship behaviour in Rooks. In theory, a scarce resource used by all individuals, and presented clearly visible for conspecifics may serve as an ample honest signal (Zahavi & Zahavi 1997) of individual quality, or parental investment. If this is so, supplementing nest materials, or in other words inflating the value of a scarce commodity associated with courtship, may allow less competitive individuals to breed, thus corroborating our findings. For instance, our results show that in the supplemented colony, twigs in nests had on average larger diameter, yet the heights of the nests at both colonies are similar. Also we have indication that probably less twigs were used per nest in the supplemented colony. From an individual's perspective this may result in less time used for nest building, allowing allocating resources into mate choice, nest/mate guarding etc. In any case, future investigations may focus on whether relationship exists between nest quality and individual fitness, and thus help reveal the mechanisms of how supplementary nest material provisioning alters breeding behaviour of Rooks.

From a conservation perspective, nest-material provisioning carried out on a large spatial scale may have a substantial effect on strengthening or even increasing the number of rook pairs breeding in non-urban habitats. It may also be possible that provisioning nest material in areas where the expected intensity of human conflicts is low would lure the Rooks to breed there and thus allow a non-invasive conflict management of the species. Stabilizing already existing colonies or even increasing their number in grassland type habitats would also aid the sustainability of the Red-footed Falcon population (Palatitz *et al.* 2015). Our results show that a medium sized colony of under 200 pairs may use large quantities of provisioned nest-material. Acquiring and transporting large quantities of sticks and twigs may be problematic and/or expensive, potentially limiting the usability of the method on a large scale. However, local municipalities near our study site proved to be helpful in providing and even transporting the nest material once the aims of the usage was explained. We believe that their willingness will set an example for other communities throughout the country. Various other sources may be also be requested to provide large quantities of sticks and twigs, like forestries, tree nurseries, sawmills or potentially cleaned and chopped Christmas trees may also be exploited for this purpose. However, we emphasize that as with all direct conservation measure tools, one has to first understand the effects of the manipulation, and consider potential side effects. Therefore we recommend that further studies have to carried out to evaluate the mechanisms and ultimate consequences of nest material provisioning near rookeries prior to large scale adaption of the method.

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Hunting efficiency of Red-footed Falcons in different habitats

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Péter Palatitz, Szabolcs Solt, Éva Horváth & László Kotymán 2015. Hunting efficiency of Red-footed Falcons in different habitats. – Ornis Hungarica 23(1): 32–47.

Abstract We studied hunting success of 13 male Red-footed Falcons by radio-telemetry in the second phase of chick rearing. We coded 484 hunting events, and the success measured in captured prey biomass/minute was exceedingly high in corn fields. This is mainly caused by the fact that the effectiveness of hunting for vertebrate prey was high on the harvested stubble fields. Moreover the observed falcons hunted for insects in these stubble field and alfalfa fields most successfully. In the studied habitat the chick feeding period of Red-footed Falcons coincide with the harvest of cereal fields, and the suddenly created lower vegetation cover increases temporarily the accessibility of prey items.

Till they were available and could be efficiently harvested, the falcons hunted on the fields within a 1 km radius from the nesting colony for the more profitable vertebrate prey. Thereafter they searched for vertebrate prey on the fields located at average 1–2.5 km distance from the colony. In the later zone falcons started to hunt insects, too, but approximately third of the captured insects (36.4%) was consumed immediately and was not delivered to the colony. Conversely larger prey was almost always (98.1%) carried directly to the nest site. Only one part of the Field Voles was observed to be eaten regularly: the brain. Finally later in the breeding season falcons were observed more and more often to hunt in the nearest fields again, this time for insects. Probably due to the depletion of the distant plots, the closer fields with lower investment became a competitive alternative for the birds.

Our results highlight the fact that even for such characteristic short-grass specialist birds as Red-footed Falcons the prey sources offered by arable lands might be temporarily exploited with success. Hence it is very important to integrate the measures offered by agri-environment schemes into the management of this threatened species.

Keywords: radio-telemetry, habitat use, resource utilization, *Falco vespertinus*, agro-environmental scheme

Összefoglalás A fiókanevelési időszak második felében követéses rádiótelemetriával vizsgáltuk 13 kék vércse hím vadászati sikerét. Összesen 484 vadászatot kódoltunk le, a vadászati sikert az átlagosan 1 perc alatt zsákmányolt biomasszában (g) mértük. A vizsgált egyedek vadászati sikere kiemelkedő volt a kalászos kultúrákban. A gerinces préda zsákmányolási hatékonysága magas volt a gabonatarlókon, de rovarokra emellett lucernatáblákon is sikeresen vadásztak. Ennek oka lehetett, hogy a vércsék fiókanevelése egybeesett a kalászosok betakarítási időszakával, amikor a növényzeti borítás megszűnése a madarak táplálékául szolgáló fajok elérhetőségét időszakosan megnövelte.

Ameddig eredményesen kiaknázhatóak voltak, a kék vércsék a fészektelep körüli, 1 kilométernél közelebbi táplálkozó területeken nagyobb profittal megszerezhető gerinces prédát zsákmányolták. Ezt követően az átlagos távolságú (1–2,5 km közötti) táblákon keresték a gerinces zsákmányolás lehetőségét. Ha ilyen távolságba eltávolodtak a fészkeiktől, már rovarokat is zsákmányoltak, de ezek mintegy harmadát (36,4%) saját maguk fogyasztották el. Ellenben a mezei pockoknak csak az agyvelejét ették meg, a többit szinte minden esetben a fészekhez vitték (98,1%). Mivel vélhetően a távoli (>2,5 km) zónában való táplálékkeresés és vadászat költsége legfeljebb gerinces zsákmányolás esetén térül meg a madaraknak, a költés végéhez közeledve egyre gyakrabban jelentettek versenyképes alternatívát a legközelebbi területeken megfigyelt rovarvadászatok.

Eredményeink felhívják a figyelmet arra, hogy még egy olyan tipikusan pusztai fajnak tartott ragadozó madár, mint a kék vércse, időszakosan hatékonyan aknázhatja ki a mezőgazdasági élőhelyek kínálta forrásokat. Fontos ezért, hogy a faj természetvédelmi kezelésébe bevonjuk az agrár-környezetvédelem nyújtotta eszköztárat is.

Kulcsszavak: rádió-telemetria, élőhelyhasználat, forráshasználat, *Falco vespertinus*, agrár-környezetvédelmi támogatás

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Introduction

Red-footed Falcons *(Falco vespertinus)* are gregarious in all phases of their life cycle from breeding to migration. Single bids and flocks can be observed throughout the whole year regardless of the age group or sex of the bird. The composition of these groups, the role of individuals in searching for food, or the true complexity of hunting behaviour are all not yet discovered in this species. In other communal feeding bird species (Wright *et al.* 2003, Weimerskirch *et al.* 2010), information exchange (Ward & Zahavi 1973), recruiting function (Richner & Heeb 1996) and the joint exploitation of food resources (Krebs *et al.* 1972) are supposed to be the most probable reasons to form groups. We have very scarce knowledge on the time and space pattern of hunting of aggregated individuals, and the factors influencing this phenomenon in most of the bird species.

The Red-footed Falcon is considered a generalist predator (Cramp & Simmons 1980). Dietary analyses are based on observations of nestling prey provisioning or the analysis of non-digested parts of the prey remains. In the Carpathian Basin Red-footed Falcons feed their chicks predominantly with insects (Insecta) (Keve & Szijj 1957): mainly larger representatives of the following orders: Orthoptera, Coleoptera and Odonata. Falcons can practically snatch any insect either from the air, surface of vegetation or from the ground (Haraszthy *et al.* 1994, Purger 1998). There might be as many as 30–100 insect species in the diet, and even the small 5–10 mm sized arthropods are regularly caught by the Falcons. On a typical steppe grassland with short vegetation cover as the Hortobágy, the following species were most often preyed upon: *Elaphrus riparius*, *Calliptamus italicus, Decticus verrucivorus*, *Harpalus affinis*, *Gryllotalpa gryllotalpa*, *Zabrus tenebrioides*, *Geotrupes mutator* and *Amara aenea* (Haraszthy *et al.* 1994). At some habitats the following vertebrate animals can also be important, especially when they are superabundant in gradation years: Common Spade-foot Toads *(Pelobates fuscus)* (Horváth 1963) and some small rodent species, especially the Field Vole *(Microtus arvalis)* (Keve & Szijj 1957, Haraszthy *et al.* 1994). Besides the above mentioned species lizards (*Lacerta* sp.) and sometimes small passerines (e.g. *Sylvia* sp., *Alauda* sp.) are also captured by Red-footed Falcons (Fülöp & Szlivka 1988).

Red-footed Falcons have two distinct foraging tactics: active hunting and perch hunting. In the former the bird catches large insects in flight, or it might hover with fast wing-beats above a spot, and then swoops down on the prey. Perch hunting is performed from various elevated observation posts: from the ground, vegetation, pylons or wires of power lines. The bird sits on these objects, and waits until a prey item passes by near enough to launch a successful attack either with a short glide or some powerful wing-beats.

Red-footed Falcons prefer grassy habitats for nesting (Haraszthy *et al.* 1994), colonies are often found in the near vicinity of grazed pastures (Purger 1996). The current breeding distribution of the species in Hungary negatively correlates with the ratio of forest cover within a 3 km radius circle around the colony (Fehérvári *et al.* 2009). The artificial nesting colonies that harbour more than two thirds of the Hungarian population (Palatitz *et al.* 2010) were assigned to areas where larger natural or semi-natural grasslands are present (Fehérvári *et al.* 2012). Regular breeding pairs in some places of the Hungarian extensive agricultural landscape show that in some extent birds can tolerate the lack of natural grassland habitats. There are reports from the Bachka Region/Serbia on Red-footed Falcon colonies that existed for decades surrounded almost exclusively with arable lands (Fülöp & Szlivka 1988).

Resource utilisation of the species is not yet described in the scientific literature, only some indirect assumptions are listed. Observations carried out on the Hortobágy suggest that Red-footed Falcons hunted in the close vicinity of their colonies on grasslands, catching Orthopterans, in wet year Common Spade-foot Toads while in dry years Field Voles were carried in large quantities to the nest (Haraszthy *et al.* 1994). In the literature and species descriptions diverse natural and agricultural habitats are listed, where Red-footed Falcons hunt successfully (Haraszthy *et al.* 1994, Purger 1997, Haraszthy 1998). The studied radio-tagged individuals clearly avoided dense, closed woody vegetation patches. These individuals most often visited grasslands, but neither these, nor the also frequently visited alfalfa fields were preferred positively compared to the availability of the habitat types within the home-range. Despite low sample sizes two groups of birds could be clearly distinguished in our previous analysis: the members of the first group visited mainly alfalfa fields besides grasslands while the other choose cereal fields besides grasslands (Palatitz *et al.* 2011).

In this work we analyse the same dataset (Palatitz *et al.* 2011) and try to find the reasons for the individual fine-scale hunting habitat choice and describe temporal and spatial pattern of the hunting of Red-footed Falcons in the chick rearing phase of nesting.

Methods

The field work was carried out in the Kardoskúti Fehértó region of the Körös-Maros National Park Directorate (KMNPI) at the Red-footed Falcon study area between 2006–2008 (Fehérvári *et al.* 2008). We used the digital map with reference to individual arable land plots, that enabled us to individually recognise each plot (Kristóf *et al.* 2007, Palatitz 2012). This typical Great Plain habitat, containing high percent of seminatural grassland housed three artificial nestbox colonies, where in the study years 55–95 pairs of Red-footed Falcons bred (Kotymán *et al.* 2015).

We captured adult birds according to the permit of the Nature Protection Authorities: after the eggs hatched the adults were captured near the nest using decoy birds and mist nets (Bub 1991). During the study 40 birds were tagged with 3.5 gr miniature radio-transmitters attached to tail feathers, which were tracked from the ground with receivers. We used the radio-tracking data to describe the hunting of Red-footed Falcons by following the tagged individuals (Palatitz *et al.* 2011).

The term ‘hunt’ was used to describe the behaviour elements in a field to find and capture prey. The duration and pattern of the hunts of females were considerably different form that of males' (Palatitz *et al.* 2015), probably due to the different roles of the sexes during nesting. The majority of food provisioned to the chicks was carried to the nests by the males. Therefore we only analysed the hunts of male individuals. In order to avoid bias only those hunts were entered into the analyses, where the entire length of the hunt was coded (from entering the actual plot till leaving). Previous analyses clearly indicated that the time spent with hunting in a given study plot was dependent first of all on the applied hunting technique (active versus perch hunting). We assume not only the average length (time allocation), but also the energy gain per time unit also varies according to the hunting technique. Active hunting involving hovering requires significant amount of muscle work. On the other hand the energy requirement of perch hunting is much lower (Masman & Klaasen 1987, Pennycuick 2008). Therefore we only analyse in this study the active hunts. Each data form gave information whether the hunt was successful or unsuccessful, or whether the observer was uncertain. If possible we also took note of the prey with the best possible taxonomic resolution (most often we could only distinguish vertebrate and invertebrate prey). We also recorded whether the prey item was consumed, or the bird left the study plot with the prey (Palatitz 2012).

Hunting success was measured as the biomass of prey gained per time unit. To estimate the biomass of invertebrate and vertebrate prey we used our own measurements based on live (wet) weight of the prey taxa from similar habitats. As the standard deviation of the two main prey category (insects and voles) were quite large, we gave a value of 20 to vertebrate prey and a value of 1 to insect prey in order to avoid overestimating the significance of vertebrate prey items (Palatitz 2012). The dependent variable of hunting success was formed as the potentially available prey biomass per time unit = (log(prey total weight [grams]/duration of hunt [minute]).

To analyse the success of hunts we used decision trees (Breiman *et al.* 1984). We studied the effect of the following potentially effective grouping variables: hunting location (code of the arable field), individual, nesting location, nesting type (solitary vs. colonial), hunting strategy (=cereal or alfalfa (see in detail Palatitz *et al.* 2011), habitat type (grassland, cereal, alfalfa, intertilled crops) and Julian date.

Based on the distance of the hunt from the nest we assigned all hunting events by cluster analyses into three natural categories: 1 (near) distance < 1 km; 2 (average) distance: 1–2.5 kms and finally 3 (distant) 2.5–5 kms (Palatitz 2012).

QGIS 1.7.3 'Wroclaw' (Quantum GIS Development Team 2011) and R 2.13.1 software were used to carry up the analyses (Calenge 2006, R Development Core Team 2011).

Results

We succeeded to code altogether 484 active hunts in full length of 13 male Red-footed Falcons. When the outcome of the hunt was known, 223 proved to be successful (48.3%) and 239 unsuccessful (51.7%). Their distribution by habitat type is given in *Table 1.*

We could assign prey category and biomass estimate to 190 hunting events. Our analysis distinguished two significantly different (p=0.008) groups of huntings *(Figure 1)*. While in cereal fields (n=88) the average of biomass per unit time (grams/minute) is

Observed active hunts	Total	Habitat type			
		Grass land	*Cereal stubble*	*Inter tilled crops*	*Alfalfa fields*
The ratio of all hunts	484	41.3%	43.6%	4.3%	10.7%
The ratio of successful hunts	223	44.4%	45.3%	1.8%	8.5%
Success rate*		*51.8%*	*50.0%*	*19.0%*	*39.6%*

* number of successful hunts/number of total hunts

Table 1. The distribution of active hunts and estimated hunting success rate of Red-footed Falcons by habitat type

1. táblázat A kék vércsék aktív vadászatainak élőhely típusonként becsült sikeressége

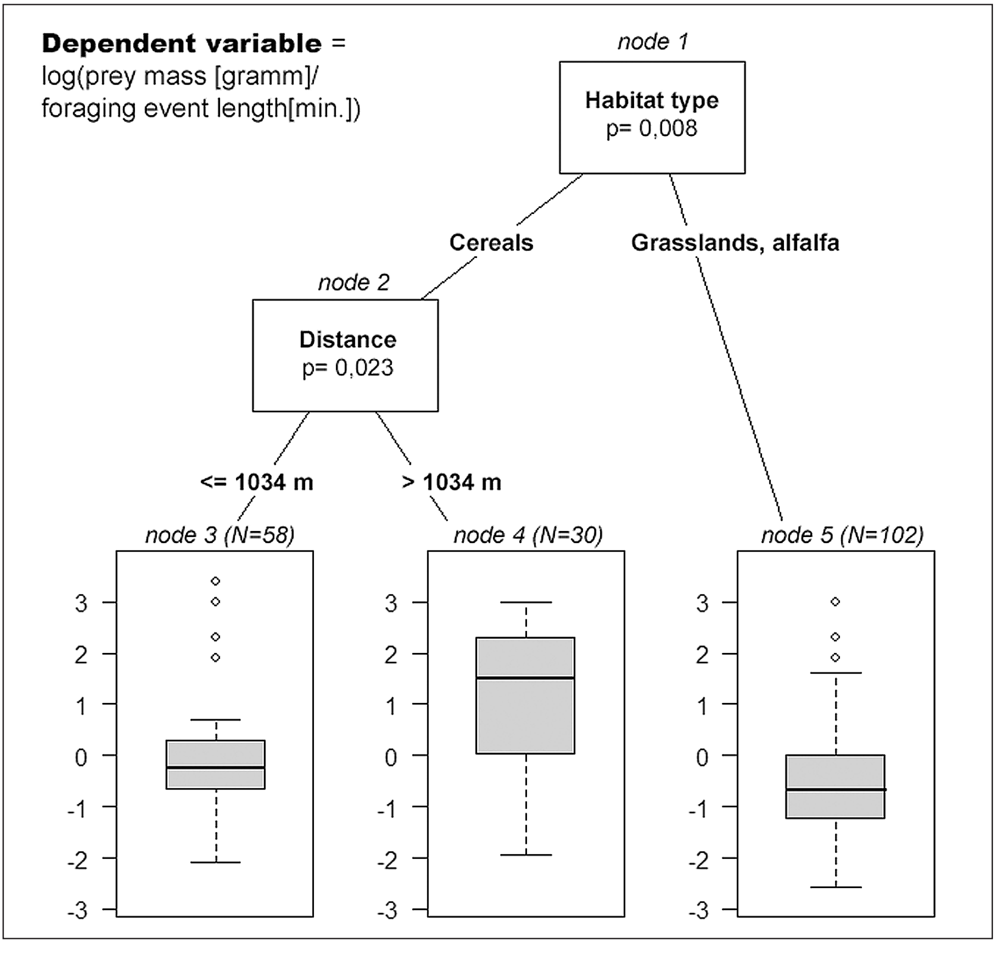

Figure 1. Factors affecting the success (biomass (gramm)/minute) of active hunting events of Red-footed Falcons

1. ábra A kék vércsék aktív vadászatainak sikerességét (biomassza (gramm)/ perc) befolyásoló változók döntési fája

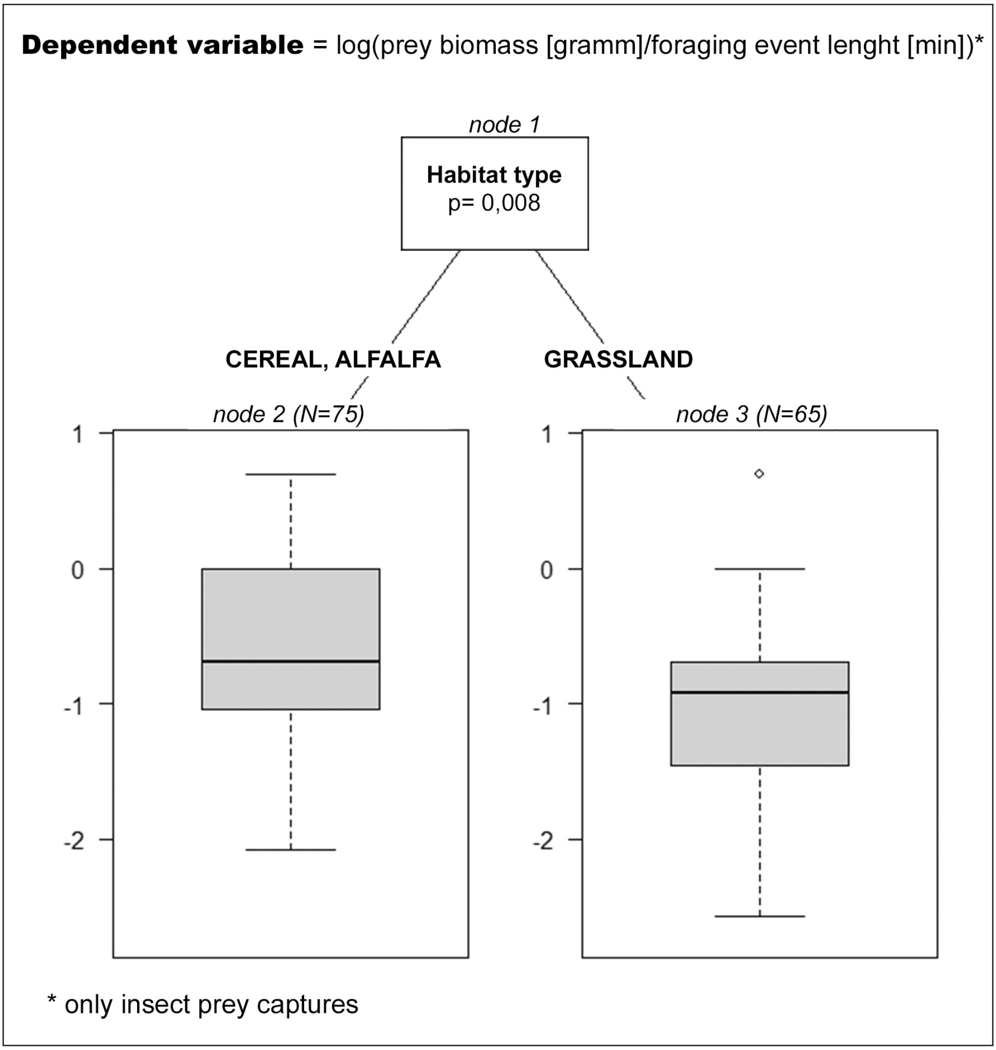

Figure 2. Factors affecting the success (biomass (grams)/minute) of active insect hunts of Red-footed Falcons

2. ábra A kék vércsék rovar zsákmánnyal végződő vadászatainak sikerességét (biomassza (gramm)/perc) befolyásoló változók döntési fája

1 (min.: 0.125; max.: 22), in grasslands and in alfalfa fields this value is 0.5 (min.: 0.08; max.: 20; n=102).

The huntings performed in cereal fields can be further grouped into two significantly different groups (p=0.023) depending on how far they happened from the colony *(Figure 1)*. In the case of hunts in the near group (within 1 km) (n=58) the average of biomass per unit time (grams/minute) is 0.75 (min.: 0.125; max.: 22), while in the case of huntings performed in the average distance category (min.: ~1 km) (n=30) this value was 4.5 (min.: 0.14; max.: 20). The reason for this great difference is that in the distant cereal fields 2 out of 3 huntings resulted in verteb-

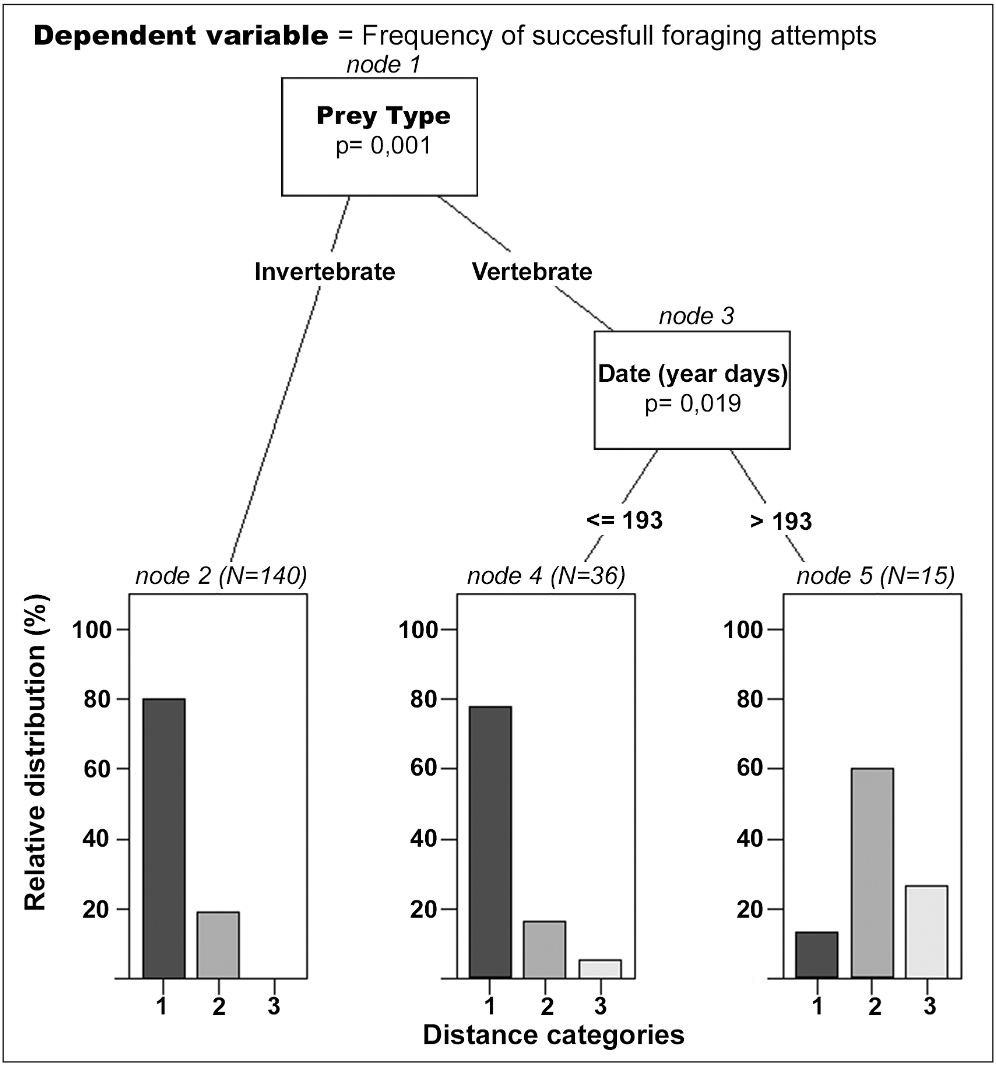

Figure 3. Decision tree on the temporal and spatial pattern of successful Red-footed Falcon hunts (distance categories: 1= distance <1 km from the nest; 2=1–2.5 km from the nest; 3= more faraway than 2.5 km from the nest)

3. ábra Döntési fa a kék vércse vadászatok sikerességének tér- és időbeli függésére (távolság kategóriák: 1: < 1 km-re a fészektől, 2: 1-2,5 km-re a fészektől, 3 >2,5 km-re a fészektől)

rate prey items, (n=20), while in the case of hunts closer to the colony only in 17% (n=10) of the cases were vertebrates caught.

The necessary time to capture vertebrate prey in grasslands and alfalfa fields was 3 minutes, while in corn fields only 2 minutes.

However the estimated success of Red-footed Falcon hunts in the different habitat types not always depends on the chance to catch the much larger vertebrate prey items. If we analyse the successful insect hunts (n=140) with decision trees, the difference among habitat types is significant again (p=0.007) *(Figure 2).*

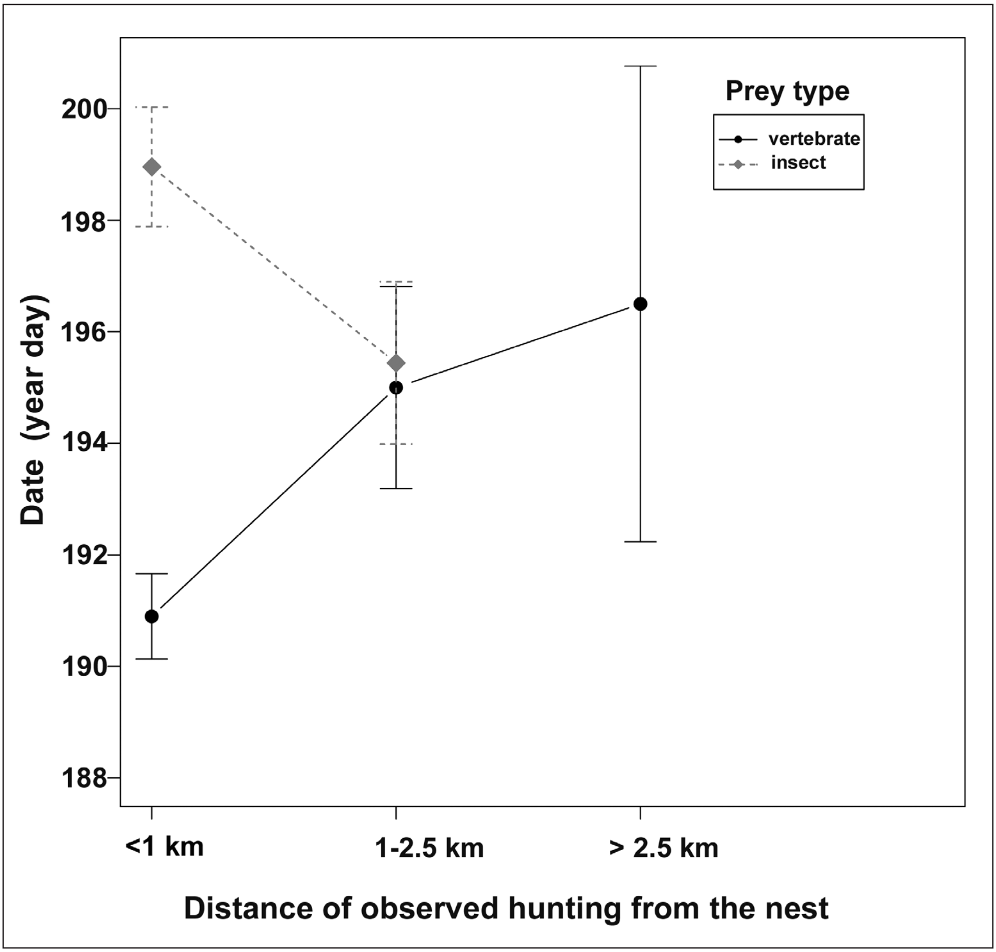

Figure 4. Temporal and spatial pattern of the relative frequency of successful hunts of Red-footed Falcons

4. ábra A kék vércse sikeres vadászatai relatív gyakoriságának tér- és időbeli függése

In the case of insect hunts the average of biomass per unit time (grams/minute) is 0.5 (min.: 0.125; max.: 2) in alfalfa and cereal plots (N=75) regardless of distance, while in grasslands (n=65) the average was 0.4 (min.: 0.08; max.: 2). These differences practically mean that on average a successful insect hunt lasts for 4 minutes in grasslands, 2 minutes in alfalfa fields, while 3 minutes in cereal fields.

We also analysed the temporal and spatial pattern of successful hunting events. Dependent variable was the frequency of successful hunts, independent grouping variables were: prey-type, continuous and category distance parameters, and day of year *(Figure 3–4)*.

The vast majority of hunts were performed less than 2.5 kilometres from the colony, and what is more important, there is a significant difference between the spatial pattern of insect hunts and vertebrate hunts (p=0.001). About 80% of all insect hunts (n=140) were recorded closer than 1 km from the nest, and the remaining 20% were recorded within 2.5 kms. The observed successful vertebrate hunts (n=51) showed a markedly different distribution: 60% were performed in areas located near to the nest (within 1 km), a further 30% were closer than 2.5 kms, and the remaining 10% were performed in distant areas (more than 2.5 kms).

The second level of the decision tree shows the temporal pattern of vertebrate hunts, and two significantly different (p=0.019) groups can be differentiated *(Figure 3)*. As the year advances the ratio of vertebrate hunts changes in the closer hunting plots. Earlier Red-footed Falcon catches predominantly vertebrate prey items in the vicinity of the colony *(Figure 4)*. The observed hunts shifted to more distant locations, as the breeding season advance, and insects were also caught later on. In the latest phase of observations the importance of insects caught near the nest increased. The observed change in hunting pattern was independent from the nesting phase of the individual, it was determined by the calendar date.

Discussion

A bird in the hand is worth two in the bush?

Colonially breeding bird species as Red-footed Falcon are mostly characterized by central place foraging and feeding on spatially aggregated food resources (Orians & Perason 1979). In case of the falcons – that are unable to stock the prey – this means that after every successful hunt the food item has to be carried back to the nest. The nutritional value of the given prey item, its digestibility, searching and handling time, catching and transporting prey all counts when we try to calculate the net energy gain of a hunt.

The nutritional value of insects calculated for dry weight is 20–25 kJ/g (Bell 1990), while that of Field Voles varies largely with their size, but always more than 25 kJ/g (Sawicka-Kapusta 1970). The nutritional value of the two main prey types of Red-footed Falcons therefore show a similar magnitude per unit of weight. The digestibility of the two prey type is not known, but both of them contain quite large quantity of nondigestible remains that can be found in the pellets of the falcons (mammals: bones and fur, while insects: chitin).

The handling time of insects is evidently smaller than that of mammals, especially in case of smaller nestlings, when parents have to feed each offspring carefully. However in the second half of the chick rearing period investigated in our study the chicks either swallow the prey as a whole, or the female tears it apart for them. Hence in the case of male Red-footed Falcons we do not have to take into count the handling time differences of insect and mammal prey.

The transport of an insect to the nest costs less energy than that of relatively large vertebrate prey. Falcons are excellent flyers, and compared to the very high cost of finding and catching prey, the cost of the transport has probably much less importance (Kvist *et al.* 2001, Nudds & Bryant 2002).

To sum up besides the size of the prey item and the effectiveness of its capture (these parameters together form hunting success parameter of our analysis), the time invested into finding the right hunting grounds may be the other major component affecting the profitability of each hunt.

Hunting success in different habitat types

Although the estimated biomass of mammals is considerably higher then, that of insects, in the appropriate hunting area the average time needed to catch them can be even shorter. According to our observations the active hunt for mammal prey depending on the habitat type takes 2–3 minutes on average, while that of insects 2–4 minutes. With the same investment the catching of mammals is probably much more profitable for Red-footed Falcons. If the energy expenditure is equal probably catching mammal prey is more profitable for Red-footed Falcons, than that of insects. Consequently the net energy gain for a small insect carried back to the nest is diminishing as the distance from the place of catching prey to the nest increases (diminishing return is an inverse function of distance), while for a larger mammal the transport cost cannot fully burn up the energy gain.

Catching of vertebrate prey (predominantly Field Voles) was fastest in cereal stubble fields then in other habitat types, it was a very important factor in the decision of choosing hunting sites, and hence largely affected the spatial pattern of space use. Another indirect indicator of the importance of mammal prey is that in Field Vole gradation years the breeding success of Red-footed Falcons is significantly higher than in other years (Palatitz *et al.* 2010).

Moreover hunts resulted in insect catching on alfalfa and cereal stubble fields proved to be more successful than those carried out on grasslands. In the study period on our study area considerable proportion of landowners applied for agri-environmental subsidies (Ángyán *et al.* 2003), and the nature protection oriented management by the National Park Directorate ensured that in all the studied habitat types nature conscious biodiversity oriented management regimes were applied. Although there were some assessments in order to monitor the yearly change of food resources on the study area (Böde 2008, Juhász 2008, Szövényi 2015), we do not have strong evidence to assess the difference of food availability on the habitat types. The importance of grasslands and alfalfa plots in conserving biodiversity is widely accepted. Probably these periodically stable habitats provide favourable conditions for the Orthoptera species and Field Voles that form the bulk of food carried for the young of Red-footed Falcons (Báldi & Kisbenedek 1997, Böde 2008). However these prey groups are prone to large population fluctuations and during gradation might appear in virtually any habitat types that provide minimal conditions for them (Delattre *et al.* 1996, Michel *et al.* 2006). Therefore it is probable that they were present in high quantity and density in many habitat types, when their gradation was confirmed in our study area. Our field observations and the results of trapping also confirm this assumption.

The accessibility of prey has differed substantially among the habitat types. In the study area the mowing of grasslands usually starts on the 15th of June. The first mowing of alfalfa fields continuously happened from the second half of May, while the harvest of cereals started in the last week of June and went on for about a month (personal observation). This meant that in the study period the grasslands mowed earlier in the season were mostly covered with growing vegetation. To a lesser degree where mowing was not carried out yet, or the plot was grazed a mosaic-like various vegetation height prevailed. The alfalfa fields that were mowed earlier than grasslands showed various vegetation height depending on the date of mowing, the general characteristics of the plot and the applied mowing technique. The harvest of corn fields was performed parallel with our observation period, so during the studies we could find all phases of wheat and corn fields from the not yet cut plots through the stubble fields to the already tilled fields. Two characteristics of the cereal fields were very different from grasslands and alfalfa fields: they became open for birds during the study period, and the mowed fields were covered with very short vegetation. According to our data all the observed Red-footed Falcon hunts in cereal fields were performed in stubble fields, often on those fields that were tilled right after harvest. Probably the agricultural activities significantly improved the chance of successful hunts. The lack of vegetation cover and the disturbed burrows of voles could contribute largely to the observed hunting success of falcons for this prey type on stubbles. Therefore low vegetation cover and hence the good detectability of vertebrate prey on stubble cereal fields might have led to higher hunting success in these fields than in grasslands or alfalfa fields respectively.

Our earlier experiments showed that Orthopterans emigrate from mowed fields and try to find cover in the adjacent edge habitats (Juhász 2008). Territorial small mammals probably react differently to mowing. The earlier mowed, and then re-grown alfalfa fields provided mosaic-like, massive green mass for insects (Bretagnolle *et al.* 2011). The abundance of Orthoptera species could be higher than in other habitat types. Probably this explains why Red-footed Falcons captured insects more efficiently in the sparsely vegetated patches and edges of alfalfa fields.

The phenomenon described her is not unique, Lesser Kestrels in Spain mainly hunt at the edges of arable fields and set aside fields, and the extensively cultivated cereal fields (Bustamante 1997, Franco & Sutherland 2004, De Frutos *et al.* 2009). Lesser Kestrels also catch prey faster in ploughed fields than in natural grasslands or in the edges of vegetation (Rodriguez *et al.* 2006), and the hunting success is closely related to the used agrotechnics (Ursua *et al.* 2005, Catry *et al.* 2011).

Despite our results in the given period and study site it would be a mistake to underestimate the importance of natural habitats. The role of grasslands in the choice of nesting sites is not a mere coincidence (Fehérvári *et al.* 2009, Fehérvári *et al.* 2012), on the other hand in the period prior chick rearing, or in years with different food availability (for example when Field Vole density is lower), probably their importance is relatively more significant.

Spatial and temporal patterns of hunting success

We observed that Red-footed Falcons effectively hunted for vertebrate prey at the close proximity of the nest sites at the early phase of our studies. After a few days they started to hunt at more faraway plots, and we could only observe successful vertebrate hunts 1–2.5 kms from the nest, or even more far away.

In colonially breeding birds the competition for food increases as the number of breeding birds increases (Furness & Birkhead 1984, Brown & Brown 2001, Ainley *et al.* 2004). Unfortunately we have no data whether the relative larger predation pressure near the colonies, where hunting could be performed with lover travelling cost, is reducing either the availability or abundance of the prey types. In Lesser Kestrels a similar phenomenon was described, when the decrease in prey density influenced the fitness of the birds in a measurable fashion (Bonal & Aparicio 2008).

Some prey taxa of the falcons, for example the small rodents that exhibit complex behaviour can adapt to the elevated predation pressure (Korpimäki *et al.* 1996). Their behaviour changes: the daily activity decreases and night activity increases, and hence the chance of getting caught by day-time predators, as birds of preys is lessened. We assume that due to strong predation pressure near the colony the availability of voles changed, and hence as the season advanced Red-footed Falcons were not able to deplete these resources effectively.

The shift to more far away fields to hunt rodents, and the appearance of insect hunting coincided in time. In the mid-term of our observations Red-footed Falcons started to hunt insects in fields nearer than 2.5 kms to the colonies. Then after in the third term of the chick feeding, insect hunts closer than 1 km to the nest site were performed the most frequently.

The spatial and temporal pattern of the successful hunts for the two main prey type showed an opposing trend. To hunt mammal prey items offering higher net energy gain the birds went more and more away from the colonies, while they were hunting for insects nearer and nearer as calendar date advanced. In some aspects hotly debated (Pyke 1984, Ydenberg *et al.* 1994) however optimal foraging theory (Stephens & Krebs 1986) is still often used as a theoretical framework for studies on animal foraging. It predicts that the more distant a feeding area is, the higher net energy intake rate it must offer, otherwise its use is not profitable. Above a certain distance threshold it is not worth investing in searching a more profitable hunting area (Fauchald 2009). It is possible that the nearer foraging areas, rich in insects, offering lower energy intake but costing less in terms of travel were chosen for this reason by falcons in our study.

It is very difficult to assess at what food availability level which distance will be still efficient to hunt for food to feed the offsprings (Rodriguez *et al.* 2006). We observed that there was only a single case from the 52 successful mammal hunts (1.9%), when the prey was not carried back to the nest. But we often observed that the most energy-rich part, the brain was removed and eaten frequently by the hunting bird, so a headless carcass was passed on to the female or chicks. From the insect hunts (n=140) in 36.4% the observed bird consumed the caught insect itself, and continued hunting.

From our data we can not tell, whether in vole gradation years Red-footed Falcons actively search for rodent-rich plots in their home range, where they can very efficiently hunt? Probably in these periods insects only serve as a supplementary food resource regarding the total biomass of the chick diet. The percentage of insects in the diet is always higher than that of mammals', even in the periods when the later constitute the primary prey choice (Böde 2008). Both the breeding success of Red-footed Falcons and the condition of chicks suggest that Field Voles are the corner stone of hunting in gradation years (Palatitz *et al.* 2010).

Probably it is not easy to find good Field Vole yielding plots, and as they become depleted very fast, more and more faraway plots needs to be visited. The feeding ecology of aggregated predators long been studied by ecologists. In larger colonies information from other birds could be obtained on potential feeding grounds, and hence larger areas can be profitably exploited (Rafacz & Templeton 2003). This suggests that the home range of Red-footed Falcons nesting at larger colonies was larger than that of birds nesting in smaller colonies or breeding solitarily (Palatitz *et al.* 2011). Feeding in groups is more efficient for those animal food sources that are either patchy, or very short-lived because of depletion due to predation or emigration (Jacob & Brown 2000). At the same time competition is stronger at colonies (Brown & Brown 2001). If due to low food availability the time necessary to find food increases (Fauchald 2009) birds breeding at colonies the formerly listed advantages might easily turn into disadvantages. As in Red-footed Falcons both solitary and colonial breeding coexists in the same habitat (Kotymán *et al.* 2015) for a long evolutionary time, their feeding strategies are expected to be even more refined (Barta & Giraldeau 2001), and therefore the analyses of their feeding behaviour by mechanistic modelling (Moorcroft *et al.* 1999) will be even more intriguing.

When applying our results for management and protection it is worth keeping in mind, that the results were obtained in an extremely food-rich breeding season (Field Vole gradation year), at a single Red-footed Falcon breeding habitat. We hope that the zonal partition of our feeding areas will form a good basis when planning more complex research projects as in Lesser Kestrel (Franco & Sutherland 2004, Catry *et al.* 2011) or for the planning of nature protection oriented management of agro-ecosystems (Young *et al.* 2005, Kleijn *et al.* 2009).

Our results highlight the fact that even for such characteristic grassland specialist birds as Red-footed Falcons the prey sources offered by arable lands might be temporarily important. If we utilise this knowledge in the management of habitats, it might facilitate the harmonisation of the needs of different species, and it might enlarge the scope, spatial dimension and efficiency of habitat management.

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Orthopteran insects as potential and preferred preys of the Red-footed Falcon *(Falco vespertinus)* in Hungary

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Abstract Orthopterans play an important role in Red-footed Falcon diet, however, most studies focus only on its qualitative food composition, and less on quantitative composition and preferences of the taxa identified as prey. During the present research, an extensive orthopterological investigation was carried out in the Red-footed Falcon study area, Vásárhelyi Plain (SE-Hungary) between 2006 and 2008. Grasshoppers were sampled in their main habitats by sweep netting and pitfall trapping, and orthopterans were identified in the food remnants collected from the nests, both artificial and natural ones. 26 species were detected during the field works, 18 species from the food remnants. Altogether 32 species were identified. Prey preference values for all species for each year were calculated. More than two thirds of the identified preys were *Decticus verrucivorus*, and nearly 20% were *Tettigonia viridissima*. Other common prey species were *Melanogryllus desertus, Platycleis affinis, Gryllotalpa gryllotalpa, Calliptamus italicus* and *Gryllus campestris*. Based on the prey preference analysis, the most preferred species was *Decticus verrucivorus* with extreme high values, and the other preferred ones, overlapping with the previous list, were *Platycleis affinis, Bicolorana bicolor, Tettigonia viridissima, Calliptamus italicus* and *Roeseliana roeselii*. These results may help in the development of Red-footed Falcon-friendly habitats through the application of habitat management favourable for the preferred prey species.

Keywords: Red-footed Falcon, Hungary, Orthoptera, prey composition, prey preference

Összefoglalás A kék vércse táplálkozásában az egyenesszárnyúak kiemelkedő fontosságúak, a táplálkozás-vizsgálattal foglalkozó kutatások azonban jobbára csak a táplálék összetételére vonatkoznak és fajlistákat közölnek, mennyiségi és preferencia-viszonyokat kevésbé tárnak fel. A munka során 2006–2008-ig a Vásárhelyi-pusztán kialakított Kékvércse-védelmi és Kutatási Mintaterületen végeztem a helyi kék vércse populáció táplálkozóhelyein kiterjedt orthopterológiai vizsgálatokat. A főbb jelen lévő egyenesszárnyú élőhelyeken fűhálózással és talajcsapdázással végeztem mintavételeket, illetve a kék vércsék fészkeiből gyűjtött táplálékmaradványokból azonosítottam az egyenesszárnyúakat. A terepi mintavételek során 26, a táplálékmaradványokból 18, összesen 32 fajt sikerült kimutatni a területről. Az egyes zsákmány fajok preferenciáját az egyes évekre külön kiszámoltam. A zsákmányolt fajok közül a szemölcsevő szöcske *(Decticus verrucivorus)* több mint a zsákmány kétharmadát, a zöld lombszöcske pedig közel 20%-át alkotta, a további gyakoribb prédái a *Melanogryllus desertus, Platycleis affinis, Gryllotalpa gryllotalpa, Calliptamus italicus* és a *Gryllus campestris* voltak. A preferencia elemzés alapján a legkedveltebb préda szintén a szemölcsevő szöcske volt extrém magas értékekkel, a többi pedig részben átfedően az előzőekkel a *Platycleis affinis, Bicolorana bicolor, Tettigonia viridissima, Calliptamus italicus* és a *Roeseliana roeselii* volt. Az eredmények a preferált prédafajoknak kedvező élőhely-kezelések alkalmazása révén segíthetnek a kék vércse-barát élőhelyek kialakításában.

Kulcsszavak: kék vércse, Magyarország, egyenesszárnyú rovarok, zsákmány összetétel, zsákmány preferencia

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Introduction

The Red-footed Falcon *(Falco vespertinus)* is a general avian predator (Cramp & Simmons 1980) widely distributed in the Eurasian steppe zone. In its breeding season it prefers different types of open habitats including steppes, forest-steppes and extensively cultivated agricultural landscapes as well, where forest patches or small groups of trees provide it with suitable nesting places and grasslands or mosaic agricultural fields, which supply it with enough food (Palatitz *et al.* 2009, 2015). It preys mammals, reptiles, amphibians and different insects (Palatitz 2012) of a wide range of size down to 1–2 mm (Haraszthy *et al.* 1994). During the breeding season Red-footed Falcons feed on small rodents, anurans, spiders and different insects, especially on Orthoptera, Odonata and Coleoptera (Keve & Szijj 1957) species. Most of data available on its diet are mainly based on prey remnants collected from nests, and these show that orthopteran insects form a considerable and stable part of the food for the young birds. An extensive study of Haraszthy *et al.* (1994) conducted in the Hortobágy region (East Hungary) found that orthopteran prey items form the largest part of the detectable prey biomass. The breeding population of the Red-footed Falcon shows a considerable decline during the past decades throughout most of its distribution range (Palatitz *et al.* 2009, 2015), thus the knowledge about its diet is crucial for the appropriate habitat management in its breeding and feeding habitats.

Although previous studies on the diet of the Red-footed Falcon provided detailed information on food composition, until now, a quantitative analysis about their real prey preference in ecological terms has not been published. Thus, the main aim of the present investigation was to obtain relevant information on the potential orthopteran prey availability of a Red-footed Falcon population in Hungary, and to determine their prey preferences in order to provide a basis for the falcon-friendly management of these habitats.

Material and methods

Study area

Field investigations were carried out in the Red-footed Falcon study site, Vásárhelyi Plain (SE Hungary), between 2006 and 2008 (Kotymán *et al.* 2015). This area – named after a shallow alkali lake located here –, together with the surrounding grasslands is among the largest continuous steppic remnants of south eastern Hungary. A stable population of Red-footed Falcons breeds here, mainly in artificial nest-boxes (Palatitz *et al.* 2011, 2015, Kotymán *et al.* 2015). The above indicated, 10×10 km long term study site was designated here in 2006, in a frame of a conservation project funded by the LIFE Nature Fund for studying the ecology and conservation of the Red-footed Falcon in Hungary. The main habitat types of the study area and their proportions were precisely identified for each study year, using remote sensing techniques (Palatitz 2012). The main habitat categories were: grasslands, cereals, alfalfa fields, intertilled crops (e.g. maize and sunflower), artificial surface (e.g. roads, farm buildings), reedbeds, water surface and woods. The applied remote sensing methodology did not allow the separation of fallow land from grasslands. Since grasshoppers inhabit mainly open terrestrial habitats in this region, artificial surfaces, reedbeds, water surface and woods were excluded from the orthopterological investigation. Additionally, after the first study year, intertilled crops (maize fields) were also neglected, because the sampling methods used for grasshoppers were partly inapplicable in this habitat type and extremely low density of orthopteran insects was detected during the first year of field works.

Sampling methods

Two methods of different sensitivity were applied for sampling the potential Orthoptera prey availability in the studied habitats, including the grasslands and fallow as real habitat types separately (separated by recorded history of each arable field), because the local Orthoptera assemblages of these two latter habitat types showed considerable differences. Grasslands were also divided into two categories in 2006 (hayfields and pastures), but in 2007–2008 only hayfields were sampled.

Pitfall traps were used for the effective collection of ground-level inhabiting species (mainly crickets), while species living in the vegetation (mostly bush crickets and grasshoppers) were collected by sweep netting completed by visual and acoustic searching for species that are difficult to detect or rare (Ingrisch & Köhler 1996, Southwood & Henderson 2000). Two sampling plots were selected for each studied habitat type in each year. Pitfall traps (a line transect of 9 traps of 10 cm diameter, half filled with ethylene-glycol on each plot) were exposed for one month between June and July. In sweep netting, the sampling effort was 300 sweeps (net diameter: 40 cm) for each sampling plot once a year between the end of June and the end of July. Field samplings were carried out during the nesting period of Red-footed Falcons. The materials of pitfall traps were identified in laboratory, while most specimens collected by sweeping were identified on the field and released afterwards alive in the same habitat in order to minimise the invasiveness of data collecting methods applied in the protected study area.

The food composition of a bird of prey, such as the Red-footed Falcon can be studied by analysing the food remains left in the nests (Haraszthy *et al.* 1994). This method provides reliable data with restrictions, since it shows mainly the food composition of nestlings, but, on the other hand, the food quality consumed by them has a strong effect on their future life perspective, thus the prey items detectable by this way probably demonstrate well the real food preferences of the species. Moreover, Red-footed Falcons commonly eat numerous insects which are generally seriously damaged during the digestion and/or after it in the nest, and the small parts like wings or legs of a grasshopper often disappear form the nest. This makes the exact identification of insect prey items at species level hard or sometime impossible. Food remnants were collected from several nests after the nesting period (in July or August) in the study area in each year in order to get enough data for the prey preference analysis. Prey remnants in collected samples were classified into larger groups (mammals, birds, amphibians, reptiles and arthropods) and Orthoptera remnants were indentified in laboratory using the identification keys of Harz (1969, 1975) and a comparative collection with separated body parts of species occurring in the study area based on the collected Orthoptera samples and the already published data (Nagy & Szövényi 1998, Szövényi & Nagy 1999) on the region's grasshoppers. A minimal number of specimens for each taxa identified in each sample (prey remnants collected from one nest) were obtained on the basis of the combination of body parts belonging to the minimal number of specimens of a taxa (e.g. a pair of mandibles, a pair of hind, middle and fore legs, wing parts, pronotum, head).

Data analysis

Prey availability

After the determination of all materials investigated, a list of taxa with number of individuals belonging to each was obtained for each sampling plot, each year and both sampling methods separately. Since the Orthoptera prey items identified from the food remnants could be captured by the Red-footed Falcons from any part of the study area suitable for grasshoppers, average data on availability of each orthopteran species were calculated for the whole study area. Main steps of this calculation are listed below.

Step 1: The lists of two sampling plots per real habitat types were summarized (numbers of specimens were added up) for each year and each sampling method separately.

Step 2: The numbers of specimens for each taxa were summed for each main habitat type category, for each year and each sampling method separately, when more than one real habitat type were sampled in one main habitat type category (e.g. for grasslands and oldfields). These were converted to percentage dominance values for each dataset. When only one real habitat type was sampled in one main habitat type category, the results of step 1 were converted into percentage values for each dataset.

Step 3: The percentage dominance lists created in step 2 were averaged for the two sampling methods separately in each main habitat type category and each year.

Step 4: The averaged percentage dominance datasets of the main habitat type categories for each year were weighed by their proportion to the whole area in the study area for each year (detailed in Palatitz 2012) and then averaged for the whole study area separately for each year.

Finally one list was obtained for each year containing all taxa detected during the field works in a particular year with their average dominance considering both sampling methods and the actual relative percentage proportion of each main habitat type category sampled.

It was hypothesized that Orthoptera samples are representative for their habitat type, and that the two applied sampling methods considered in equal weight represent well the real composition of the local assemblages and therefore the availability of the potential orthopteran prey species for the Red-footed Falcon. Although it is a highly simplified approach, but it is the only way in which the results can be made comparable with the prey consumption data obtained.

Prey consumption

Since the exact origin of prey specimens identified from the food remnants was unknown, prey ‘specimens’ from all nest samples were pooled into one list and average percentage frequency values of detected taxa were calculated for the whole data pool. The investigation of Palatitz *et al.* (2011) on the foraging habitat selection of this Red-footed Falcon population confirmed that presumably most of preys were captured inside the designated study area.

Prey preference

The lists of averaged dominances, which denote potential orthopteran prey species availability for the whole study area in each year and the lists of summarized percentage prey frequency for the whole Red-footed Falcon population breeding in the study area in each studied year make it easy to calculate ecological preference values of this population for each prey species and each year. It was calculated by a simple division (prey consumption frequency divided by the prey dominance). When the preference value was above 1, the consumption of that prey species was larger than its averaged availability, which means that this species was preferred by the Red-footed Falcons in that year, while when the value was between 1 and zero, it means that these species were not actively chosen by the birds. In the special case when only one list contained a potential species, the preference value could not be calculated. If the particular species was not detected during the Orthoptera sampling, however it was found in the food remnants, it could be considered to be highly preferred, and in an opposing case it was avoided.

Results

Potential orthopteran prey availability and food composition

During the 3 year-long study, 5879 specimens of Orthoptera were sampled and identified in the field samplings in the Kardoskút study site (3504 by sweeping and 2375 by pitfall trapping) belonging to 26 species *(Table 1)*. 26.7 percents of it were nymphs, identifiable only at genus level. The minimal number of Orthoptera specimens identified in Red-footed Falcon food remnants was 5164 during the whole investigation (2006: 544 specimens from 39 nests; 2007: 1450 specimens from 130 nests; 2008: 3170 specimens from 54 nests) belonging to 18 identifiable species *(Table 1)*. Here only 2 percent of all specimens were identifiable only at higher levels (genus or family). Altogether 32 Orthoptera species were detected during the whole study *(Table 1)*, 14 species were found only during the field samplings, but individuals of six species were preyed on only by the Red-footed Falcons.

Prey preferences

Prey preference values of all orthopteran species found in the food remnants were calculated for each year and these values were averaged as well *(Table 2)*. Species which were preferred by Red-footed Falcons at least in one studied year according to the calculated preference values were indicated with bold letters in *Table 2*.

Discussion

The extensive field sampling showed that the study area is rich in orthopterans; 25% of the species occurring in Hungary (Panrok & Szövényi 2013) were found here. Some nationally protected species were among them *(Gampsocleis glabra, Tettigonia caudata)*, a cricket *(Modicogryllus truncatus)*, which since then also became protected, proved to be new for the Hungarian fauna (Szövényi 2011) and some of them *(Stethophyma grossum, Platycleis albopunctata grisea)* were not published before in the administrative area of the Körös-Maros National Park Directorate (Nagy & Szövényi

	Field sampling			Food remnants		
	2006	2007	2008	2006	2007	2008
Ensifera						
Leptophyes albovittata	+	+	+			
Conocephalus fuscus		+	+			
Conocephalus dorsalis			+			
Ruspolia nitidula				+		
Decticus verrucivorus	+	+	+	+	+	+
Bicolorana bicolor	+	+	+	+	+	+
Roeseliana roeselii	+	+	+	+	+	+
Platycleis affinis	+	+	+	+	+	+
Platycleis albopunctata grisea					+	
Tessellana veyseli	+	+	+	+	+	+
Gampsocleis glabra	+					
Tettigonia caudata				+	+	+
Tettigonia viridissima	+	+	+	+	+	+
Gryllus campestris	+	+	+	+	+	+
Melanogryllus desertus	+	+	+	+	+	+
Modicogryllus bordigalensis	+		+			
Modicogryllus truncatus			+			
Oecanthus pellucens		+	+			
Gryllotalpa gryllotalpa				+	+	+
Caelifera						
Tetrix subulata	+					
Calliptamus italicus	+	+	+	+	+	+
Pezotettix giornae	+	+	+	+		
Chorthippus brunneus	+	+	+			
Chorthippus dichrous		+				
Chorthippus oschei	+	+	+	+	+	
Dociostaurus brevicollis	+					
Euchorthippus declivus	+	+	+			
Omocestus rufipes	+	+	+			
Pseudochorthippus parallelus	+	+	+			
Aiolopus thalassinus	+	+	+	+	+	+
Oedaleus decorus				+		
Stethophyma grossum					+	

Table 1. Orthoptera species identified during the field sampling (sweep netting and pitfall trapping) and in the food remnants of Red-footed Falcons in the Red-footed Falcon study site between 2006 and 2008

1. táblázat A terepi mintavételek során (fűhálózás és talajcsapdázás) és a kék vércsék táplálékmaradványaiból azonosított Orthoptera fajok a Kékvércse-védelmi és Kutatási Mintaterületen 2006 és 2008 között

	Total % proportion	2006 pref.	2007 pref.	2008 pref.	Average pref.
Ensifera					
Ruspolia nitidula	0.02	OR			
Decticus verrucivorus	64.18	719.87	369.87	251.21	446.98
Bicolorana bicolor	0.21	7.58	5.78	1.13	4.83
Roeseliana roeselii	0.37	0.83	0.26	1.13	0.74
Platycleis affinis	3.66	19.24	26.55	9.35	18.38
Platycleis albopunctata grisea	0.02		OR		OR
Tessellana veyseli	0.41	0.09	0.1	0.2	0.13
Tettigonia caudata	0.08	OR	OR	OR	OR
Tettigonia viridissima	19.69	7.45	1.27	2.23	3.65
Gryllus campestris	1.3	0.46	0.23	0.17	0.29
Melanogryllus desertus	5.23	0.6	0.48	0.08	0.39
Gryllotalpa gryllotalpa	2.46	OR	OR	OR	OR
Caelifera					
Calliptamus italicus	2.4	4.22	0.51	1.02	1.92
Pezotettix giornae	0.02	0.11	OS	OS	0.04
Chorthippus oschei	0.41	0.22	0.08	OS	0.10
Aiolopus thalassinus	0.52	0.42	0.47	0.73	0.54
Oedaleus decorus	0.02	OR			OR
Stethophyma grossum	0.02		OR		OR

Table 2. Prey preference values for Orthoptera species identified from the food remnants of Red-footed Falcons in the study site between 2006 and 2008 (Total % – percentage proportion in the total pool of food remnants collected during the whole study period including specimens not identifiable at species level; OR – species found only in food remnants; OS – species found only by Orthoptera sampling)

2. táblázat A kék vércse táplálékmaradványaiból azonosított Orthoptera fajok préda preferencia értékei a Kékvércse-védelmi és Kutatási Mintaterületen 2006 és 2008 között (Total % – százalékos arány a vizsgálat teljes ideje alatt gyűjtött táplálékmaradványokban a faji szinten nem azonosítható példányokat is beleértve; OR – csak táplálékmaradványból előkerült faj; OS – csak az egyenesszárnyú mintavételek során előkerült faj). A vastaggal szedettek a preferencia szerint 1 fölötti értékkel szereplő fajok, azaz az aktívan választott, keresett zsákmányok

1998, 1999, Szövényi & Nagy 1999). At the same time, the fact that six species were detected only in the food remnants, locally rare species among them, well indicates that the sampling efforts were far not enough even, for the complete faunistical exploration of the study area. Beside the high abundance, the relatively high diversity of potential Orthoptera preys occurring in the feeding habitats of the studied Red-footed Falcon population, similarly to the Lesser Kestrel *(Falco neumanni)* (Rodrigez *et al.* 2010), also may indicate the good quality of this habitat complex for them. The results of Palatitz *et al.* (2011) on the foraging habitat selection of this population (preferences to grasslands and fallow land, neutrality to alfalfa and cereal fields and avoidance of intertilled crops, water surface, woods and artificial surfaces) confirm the representativity of the sampling method used from the point of view of sampled habitat types.

The prey composition of the studied Red-footed Falcon population (for a summary of all prey taxa found here in 2006 and 2007 see Böde 2008) was similar to the previous studies on the diet of this species (e.g. Keve & Szijj 1957, Horváth 1964, Bezzel & Hölzinger 1969, Fülöp & Szlivka 1988, Haraszthy *et al.* 1994, Purger 1998, Molnár 2000). However, according to Purger (1998), the larger prey items are generally overrepresented in the food remnants collected from nests, because the larger parts are preserved better than the smaller, and therefore the more fragile pieces disappear. This opinion may have a real basis, but is controversial with the results of Haraszthy *et al.* (1994), who found small sized preys (between 5 and 10 mm) to have the largest proportion in food remnant samples collected from nests.

Some widely distributed Orthoptera genera of large bodied species, like *Tettigonia, Decticus, Platycleis, Gryllus, Gryllotalpa* or *Calliptamus* (especially the females is this latter genus) seem to play an important role in the nutrition not only of the Red-footed Falcon in Central and Southeast Europe, but also of the similar Lesser Kestrel in Spain (Rodrigez *et al.* 2006). Considering only the composition of the food remnants, similarly to other studies, the most important prey species was the Wartbiter *(Decticus verrucivorus)*, composing nearly 2/3 of all prey specimens in the study area, while the Great Green Bush Cricket *(Tettigonia viridissima)* was the second most numerous species with a nearly 20% proportion altogether. The other species of larger proportion (more than 1%: *Melanogryllus desertus, Platycleis affinis, Gryllotalpa gryllotalpa, Calliptamus italicus, Gryllus campestris*) were much less dominant. The preference values obtained have shown partly different patterns in term of the importance of preyed orthopteran species. These results confirm the importance of Wartbiter in the nutrition of species, even considering the opinion of Purger (1998) on the biases of the applied food remnant sampling method, since the preference values of this species were extremely high, between 720 and 251 during three consecutive study years, while the next category on the preference values was a mere 26 in case of the *Platycleis affinis*. Species preferred at least in one year largely overlapped with species of great proportion in the food (*Decticus verrucivorus, Platycleis affinis, Bicolorana bicolor, Tettigonia viridissima, Calliptamus italicus* and *Roeseliana roeselii* in order of the average preference values). According to the food remnants, the nymphs and adults of the large bodied, underground living European Mole Cricket *(Gryllotalpa gryllotalpa)* was the fifth most frequently captured orthopteran prey in the study area, and at the same time it was not detected even by the pitfall trapping, a method otherwise appropriate for its collection, and thus this species have also to be considered as a preferred prey. It shows that the Red-footed Falcons' hunting technique is quite effective, even in the case of a mostly underground insect. Another interesting phenomenon, which underlines the importance of the preference analyses, is the case of *Melanogryllus desertus*. This cricket species was the third most frequent species among the prey items, however, it was not actively chosen by the birds according to the preference analysis (average value: 0.39), highlighting the importance of such an analysis compared to the use of merely food composition for the evaluation of the importance of different prey species.

The results of the present study may help to form the preferred habitat types into a better source of foods for the Red-footed Falcons during their breeding period by optimizing the availability of the preferred prey species through the perfect timing of different interventions (mowing, grazing etc.) in the habitats of these species.

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Louse (Insecta: Phthiraptera) infestations of the Amur Falcon *(Falco amurensis)* and the Red-footed Falcon

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Abstract Little is known about the louse species harboured by Red-footed and Amur Falcons despite the fact that various life-history traits of these hosts make them good model species to study host-parasite interactions. We collected lice samples from fully grown Amur (n=20) and Red-footed Falcons (n=59), and from nestlings of Red-footed Falcons (n=179) in four countries: Hungary, India, Italy and South Africa. We identified 3 louse species on both host species, namely *Degeeriella rufa, Colpocephalum subzerafae* and *Laembothrion tinnunculi.* The latter species has never been found on these hosts. Comparing population parameters of lice between hosts we found significantly higher prevalence levels of *D. rufa* and *C. subzerafae* on Amur Falcons. Adult Red-footed Falcons had higher *D. rufa* prevalence compared to *C. subzerafae*. For the first time we also show inter-annual shift in prevalence and intensity levels of these species on Red-footed Falcons; in 2012 on adult hosts *C. subzerafae* had higher intensity levels than *D. rufa*, however in 2014 *D. rufa* had significantly higher intensity compared to *C. subzerafae*. In case of nestlings both louse species had significantly higher prevalence levels than in 2014. The exact causes of such inter-annual shifts are yet to be understood.

Keywords: ectoparasite, lice, *Degeeriella rufa*, *Colpocephalum subzerafae*, *Laembothrion tinnunculi*, descriptive statistics

Összefoglalás A kék vércsék és az amúri vércsék tolltetű faunájáról és a fajok ökológiájáról keveset tudtunk, pedig különleges életmenet-sajátosságaik jó modellrendszerré teszik őket parazitaökológiai vizsgálatokra. Felnőtt amúri vércsékről, valamint felnőtt és fióka kék vércsékről gyűjtöttünk ektoparazita mintákat. A *Degeeriella rufa* és *Colpocephalum subzerafae* már korábban is ismert volt mindkét gazdafajról, azonban a *Laembothrion tinnunculi*-nak ez az első ismert elfordulása mindkét madárfajon. Mind a *D. rufa*, mind a *C. subzerafae* prevalenciája magasabb volt az amúri vércséken a kék vércsékhez viszonyítva. A felnőtt kék vércséken a *D. rufa* prevalenciája meghaladta a *C. subzerafae*-jét. 2012-ben a *C. subzerafae*, 2014-ben a *D. rufa* átlagos intenzitása volt magasabb. Mindkét vizsgált tetűfaj prevalenciája magasabb volt a fiókákon 2012-ben mint 2014-ben. Az eredmények alapján a tetvek abundanciája eltérést mutat évek között a kék vércse fiókákon. Ennek az évhatásnak a kialakító tényezői még nem ismertek.

Kulcsszavak: ektoparazita, tolltetű, *Degeeriella rufa, Colpocephalum subzerafae, Laembothrion tinnunculi*, leíró statisztika

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Introduction

Relationship of avian hosts and their ectoparasites has been widely studied from macroevolutionary (Vas *et al.* 2013, Rózsa & Vas 2015) to ecological perspectives (Brooke 2010, Brown *et al.* 1995). Lice (Insecta: Phthiraptera) are the only insects that complete their full life-cycle on the surface of their avian or mammalian hosts. They also have relatively low pathogenicity levels compared to other ectoparasites (Clayton & Tompkins 1994, 1995). Despite this, avian lice may have considerable effects on their hosts (Brown *et al.* 1995, Møller & Rózsa 2005) thus constitute an important aspect of avian evolutionary ecology. Comprehensive overviews of the genus and species composition of lice on various host species are available through worldwide and regional open source databases and checklists (Price *et al.* 2003, Vas *et al.* 2012). However, quantitative data describing population level parameters of ectoparasites are seldom reported. Moreover, studies aiming to assess aspects of louse life history often neglect inter-annual differences in these parameters (but see Hamstra & Badyaev 2009, Monello & Gomper 2009).

The Amur Falcon *(Falco amurensis)* and the Red-footed Falcon *(Falco vespertinus)* are closely related sister species of the Falconidae family (Fuchs *et al.* 2015). Both are small-bodied birds of prey exhibiting marked sexual dimorphism. The Amur Falcon breeds in east Asia from Transbaikalia to Amurland, southward to Eastern China, while the breeding area of the Red-footed Falcon extends from Central and Eastern Europe to Northern Central Asia (Ferguson-Lees & Christie 2001). They are both long-distance migrants wintering in similar habitats of southern Africa. During their annual migration cycle the Amur Falcon uses vast roosting sites in Nagaland (India) where many hundreds of thousands of birds can congregate (Kumar 2014). Their wintering areas may overlap with those of the Red-footed Falcon, where they can share roosting sites, making direct bodily contacts between the two species possible (pers. obs.). The louse faunae of Amur Falcons and Red-footed Falcons has been scarcely studied to date (but see Tendeiro 1988). According to Price *et al.*'s (2003) world checklist of lice, two common species were reported from Amur Falcons: *Degeeriella rufa* (Ischnocera: Philopteridae) and *Colpocephalum subzerafae* (Amblycera: Menoponidae) and both of them also can be found on Red-footed Falcons. The only other species known to occur on Red-footed Falcons is *Nosopon lucidum* (Amblycera: Menoponidae). In this study we aim to a) describe the louse faunae of these two falcon species and, b) give precise population level estimates of louse infestations based on relatively large samples and c) investigate potential inter-annual differences in these parameters.

Materials and Methods

Louse samples from Amur falcons were collected in Nagaland, India in November 2013 and from South Africa in March 2014. Fully developed individuals were trapped and sampled at both locations. Red-footed Falcons were sampled in Körös-Maros National Park, Hungary (Kotymán *et al*. 2015) with the aid of MME-Birdlife Hungary's Red-footed Falcon Working Group. In 2012 fledglings in 2014 both fledglings and adult birds were sampled. Only nestlings 0-7 days prior to leaving the nest were sampled. At this stage the feathers flight feathers are fully developed and most of the contour feathers have appeared. Additionally 5 adult were sampled near Parma (Italy) in 2014.

Ectoparasite samples were collected by using the most widespread sampling method (Johnson & Clayton 2003, Rózsa 2003). The birds' plumage were treated with pyrethrin powder (marketed drug in veterinary practise for pet birds), and then we moved through gently the birds' plumage with a forceps above a white tray for a standard 5 minutes sampling time. Lice were collected per hosts into a 1.5 ml centrifuge tube containing 70% ethanol. In case of Red-footed Falcon nestlings, we excluded all individuals where the parents were treated with pyrethrin in previous years. The identification of lice was carried out by specialists using a stereoscopic microscope.

Descriptive statistics and statistical tests were calculated using Quantitative Parasitology 3.0 (Reiczigel *et al.* 2005). Following Rózsa *et al.* (2000) the prevalence, mean and median intensity of the infestation and their 95% confidence intervals are reported. To compare prevalences we used an exact unconditional test described in (Reiczigel *et al.* 2008).

Results

A total of 20 Amur Falcons were sampled and three louse species were identified: *Degeeriella rufa*, *Colpocephalum subzerafae* and *Laembothrion tinnunculi*. To our knowledge, this is a new host record for *L. tinnunculi* that was present in two birds (1 female, 1 nymph).

We identifed three louse species form the samples taken from the 238 Red-footed Falcons. The two most prevalent species were *Degeeriella rufa* and *Colpocephalum subzerafae*. *Laemobothrion tinnunculi* was found on 3 adult birds (one from Italy and two from Hungary) represented by a male, a female, and nymphs in two of the samples, and only nymphs in the third sample. The descriptive statistics of infestations are presented in *Tables 1–3*.

Comparing the infestation of the two most common lice on fully grown Amur and Red-footed Falcons, both *D. rufa* and *C. subzerafae* were more prevalent on Amur Falcons (p-value=0.0045) while there was no significant difference in mean (p-value=0.2515) or median intensity (p-value=0.547) between the two host species (see also *Tables 1–2*).

Examining the infestation patterns of the two most prevalent louse species on adult Red-footed Falcons, *D. rufa* was found to

N=20	***D. rufa***	***C. subzerafae***	***L. tinnunculi***
Prevalence	90%	70%	10%
95% CI	68%–98%	47%–86%	1%–31%
Mean intensity	4.39	2	1
95% CI	3.28–6.06	1.43–2.71	NA
Median intensity	3	1.5	1
CI	95.1%: 2–5	99.3%: 1–3	NA

Table 1. Descriptive statistics and their confidence intervals of the louse infestations of fully grown Amur Falcons. N is the number of birds. Calculating the confidence intervals for *L. tinnunculi* was not possible

1. táblázat Az amúri vércséken talált tetűfajok, azok leíró statisztikái és a becsült paraméterek konfidencia intervallumai (CI). N a madarak egyedszáma. A *L. tinnunculi* esetén nem lehetett konfidencia intervallumot számolni

N=59	***D. rufa***	***C. subzerafae***	***L. tinnunculi***
Prevalence	56%	20%	0.034%
95% CI	43%–68%	12%–33%	NA
Mean intensity	6.79	12.08	3.5
95% CI	4.21–12.03	4.17–37.08	NA
Median intensity	2	3.5	3.5
CI	95.8%: 2–3	98%: 1–13	NA

Table 2. Descriptive statistics and their confidence intervals of the louse infestations of fully grown Red-footed Falcons. N is the number of birds. Calculating the confidence intervals for *L. tinnunculi* was not possible

2. táblázat A kék vércséken talált tetűfajok, azok leíró statisztikái és a becsült paraméterek konfidencia intervallumai (CI). N a madarak egyedszáma. Az *L. tinnunculi* esetén nem lehetett konfidencia intervallumot számolni

be more prevalent (p-value=0.0001), while its mean (p-value=0.5127) and median intensity (p-value=0.325) do not significantly differ from that of *C. subzerafae (Table 2).*

In 2012, there was no difference in prevalence between *D. rufa* and *C. subzerafae* on Red-footed Falcon nestlings (p-value=1), but the mean (p-value=0.0006) and median intensity (p-value=0.002) for *C. subzerafae* was significantly higher. On the other hand, in 2014 the prevalence of *D. rufa* exceeded (p-value=0.0003) that of *C. subzerafae* while there was no significant difference in their median and mean intensities (p-value=0.5724 and 0.633, respectively).

The prevalence of *D. rufa* on Red-footed Falcon nestlings was significantly higher in 2012 than in 2014 (p-value=0.0308), but the mean (p-value=0.5107) and median intensities (p-value=0.5107) showed no significant differences. In case of *C. subzerafae* the prevalence (p-value<0.0001), and both the mean (p-value<0.0001) and median intensities (p-value<0.001) were significantly

N=95	***D. rufa***	***C. subzerafae***
Prevalence	78%	78%
95% CI	68%–86%	68%–86%
Mean intensity	3.66	6.73
95% CI	3.07–4.53	5.58–8.28
Median intensity	2	5.5
CI	99.9%: 2–4	99.5%: 4–7

Table 3. Descriptive statistics and their confidence intervals of the louse infestations of Red-footed Falcon nestlings in 2012. N is the number of nestlings

3. táblázat Kék vércse fiókákon 2012-ben talált tetvek leíró statisztikái és azok konfidencia intervalluma. N a madarak egyedszáma

N=84	***D. rufa***	***C. subzerafae***
Prevalence	63%	34%
95% CI	52%–73%	25%–45%
Mean intensity	3.28	2.86
95% CI	2.57–4.4	2–4.31
Median intensity	2	2
CI	95.1%: 2–2	96.9%: 1–2

Table 4. Descriptive statistics and their confidence intervals of the louse infestations of Red-footed Falcon nestlings in 2014. N is the number of nestlings

4. táblázat Kék vércse fiókákon 2014-ben talált tetvek leíró statisztikái és azok konfidencia intervalluma. N a madarak egyedszáma

higher in 2012. Moreover, the distribution of *D. rufa* and *C. subzerafae* infestation classes on nestlings was significantly different in the two years (Goodness-of-fit tests: χ^2:120.09, df=80, p=0.002 and χ^2:112.06, df=48, p<<0.001, respectively. see also *Figures 1-2*).

Discussion

We recorded the occurrence of the same three louse species on both Amur and Red-footed Falcons. *L. tinnunculi,* which can be found on several species in the genus *Falco*, is reported here for the first time to infest Amur Falcons and Red-footed Falcons. *Laemobothrion* species differ in many characteristics from other lice. They have considerably larger body size (Price *et al.* 2003) and appear to be more mobile, while their intensity tend to be low. We hypothesize that *Laemobothrion* lice might have a peculiar life cycle that calls for innovative new methods to be developed.

Both of the two smaller louse species had significantly higher prevalences on Amur Falcons than on Red-footed Falcons. The host species have similar body and bill sizes, possess similar plumage patterns in

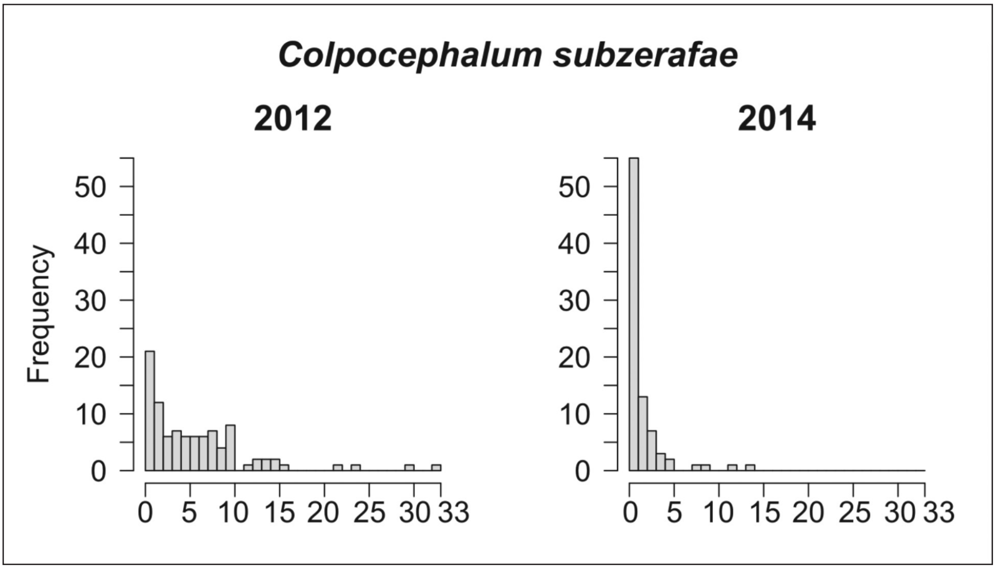

Figure 1. The distribution of *D. rufa* infestation classes on sampled Red-footed Falcon nestlings. The number of sampled birds is 95 in 2012 and 84 in 2014

1. ábra A *D. rufa* tetűfaj fertőzöttségi osztályainak eloszlása kék vércse fiókákon. A mintázott fiókák száma 2012-ben 95 példány, 2014-ben 84 példány

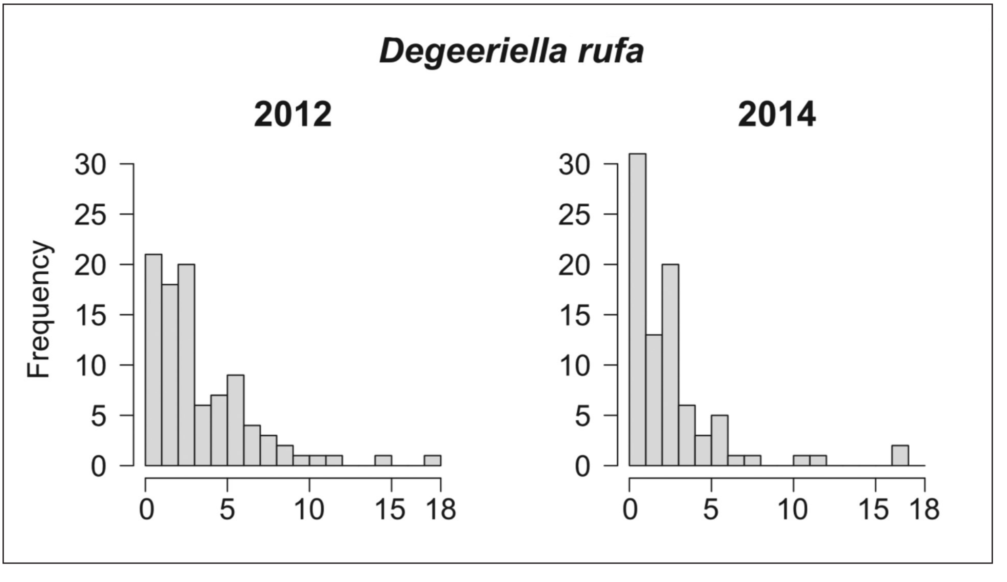

Figure 2. The distribution of *C. subzerafae* infestation classes on sampled Red-footed Falcon nestlings. The number of sampled birds is 95 in 2012 and 84 in 2014

2. ábra A *C. subzerafae* tetűfaj fertőzöttségi osztályainak eloszlása kék vércse fiókákon. A mintázott fiókák száma 2012-ben 95 példány, 2014-ben 84 példány every age and sex groups, thus making it unlikely that they provide considerably different habitats for lice. Increased rate of horizontal transmission (lice infesting unrelated hosts) due to coloniality (Rózsa *et al.* 1996) or frequency of congregations of the hosts is hypothesized to increase ectoparasite prevalence. In our case, samples were collected from Amur Falcons at the two largest known migratory (Nagaland, India: >1 million birds present) and wintering (Newcastle, South Africa: 5–10 thousand birds present) roost sites of the species, while in case of Red-footed Falcons the sampled individuals were taken from breeding colonies (10–200 adult individuals present) making the number of birds 2–5 orders of magnitude lower. This in itself may cause differences in prevalence. However, Red-footed Falcons are also known to aggregate in large numbers at pre-migratory roost sites (Borbáth & Zalai 2005, Fehérvári *et al.* 2014). Seasonality may also have an effect on louse population parameters (Monello & Gomper 2009). Amur Falcons were sampled in the non-breeding period while Red-footed Falcons were only sampled in the breeding season, thus the observed pattern may also be attributed to different infestation levels at different stages in their life cycle.

Inter-annual differences in prevalence and intensity of the two common louse species were detected in both adult and nestling Red-footed Falcons. We emphasize that the samples were taken from the same population, at the same location and from similar aged nestlings in the two years. We believe our data shows for the first time shifts in population parameters of avian lice species between years. It is plausible that such changes may have been caused by abiotic factors such as different average temperature or humidity, or by changes in host attributes such as deviating nestling sex ratios. In any case, such inter-annual fluctuations may be a key feature to further the understanding of host-parasite interactions.

Our results shed light on species composition and various aspects of ectoparasite demography in avian-host parasite systems. Albeit the currently used methodology to obtain ectoparasite samples yield valuable results, we believe that even a simple evaluation of infestation on a relatively large sample of hosts shows that invasive ectoparasite collection has its limits. We urge future studies to investigate the possibility of developing a precise, reliable non-invasive method to collect louse species that may allow to better enhance our understanding of host-parasite systems.

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Species specific effect of nest-box cleaning on settlement selection decisions in an artificial colony system

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Abstract Selecting a suitable breeding habitats and a nest-site within are crucial decisions birds have to make. Free ranging solitary Kestrels may use public information derived from leftover pellets and prey remnants from previous conspecific breeding attempts to assess location quality. However, this information may also indicate potentially higher nestling ectoparasite load. In colonies where habitat quality is similar for all available nests, the only information of previous nest usage may reflect expected future parasite pressure. In this study we explored whether Kestrels, Red-footed Falcons and Jackdaws rely on nest-material consisting of pellets and prey remnants when choosing a nest in a multi species artificial colony system. We also assessed potential effects of these decisions on reproductive success. We randomly selected and cleaned half (n=102) of all available nest-boxes in each of the studied 4 colonies before the breeding season. We then monitored occupancy, egg-laying date, hatching and fledging success. In case of Red-footed Falcons, we also acquired adult age and nestling condition data. Our results show that Kestrels were more likely to breed in uncleaned nest-boxes, however, eggs laid in cleaned nest-boxes were more likely to develop into fledged nestlings. There was a weak indication that lower hatching rate was responsible for this effect, rather than increased parasite load. Nest box cleaning had no effect on measured variables in case of Red-footed Falcons and Jackdaws. Colonial breeding of Kestrels, the only species to react to nest-box cleaning, is rare and is probably a consequence of extreme nest-site shortage in our study site. We conclude that Kestrels are not adapted to interpret the information carried by pellets and prey-remnants in colony nest-boxes.

Keywords: *Falco tinnunculus*, *Falco vespertinus*, *Corvus monedula*, public information, nest site choice

Összefoglalás A költőterület- és költőhelyválasztás az egyik legfontosabb döntés nem fészeképítő madárfajok esetén. Egy korábbi vizsgálat kimutatta, hogy szoliter vörös vércsék a fajtársaik által hagyott nyomokat (köpetek, táplálékmaradvány) figyelembe veszik a költőhely választásakor, mint a költőterület minőségére vonatkozó publikus információt, és korábban költenek azokon a helyeken, ahol fajtársaik nyomai fellelhetők. Annak ellenére teszik mindezt, hogy a fiókák potenciális ektoparazita fertőzöttsége magasabb azokon a helyeken, ahol korábban költés volt. A kolóniákban azonban, ahol az élőhely minősége minden fészek esetében hasonló, ez az információforrás elsősorban a potenciális ektoparazita terheltséget tükrözi. Ebben a vizsgálatban mesterséges kolóniákban vizsgáltuk vörös vércsék, kék vércsék és csókák fészekválasztását attól függően, hogy található-e benne korábbi költésekből származó köpet és egyéb táplálékmaradvány. Eredményeink szerint csak a vörös vércsére volt hatással a költőládák tisztasága. Ezeket nagyobb arányban foglalták el, azonban a fiókák kisebb valószínűséggel repültek ki a takarítatlan ládákból. Úgy tűnik azonban, hogy ez a veszteség inkább az alacsonyabb kelési siker következménye, és nem a magasabb ektoparazita nyomás okozza. A vörös vércse jellemzősen nem telepesen költ, a vizsgálati területen telepes költését feltehetőleg az extrém fészkelőhely-hiány okozza. Valószínűsítjük, hogy a vörös vércsék nem adaptálódtak megfelelően a telepeken lévő fészkekben látható maradványok hordozta információ felhasználáshoz.

Kulcsszavak: *Falco tinnunculus*, *Falco vespertinus*, *Corvus monedula*, fészkelőhelyválasztás

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Introduction

Selecting breeding habitat and breeding site within has a crucial effect on realized individual fitness of birds (e.g. Valkama & Korpimäki 1999, Serrano *et al*. 2005, Arlt & Pärt 2007, Kasprzykowski 2008). Settlement decision of prospecting breeders has to incorporate habitat quality, potential presence of predators, and nest site quality; such as orientation, exposure and potential parasite load. Acquiring a priori information before settlement is pivotal, and may rely on various sources. An individual may lean on recent personal experience such as food availability and observation of predators or on past experience, realized as high probability of philopatry. There is increasing evidence that settlers may also use public information such as reproductive success (Danchin & Wagner 1997, Aparicio *et al*. 2007, Boulinier *et al.* 2008) or the historic presence of conspecifics (Sumasgutner *et al*. 2014), and other species (Parejo 2004) with similar ecological needs. The advantage of using cues that reflect conspecific performance is that they provide insight into the net effects of various factors influencing reproductive success (Danchin *et al.* 2004). Of these, potential ectoparasite load on offspring may be a key component of settlement decisions of prospecting breeders as it may influence nestling mortality (Wimberger 1984, Richner *et al*. 1993) affect parental care investment (Richner *et al*. 1993, Tripet & Richner 1997) and reproductive success (Ontiveros *et al*. 2008). Colonial species may experience higher prevalence of ectoparasites compared to territorial breeders (Rózsa *et al*. 1996, Brown & Brown 2004) and, thus constitute one of the main costs of coloniality (Brown & Brown 1986).

Sumasgutner *et al.* (2014) have previously shown that settlement decisions of free ranging solitary breeding Kestrels *(Falco tinnunculus)* may rely on public information deriving from residual nest-material, pellets and prey remains left from previous breeding attempts of conspecifics. The birds did this despite the lower prevalence rate of a heamatophagus Carnid Fly *(Carnus hemapterus)* in nests where the nest material was cleaned prior to breeding. Apparently, assessing habitat quality via public information was more important than higher risk of ectoparasite loads for these solitary nesting falcons. The same ectoparasite is commonly found on colonial raptors including, Lesser Kestrels (Calabuig *et al.* 2010), and Red-footed Falcons *(Falco vespertinus)* (Brake 2011, pers. obs.). These flies are presumed to use the nest substrate to lay eggs, and the larvae feed on organic matter in the nest material before developing into adults or overwintering as pupae. The mass emergence of adult flies from the substrate often coincides with a specific age of the host species and predominantly feed on nestling blood (Roulin 1998, Roulin *et al.* 2003). Adult flies have two distinct life forms, the first when individuals locate new host nests (transmissive form), and the second when they lose their wings and remain in the newly colonized brood (Capelle & Whitworth 1973). Effective horizontal transmission of the transmissive form in areas with low internest distance is probably the main reason of high prevalence of flies in colonial species (Liker *et al.* 2001).

This set-up allowed us to test with an in situ experiment whether the two falcon species and Jackdaws *(Corvus monedula)* that are also exploting these boxes, cue on pellets and prey remnants as a source of public information on potential future ectoparasite load on nestlings. We hypothesized that pairs of all species will select for cleaned boxes by earlier egg laying and by higher probability of occupancy. Furthermore, we tested potential effects of cleaning on reproductive success parameters of all species and also on the condition of Red-footed Falcon nestlings. Testing these hypotheses may yield intriguing insight into settlement decision making of prospecting breeders and also allow us to assess the importance of nest-box cleaning activities. Nest-box maintenance of Red-footed Falcon colonies is an important and highly resource- and time-consuming activity in the conservation management of this species. Thus evaluating the necessity of annual maintenance may allow us a better allocation of limited resources available for active conservation measures.

Materials and Methods

Study site and nest boxes

The study was carried out in 2013 at an artificial colony system located in the Vásárhelyi Plains, Hungary (see Kotymán *et al*. 2015 for details). Here, a total of 251 nest-boxes were available in 4 larger colonies, several smaller clusters and as platforms for solitary breeding. Initially, we used a stratified randomizing procedure to select 50% of available nest-boxes in each artificial colony. The selection procedure considered the within-colony location of the boxes, thus selected boxes were not aggregated in either the centre or the edge of colonies. The selected boxes were cleaned of all nest materials by scraping all remaining prey items and pellets completely, and were filled with hay. Providing some sort of breeding substrate is necessary as nest-boxes are often tilted to some degree, thus the eggs may roll into the corners if the birds start incubating on the flat surface of the box. We chose hay as the provided nest-material in cleaned boxes as it differs both visually and in texture from the typical pellet bedding remaining in the uncleaned boxes. Nest-box design may have an impact on various parameters of reproduction (Kotymán *et al*. 2015), therefore we only involved the most common box type into our analyses. We also excluded smaller colonies and solitary boxes leaving a sample size of 102 cleaned and 135 untreated nest-boxes.

Assessing egg laying date, occupancy rate and breeding success parameters

In 2013, we recorded the species, the number of breeding pairs, first egg laying date (Julian date), clutch size, hatching and fledging success for all species breeding in the study area. sequential nesting during the same breeding season of various species in the same box is not uncommon in this area. Therefore, we only used the data of the first breeders of all species in case of both cleaned and uncleaned boxes and excluded any subsequent clutches. Our primary focus was on assessing the reproductive parameters of Red-footed Falcons and Kestrels, thus the timing and frequency of nest inspections was optimized to allow collection of precise data on these species. Long-eared Owls *(Asio otus)* and Jackdaws initiate breeding earlier than these two falcon species. The relatively low number of nest inspections from this period hindered assessing precise egg laying date for Jackdaws. Thus, to avoid this type of bias we calculated egg laying week of the year for this species. We also excluded all Jackdaw clutches where the low number of nest inspections did not allow to assess fledging status of all hatched nestlings.

Individual experience and nestling condition in Red-footed Falcons

A considerable proportion of Red-footed Falcons, breeding at the study site are marked with individually coded colour rings. We identified marked individuals breeding in the focal boxes with spotting scopes and camera traps. Age often correlates with individual quality in raptors (e.g. Penteriani *et al*. 2003, Espie *et al*. 2004), and also with competitive dominance in nest sight selection in a similar sibling species, the Lesser Kestrel *(Falco naumanni)* (Serrano *et al*. 2007). Therefore we used adult age as a measure of individual quality, with older birds having supposedly higher recruiting capability to a nest-site of choice. All nestlings of Red-footed Falcons were ringed and wing-bone, body mass and various other morphometric measurements were recorded. We used the residuals of age by body mass and age by wing length regressions as age-independent measures of nestling condition.

Statistical analyses

We used linear models to test whether egg laying date differs for cleaned and uncleaned nest boxes in case of all studied species. General Linear Models (GLM) with binomial distribution and logit link functions were fitted to assess differences in occupancy rate and fledging success for all species. For clutch size we used GLMs with a Poisson distribution and a log link function (Faraway 2006). For nestling condition (measured as age-independent body mass and wing length) we used linear mixed effects models (LME), where nest-box identity was used as a random factor (Pinheiro & Bates 2000). In general, we used nest-box treatment and colony identity as explanatory variables in case of all models fitted. We excluded colony effect whenever it was not significant, and used Akaike Information Criterion (linear models) decrease in deviance (GLM), and the likelihood ratio tests to compare model performance (Faraway 2006) of these reduced models. If the colony effect was significant we indicated it in the outputs, however, to allow concise presentation of reports we provide details only on the effect of cleaned boxes on analysed response variables. All analyses were carried out using R 3.2.0 (R Core Team 2015).

Results

Overall, 65% of cleaned and 67% of uncleaned boxes were used by the four most common species breeding in the colonies. Only two pairs of Long-eared Owls bred in the studied boxes, therefore we excluded this species from further analyses. We found no difference in the timing of breeding in case of Jackdaws, Kestrels and Red-footed Falcons *(Table 1)*. The probability of occupancy was significantly larger for uncleaned nest boxes for Kestrels, but not for Red-footed Falcons and Jackdaws *(Figure 1, Table 2)*.

Species	N	Estimate	SE	t-value	p-value
Kestrel	12/10	4.42	7.4	0.6	0.56
Red-footed Falcon*	30/27	-3.23	3.16	-1.02	0.31

*significant effect of colony identity

Table 1. Linear model parameter estimates for egg laying date in cleaned versus uncleaned boxes measured as week of the year for Jackdaws and Julian days for Kestrels and Red-footed Falcons. N denotes the number of observations in uncleaned/cleaned nest-boxes. We found no significant effect of nest-box cleaning on the timing of breeding in any of the studied species

1. táblázat A ládatakarítás költéskezdésre gyakorolt hatását leíró lineáris modell paraméter becslései. Csókák esetében az év hetével, míg a többi faj esetén az évnappal számoltunk. Az N a költések száma a takarítatlan/takarított ládákban. Nem találtunk szignifikáns eltérést a költések időzítésében a takarított és a nem takarított ládákban egyik faj esetében sem

Species	N	Estimate	SE	z-value	Pr(>|z|)
Jackdaw	23/18	0.287	0.31	0.92	0.36
Kestrel	37/21	-0.56	0.27	-2.07	0.03
Red-footed Falcon	30/27	-0.1	0.26	-0.40	0.70

Table 2. Binomial GLM parameter estimates fitted on the probability of occupying a cleaned nest-box. N denotes the number of observations in uncleaned/cleaned nest-boxes. Kestrels were significantly more likely to choose an uncleaned nest box

2. táblázat Binomiális GLM paraméter becslései a fészkelés valószínűségére. Az N a költések számát mutatja a takarítatlan/takarított ládákban. A vörös vércsék szignifikánsan magasabb arányban költöttek a nem takarított ládákban, míg a többi faj esetében nem találtunk hasonló mintázatot

Species	N	Estimate	SE	z-value	Pr(>|z|)
Kestrel	37/21	-0.1	0.08	-1.35	0.18
Red-footed Falcon*	30/27	-0.07	0.1	-0.72	0.48

*significant effect of colony identity

Table 3. Poisson GLM parameter estimated fitted on clutch size in uncleaned and cleaned nest-boxes. N denotes the number of clutches in uncleaned/cleaned nest-boxes. Clutch size was not affected by nest-box cleaning in neither of the species

3. táblázat Poisson GLM paraméter becslései a fészekalj méretre a takarított és a takarítatlan ládákban. Az N a mintaelemszámot mutatja a takarítatlan/takarított ládákban. Egyik faj esetében sem mutatkozott hatása a ládatakarításnak a lerakott tojások számában

Although clutch size was significantly different in the four colonies for Jackdaws and Red-footed Falcons, clutch size was not affected by nest-box cleaning in any of the three species *(Table 3)*. The probability of an egg to develop into a fledged nestling was significantly higher for Kestrels breeding in cleaned nest-boxes than for those in uncleaned ones, while in case of Red-footed Falcons it was similar in both box types *(Table 4, Figure 2)*.When partitioning this probability to hatching and fledging success we found a near significant trend in lower hatching probability in uncleaned boxes

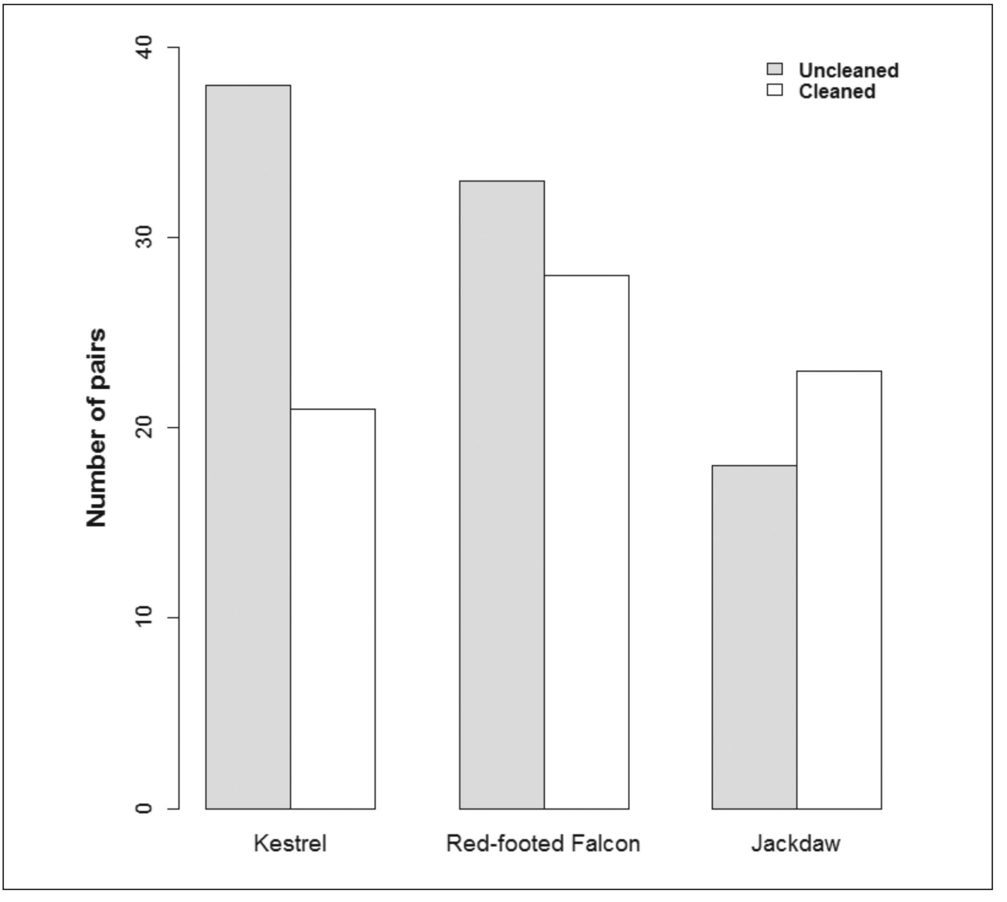

Figure 1. Number of breeding pairs of the three studied species in cleaned and uncleaned nest-boxes. Kestrels occupied significantly more uncleaned boxes, while Red-footed Falcons and Jackdaws did not differentiate between the two groups

1. ábra A három vizsgált faj párjainak száma a takarított és a takarítatlan ládákban. A vörös vércsék szignifkánsan magasabb arányban foglalták a nem takarított ládákat, azonban a kék vércsék és csókák hasonló arányban használták a két ládatípust

(Binomial GLM, Effect of cleaning: 0.58, SE:0.3, z-value=1.9, Pr(>|z|)=0.056), but not in fledging success (Binomial GLM, Effect of cleaning: 1.35, SE:1.15, z-value=1.16, Pr(>|z|)=0.24). We identified 28 individually marked Red-footed Falcons breeding in the focal nest-boxes, however age structure of these birds was similar in the two nest-box groups (Mann-Whitney U test; U=51.5, p=0.36). A total of 90 Red-footed Falcons fledged from the focal boxes. Nest-box cleaning did not influence their body mass residuals or wing feather growth residuals *(Table 5)*.

Discussion

In general, our results show that the nest-box cleaning affected only Kestrel settlement decisions and reproductive output. Albeit, giving a somewhat different re-

Species	N	Estimate	SE	z-value	p-value
Kestrel	37/21	0.77	0.32	2.43	0.01
Red-footed Falcon*	30/27	-0.67	0.45	-1.47	0.14

*significant effect of colony identity

Table 4. Binomial GLM parameter estimates fitted on the probability of fledging success. N denotes the number of clutches in uncleaned/cleaned nest-boxes. Kestrel eggs were significantly more likely to yield in fledged nestlings from cleaned boxes than those from uncleaned ones, while this pattern was absent for Red-footed Falcons

4. táblázat Binomiális GLM paraméter becslései a repítési sikerre. Az N a költések száma a takarítatlan/takarított ládákban. A vörös vércsék tojásai szignifikánsan magasabb arányban eredményeztek kirepült fiókákat a takarított, mint a takarítatlan ládákban, míg a kék vércsék esetében nem találtunk hasonló mintázatot

Category	Estimate	SE	t-value	p-value
Body mass (g)				
Uncleaned	0.03	2.62	0.01	0.98
Cleaned	1.03	3.91	0.26	0.79
Wing length (mm)				
Uncleaned	0.34	1.67	0.2	0.83
Cleaned	-1.17	2.52	-0.46	0.64

Table 5. LME parameter estimates on the residuals of body mass and wing length of Red-footed Falcon nestlings. Neither response variable was significantly different between cleaned and uncleaned nest-boxes

5. táblázat A ládatakarításnak a kék vércse fiókák tömeg és szárnyhossz reziduálisaira gyakorolt hatását leíró LME modellek paraméter becslései. Egyik függő változó esetében sem találtunk szignifikáns hatást

sponse, our results seemingly corroborate the findings that Kestrels may cue on the presence of nest-material in boxes and select for boxes where previous breeding can be visually confirmed (Sumasgutner *et al.* 2014). However, we found no evidence that egg laying date between the two nest-box groups would be significantly different. It has to be also noted that assessing egg laying date was only possible for a fraction of the clutches reducing sample size considerably. Mean clutch size was also similar, indicating that once the settlement decisions were made, Kestrels did not adjust their initial parental investment to nest-box treatment. These decisions are presumably governed by other factors such as age, habitat quality, or prey availability (Sumasgutner *et al*. 2014).

In a colony where all nests have similar surrounding foraging habitats, the value of information on habitat quality of previous breeding attempts in a particular nest is negligible. Rather, it is probably more reliable to assess future ectoparasitic load on nestlings. Despite this, Kestrels clearly opted for uncleaned boxes contradicting previous assumptions. Kestrels are mostly territorial breeders in central Europe and have only recently started to breed in artificial

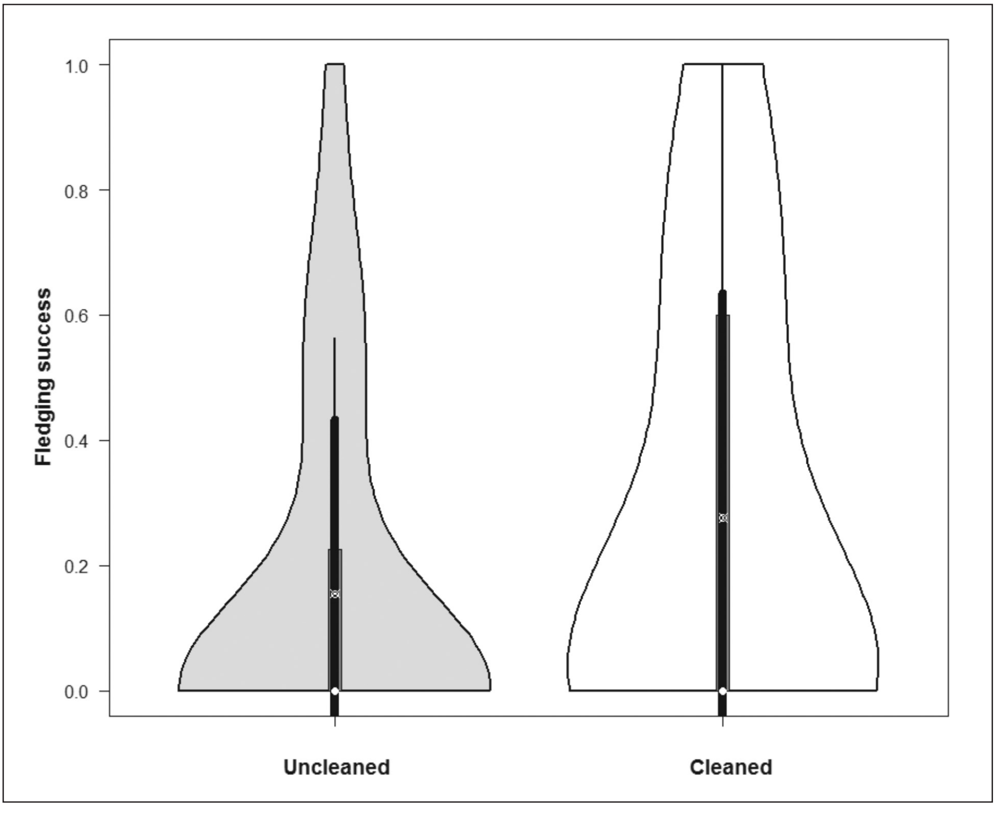

Figure 2. Violin plots (box and whisker plots with distribution densities on both sides) on Kestrel overall fledging success in cleaned and uncleaned nest-boxes. Kestrel eggs in cleaned nest-boxes were significantly more likely to develop into fledged nestlings in cleaned nest-boxes

2. ábra A hegedű ábrán a vörös vércsék költési sikerének átlag és medián értékei láthatóak, a függőleges vastag vonal a középső 50%-nyi adatot jelöli, oldalt az adatok simított hisztogramja található. A takarított ládákban a vörös vércse tojások szignifikánsan magasabb aránya eredményezett sikeresen kirepülő fiókát, mint a takarítatlan ládákban

nest-box colonies. Potentially, birds are maladapted to this situation as they had not developed mechanisms to correctly evaluate breeding site quality in colonies. They appear to rely on cues that would be of value in a territorial breeding setup. Dry hay, the substrate used in cleaned nest-boxes, differs in texture from the usual nest bedding, presenting a previously seldom seen novelty. It is likely that Kestrels – instead of selecting for uncleaned boxes – simply avoided this novel substrate. The probability of an egg to develop into a fledged nestling was significantly lower in uncleaned boxes. However, there was weak indication that this loss is more likely to occur as hatching failure rather than the loss of nestlings, suggesting that it is less likely to be caused by the negative effect of ectoparasites on nestlings. It is also possible, that increased ectoparasite load had an effect on incubating adults. Increased ectoparasite infestation could drive the birds to allocate more time into preening instead of incubation, resulting in the observed lower hatching rate. However, the phenology of Carnus Fly load in Kestrel, Starling *(Sturnus vulgaris)* and Barn Owl *(Tyto alba)* clutches are linked to nestling age, showing that the parasites optimize their life cycle to nesting hosts rather than the adults (Roulin 1998, 1999, Liker *et al*. 2001, Kaľavský & Pospíšilová 2010). In general, occupation rate and breeding success was relatively low in the study year (see Kotymán *et al.* 2015), presumably due to above average precipitation frequency and quantity throughout the breeding season. We used semi-closed nest-boxes providing shelter against rainfall, however, the large opening on the front does not completely keep the clutch dry (pers. obs). The pellet bedding in uncleaned boxes is predominantly a layer of compressed fur and various other prey remnants that may get sogged by rainfall or in highly humid air. It is possible that the lower probabilities of fledging derive from the different insulation properties of nest-materials rather than other factors.

We were unable to detect any significant effect of nest-box cleaning on the occupation rate and egg laying date of Red-footed Falcons and Jackdaws, indicating that they show no preference for cleaned boxes. Moreover, the lack of difference in clutch size indicates that the initial parental investment of females was not affected by nest-box cleaning. The natural breeding sites of Red-footed Falcons are predominantly rookeries, where the majority of nests are rebuilt annually (Horváth *et al*. 2015). Thus, cueing on previous usage of a given nest is less likely to be adaptive in choosing within colony breeding site. Nonetheless, the potential high parasite load deriving from uncleaned nest-box substrate may have an impact on nestling survival or condition. However, we found no supporting evidence for this.

Despite their wide use as effective tools in reducing nest site shortage, nest-boxes increase ectoparasite load in a wide range of avian systems (Valkama & Korpimäki 1999, Fargallo *et al.* 2001, Wesołowski & Stańska 2001, Lambrechts *et al.* 2012). Populations that depend on such artificial nest-sites are considered unsustainable on a long-temporal scale as preserving these sites needs constant maintenance that entail refurbishing, replacing, and cleaning of the boxes. This latter activity, however, is simply based on the assumption that ectoparasites accumulate and thus reduce population viability. Blood-sucking nest-dwelling ectoparasites can have various effects on avian broods, they may increase nestling mortality (Richner *et al.* 1993), decrease condition (Hoi *et al.* 2010), increase physiological stress (Martínez-Padilla *et al.* 2004), or influence parental food provisioning (Avilés *et al.* 2009, Johnson & Albrecht 1993). In case of raptors, there is increasing evidence that brood size and nestling survival are less likely to be influenced by common blood-sucking parasites on a population level (Dawson & Bortolotti 1997, Kaľavský & Pospíšilová 2010), despite their high potential prevalence on nestlings. These results taken together with our findings are intriguing, and may have direct applicability in allocating nature conservation efforts, as they suggest that nest-box maintenance works do not necessarily need to include regular cleaning. However, nest-dwelling ectoparasites have various other effects on individual condition that may affect both parents and offspring and, thus, we urge further investigations that allow deeper inference of effects before decisions should be made. In case of the

Red-footed Falcons in the Carpathian Basin, where the bulk of the pairs use artificial nest-sites (Palatitz *et al.* 2015), the effect of a potential excess parasite load in the boxes may have hidden yet influential ramifications on a population level.

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Breeding population trends and pre-migration roost site survey of the Red-footed Falcon in Hungary

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Peter Palatitz, Peter Fehérvári, Szabolcs Solt & Éva Horváth 2015. Breeding population trends and pre-migration roost-site survey of the Red-footed Falcon in Hungary. – Ornis Hungarica 23(1): 77–93.

Abstract The Red-footed Falcon is a facultatively colonial species that exploits rookeries, artificial nest-box colonies and solitary corvid nests for breeding. Moreover, the remain gregarious in the post breeding period using communal roost sites prior to migration. We developed and implemented a survey protocol to allow to precisely estimate the number of breeding pairs in all three breeding types and to assess large scale spatio-temporal changes in roost site usage. Our results show that the lowest number of breeding pairs (558) was in 2006. However, in 2014 the number of pairs showed a two fold increase, mainly due to a large scale nest-box programme implemented in the past decade. We identified a total of 105 roost sites throughout the country. The number of birds peaked in the second week of September in the past 10 years. We formulate a recommendation to maintain population monitoring efficiency by reducing the frequency of full surveys to 5 years and using designated study areas to control for temporal trends in between.

Keywords: *Falco vespertinus*, communal roost, post-nuptial migration, post-fledging period, aggregation, monitoring

Összefoglalás A kék vércse egy fakultatívan koloniális madárfaj, mely természetes körülmények között elsősorban vetési varjú telepeken fordul elő, de a fajvédelmi intézkedések keretében létrehozott ládatelepeken is nagyszámban költ. Az őszi vonulás előtti időszakban közös éjszakázóhelyeket használ. 2006-tól a faj sajátosságait figyelembe vevő, költési és vonulás előtti időszakot egyaránt monitorozó protokoll került bevezetésre. A költések monitorozása kiterjedt mind a vetési varjú, mind a ládatelepek, illetve a szoliter párok ellenőrzésére. A premigrációs időszakban új gyülekezőhelyek keresése és az ezeken végzett szinkronszámlálások zajlottak. A korábbi, nem egységesített protokoll szerint végzett felmérések eredményeit is figyelembe véve, a hazai állomány mérete 2006-ban érte el mélypontját, mely azóta növekvő tendenciát mutat. A 2014-es becsült minimális költő állomány elérte az 1250 párt, így az utóbbi évtized fajmegőrzési beavatkozásai során mintegy megkétszereződött.Összesen 105 új őszi gyülekezőhelyet azonosítottunk. A madarak száma a gyülekezőkön szeptember második hetében tetőzött. A vizsgált évek eredményei és tapasztalatai alapján egy módosított, kevesebb erőforrást igénylő, de hasonlóan pontos protokollt javaslunk. Eszerint a részletes monitoring tevékenység csak egyes kijelölt területeken zajlana minden évben, országos cenzusra pedig ötévente kerülne sor.

Kulcsszavak: *Falco vespertinus*, gyülekezőhely, őszi vonulás, állomány felmérés

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Introduction

Long-term monitoring of species specific distribution and abundance patterns provides a fundamental information source for nature conservation efforts (Nichols & Williams 2006, Gruber *et al*. 2012). Understanding the factors that play a role in shaping these patterns are crucial to assess the impact of human induced environmental changes (Eglington & Pearce-Higgins 2012), to help formulate national and international conservation policy (Gruber *et al*. 2012, Henle *et al*. 2013), or aid designating specific pin-point conservation measures (Fehérvári *et al*. 2009, 2012). Albeit avian monitoring in Hungary has a long tradition, systematic or robust design monitoring schemes have only been implemented in the past two decades (Szép *et al*. 2012). Distribution data on rare, endangered species is sporadic from the communistic era (e.g. Kovács *et al*. 2008, Horváth 2009) but in the case of Red-footed Falcons *(Falco vespertinus)*, a species of high conservation value (strictly protected in Hungary, "near-threatened" in IUCN Red List, ANNEX I of European Commission's Birds Directive 79/409/EEC), a valuable country-wide survey from the late 1940s (Keve & Szijj 1957) constitutes an important basis for assessing demographic trends. Here the authors used a questionnaire survey, followed up by a partial census to assess breeding population size in colonies. They estimated 2000–2500 pairs to breed in the country, and showed that the bulk of the population breeds in the eastern part of the country, but the species is widespread in Trans-Danubia (areas west of the Danube) and in the valleys of the foothill region of Northern Hungary (Keve & Szijj 1957, Fehérvári *et al.* 2009). The next country-wide assessment from 1990 showed similar population size as in the late '40s with an estimated 2000–2200 pairs (Haraszthy 1998). Regional scale surveys started indicating a considerable decline, for instance Tóth (1995) reports a drastic decrease in Békés County from 1990 to 1995 (550 to 280 pairs). In 1997 the estimated population size was 1300–1400 pairs, a mere half of what was in 1990 (Tóth & Marik 1999). Starting from 2003, we initiated an annual country-wide survey that used similar methods to previous estimates. This entailed a combination of estimates of local experts and data from partial census of raptors in general. The results were appalling, showing that the number of pairs is well below 1000 pairs, and continuously decreasing (725 pairs in 2003 and 654 pairs in 2005) (Palatitz *et al*. 2006).

One of the identified population limiting factors that may have largely contributed to the observed decline was the lack of rookeries, as sites for large colonies, in suitable habitats (Palatitz *et al*. 2009). Rooks have been effectively persecuted throughout the '80s and early '90s, causing a population crash when approx. 90% of the breeding population disappeared. Moreover, substantial part of the remaining rookeries shifted location to human settlements, further decreasing the number of potential breeding sites (Fehérvári *et al*. 2009). Several smaller scale initiations have proved that Red-footed Falcons are readily accepting artificial colonies as substitute breeding sites in suitable habitats where rookeries are absent (Csörgey 1908, Molnár 1999, Kotymán 2001). Thus, to halt the negative overall population trend we initiated a large scale nest-box program in 2006 (Palatitz *et al*. 2010). Initially 3500 nest-boxes were placed out in 2006, to various locations throughout the Hungarian breeding range, while today approximately 4000 boxes are readily available in suitable habitats for the birds to breed in.

One of the main motivation behind the high conservation priority of Red-footed Falcons in EU is the negative trend described from eastern Europe, and the case of the documented negative Hungarian population trend. Despite the estimated large global population (300,000–800,000 individuals) (Ferguson-Lees *et al*. 2001), sporadic observations suggests that population trends are negative in various other parts of the breeding range. The European population of 26,000–39,000 pairs suffered a large decline during 1970–1990 (Tucker & Heath 1994), and has continued to decline during 1990–2000, particularly in the key populations in the former Soviet Union countries, with overall declines exceeding 30% in ten years (BirdLife International 2004). A national scale survey conducted in Ukraine in 2009, estimated an approximate decline of 23% compared to 1990–2000 (Kostenko, M. unpubl. report). Declines have been reported from eastern Siberia, where the species may have disappeared as a breeder from the Baikal region (Popov 2000). In Serbia, population size decreased while coupled with a concentration of breeding pairs to a smaller country-wide distribution (Purger 1996, 2008, Fehérvári *et al*. 2012, Barna 2015). However, populations in central Asia appear to be stable, with the species reported as common in suitable habitats in Kazakhstan (especially in forest-steppe zone with Rook colonies), and no evidence of any population declines (Bragin, E. pers. com.).

There is hardly any data available on how these population estimates were made, yet just like in the case of the Hungarian population estimates up to 2005, they most probably lack the specificity that surveying Red-footed Falcons necessitates. Therefore, in 2006 we designed a new survey protocol that takes into account the unique breeding biology of these falcons. The most important difference from other raptors in the region is that Red-footed Falcons are facultatively colonial. Colonies are predominantly formed in rookeries (Csörgey 1908, Horváth 1956, Purger & Tepavčević 1999), while other nest aggregations like magpie nest concentrations are rare (Végvári *et al*. 2001). The other form of colonial breeding is in artificial nest-box colonies. Monitoring the number of breeding pairs in an artificial colony is straightforward, however in case of rookeries it is challenging. Rook nests are often in the upper third of the canopy, making them difficult to access. Moreover, Red-footed Falcons are relatively late breeders (mean egg laying date: May 27th, n=1113 breeding attempts, period: 1995–2014), thus tree foliage limits visibility of nests in rookeries. This species is also unique in terms of time allocated into mate and nest-site choice. Birds arriving from the wintering grounds may take weeks to finalize settlement decisions (pers. obs.). Meanwhile, their behaviour greatly resembles that of stable pairs; they vigorously defend the chosen nest site from conspecifics, and often mate in the vicinity. However, pairs occupying a given nest cannot be considered as breeders, as they will often change location and/or partners during this period and thus, observers can overestimate the surveyed population. This problem is even more emphasized in the case of solitary pairs. A surveyor, monitoring various other raptors in an area may time field visits to maximize confirmed breeding of most species, however due to the relative late egg laying date of Red-footed Falcons, this period largely coincides with the pre-breeding period, when birds are still in the process of making settlement decisions.

A recent, and at that time surprising, discovery revealed that Red-footed Falcons may regularly use communal evening roost sites in large numbers in the post-breeding (pre-migratory) period (Borbáth & Zalai 2005). Since then an array of pre-migratory roost sites have been discovered in various countries along the breeding distribution (Kostenko 2009, Fehérvári *et al*. 2014). This behaviour presents a unique opportunity to monitor spatio-temporal phenology of a little known period in the life-cycle of-migrants (De Frutos *et al*. 2007, De Frutos & Olea 2008, De Frutos *et al*. 2010, Fehérvári *et al*. 2014).

In this study we describe a novel, species specific survey protocol that allows to monitor Red-footed Falcon breeding and pre-migratory population size and extent. We present results of the implemented survey focusing on recent trends.

Methods

Breeding population monitoring

The Red-footed Falcon monitoring protocol designed specifically for the species relies on three corner stones: a) timing of field visits, b) considering detection probability differences in colony types and c) spatial units have to be surveyed (2.5 km × 2.5 km UTM square).

We restricted the timing of field visits to monitor falcon breeding in an area to June-July, with at least 2 visits at a given UTM. If a solitary pair is located and breeding cannot be unequivocally confirmed (presence of eggs or nestlings) then at least two further visits have to be made in a minimum of 10 day intervals.

In case of colonial breeding two alternative methods can be applied; either counting adult birds at least twice within June-July (preferably timing it to early mornings or late afternoons) or inspecting (climbing or using mirrors) all nests with the same temporal criteria. The number of breeding pairs in the former case is the maximum number of birds counted in the two events divided by two. Age classes, adult and 2nd calendar year are easily distinguishable based on plumage characteristics (Forsman 1999). Although 2nd calendar year birds are known to breed, but they only constitute a fraction of the breeders. However, they may appear at colonies in relatively large numbers, flocks of up to 100 individuals are not uncommon in the breeding season. Therefore it is paramount to treat the two age groups separately to avoid overestimating the number of breeding pairs at a given colony. We also defined a new category, “occupying pair” to allow retrospect inference on population dynamics. All records that are based on a single observation within the given timeframe, or no other observations confirm breeding, are considered as occupying pairs. Data collection also entailed nest type (i.e. natural nest by building species and nest-box design), geographic location of solitary pairs and colony centers and all identified various threatening factors. Where possible participants also recorded clutch size (number of eggs layed) and the number of hatched and fledged nestlings. We considered a pair’s breeding successful if at least one nestling reached an age of 18 days (feathers covering the whole body).

Field work was carried out predominantly by the professional staff of National Park Directorates and members of nature conservation NGOs (60–120 people). Although we designed the protocol to provide presence-absence data, over 90% of UTM squares had breeding records. Presumably, most of the participants had previous local knowledge of the surveyed area, had preconceptions on potential breeding locations and the habitat preference of the birds. Moreover, Natura 2000 sites were considered as top priority in surveys of not only Red-footed Falcons but for various other species. These preconceptions and the lack of spatial robust design may in theory severely bias results. Detection probability of the species depends on breeding type, however even in case of solitary pairs the chance of false negative data within a UTM square is considered relatively rare. The birds are conspicuous throughout the breeding season, are often vocal and are less shy of humans than many sympatric raptor species. Moreover, the breeding is closely associated to grasslands that are in general of high conservation value in Hungary and are well known to local experts. Thus, it is unlikely that the results are severely underestimating the general spatial extent, or the number of pairs, however we cannot exclude that solitary pairs breeding in arable habitat dominated landscapes distant from other pairs were missed by the surveyors. Nonetheless we treated the data as presence only partial point count census (Fehérvári *et al*. 2012).

The described monitoring protocol was first implemented in 2006 and was rigorously used within the project duration of an international conservation program (2006–2009). In the following years, participants had to meet the requirements of various other protocols (Biotica database, RTM, organization requirements) when monitoring bird populations; meanwhile our design became volunteer based. Consequentially, the reporting willingness and protocol compliance suffered and became spatially heterogeneous. Nevertheless, certain elements became part of good practice, like differentiating between occupying and breeding pairs and the general timing of field inspections. Therefore, we consider the general population trends as reliable but with a certain error margin. Although, this error is arbitrarily identified, it is predominantly based on annual effects and considers the spatial bias in monitoring effort. A major deficiency is that the exact location of new colonies or solitary breeding sites is not reported from the majority of regions. Thus, the spatial extent of the population in 2010–2014 cannot be assessed with similar precision as in the 2006–2009 period. To avoid bias, we only report distribution patterns from this later period. We reduced spatial data resolution to a 10×10 km UTM grid to allow a more concise presentation of results.

Roost site counts

We surveyed the number of birds present on roost sites on a weekly basis from the second week of August to the first week of October in 2004–2014. All estimates at individual sites were made on the same day, simultaneously throughout the country, either by counting birds entering the roost during the evening, or by observing the birds leaving the roost the next morning. One of the most challenging tasks was to locate roost sites, as the birds typically appear in low light conditions, thus to locate the exact place the observer has to be within a couple of hundred meters. Moreover, as opposed to other gregarious falcons (Amur Falcons – *Falco amurensis* and Lesser Kestrels – *Falco naumanni*) in their wintering roost sites, Red-footed Falcons tend to remain silent prior to roosting (pers. obs.), further making pin-pointing the precise location difficult.

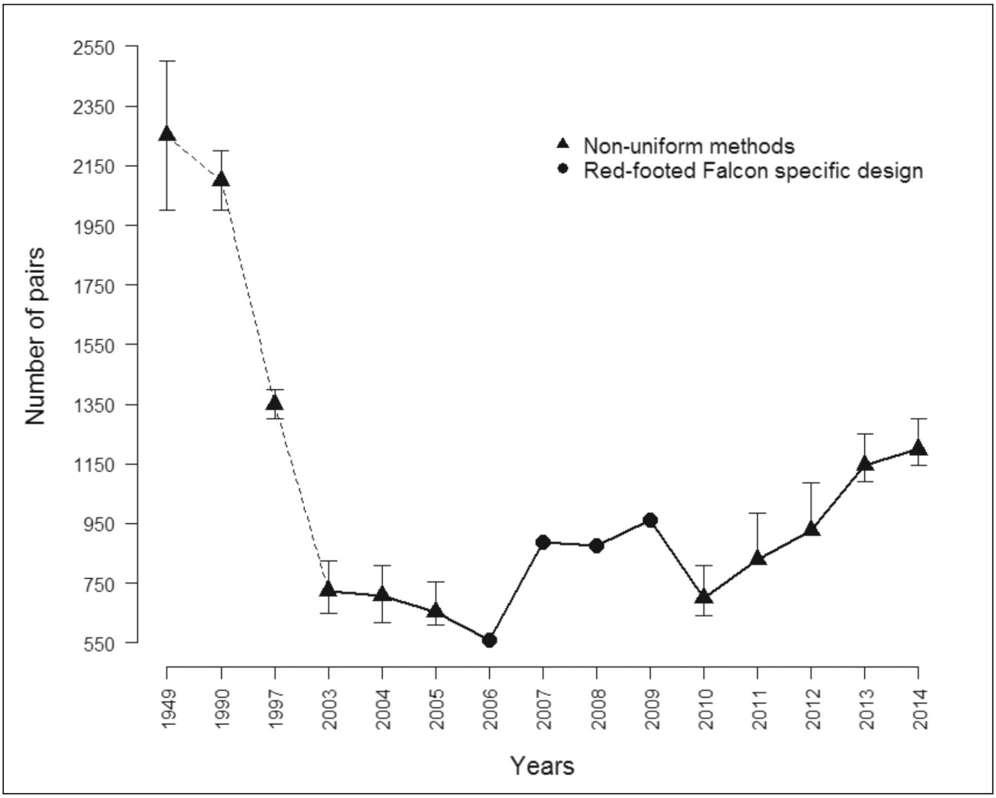

Figure 1. Population trend of Red-footed Falcons from 1949–2014. Whiskers show minimum – maximum reported estimates for a given year. In case of 2006–2009 we report the number of occupying pairs assessed via Red-footed Falcon specific survey protocol

1. ábra Kék vércse állománybecslések 1949 és 2014 között. A bajuszsávok a minimum – maximum becsléseket jelzik. 2006–2009 közötti periódusban a kék vércse specifikus monitoring protokoll szerint gyűjtött foglaló párok számát ábrázoltuk

Prior to the weekly counts, observers scanned their area to locate the roost sites in a given season. The most effective method proved to be taking advantage of the fact that the falcons will often travel directly in the direction of the roost site in low altitudes once the daily thermal activity has decreased. Typically, an observer would set out to scan the area of interest late in the afternoon, locate a group of resting individuals, and wait until they leave their location. Once the flight direction is identified, the observers would try and chase the birds and scan for other individuals that may be arriving. Experience and detailed knowledge of the area in question is important as the time period between birds starting to fly at low altitudes and sunset is relatively short. Once a roost is located, the birds tend to use the location within a season, making it possible to reliably estimate the number of birds present.

We categorized roost sites as traditional if birds have used the exact same location (i.e. the same small group of trees or bushes) in at least 3 years of the 10 year study period. All other locations roosts were considered temporary.

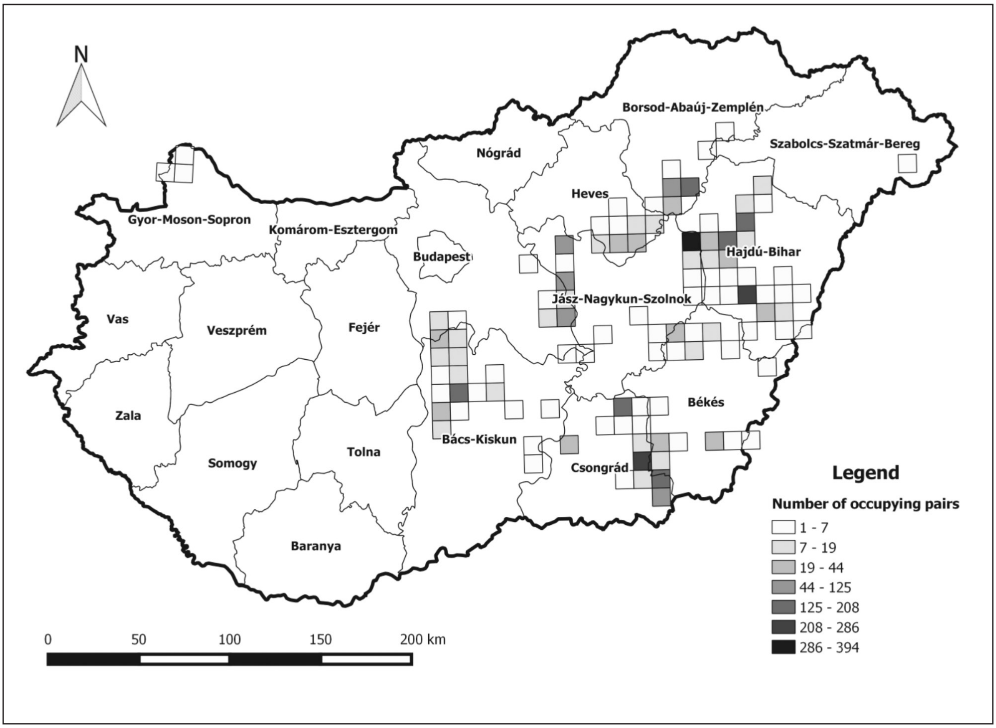

Figure 2. Spatial distribution of Red-footed Falcon occupying pairs in 2006–2009. The results are shown on a 10×10 km UTM grid

2. ábra A 2006–2009 közötti megfigyelt kék vércse foglaló párok számának térbeli eloszlása. Az adatokat 10×10 km-es UTM négyzetekben ábrázoltuk

Results

Breeding population trends

The Red-footed Falcon population suffered a dramatic over 50% decline compared to estimates in the 1940s and early ’90s *(Figure 1)*. The lowest estimated number of occupying pairs was in 2006 when only 558 occupying pairs were identified in Hungary. The following years produced a fluctuating increase, and by 2014 the estimated breeding population was 1200 pairs.

Breeding population structure and extent in 2006-2009

Altogether we recorded 3283 occupying pairs in 105, 10×10 km UTM squares within the study period of 2006–2009 *(Figure 2)*. Apart from a few pairs in north-western Hungary, the distribution is concentrated to the south-eastern lowland regions *(Figure 2)*. Despite the relative widespread distribution pattern, the population is concentrated to a handful of large clusters as 65% of all observed pairs were found in just 10 UTM squares. The proportion of pairs occupying nest-boxes increased significantly (Fisher’s exact test: $p<<0.001$) *(Figure 3a)* and so did the number of colonial pairs (Fisher’s exact test:

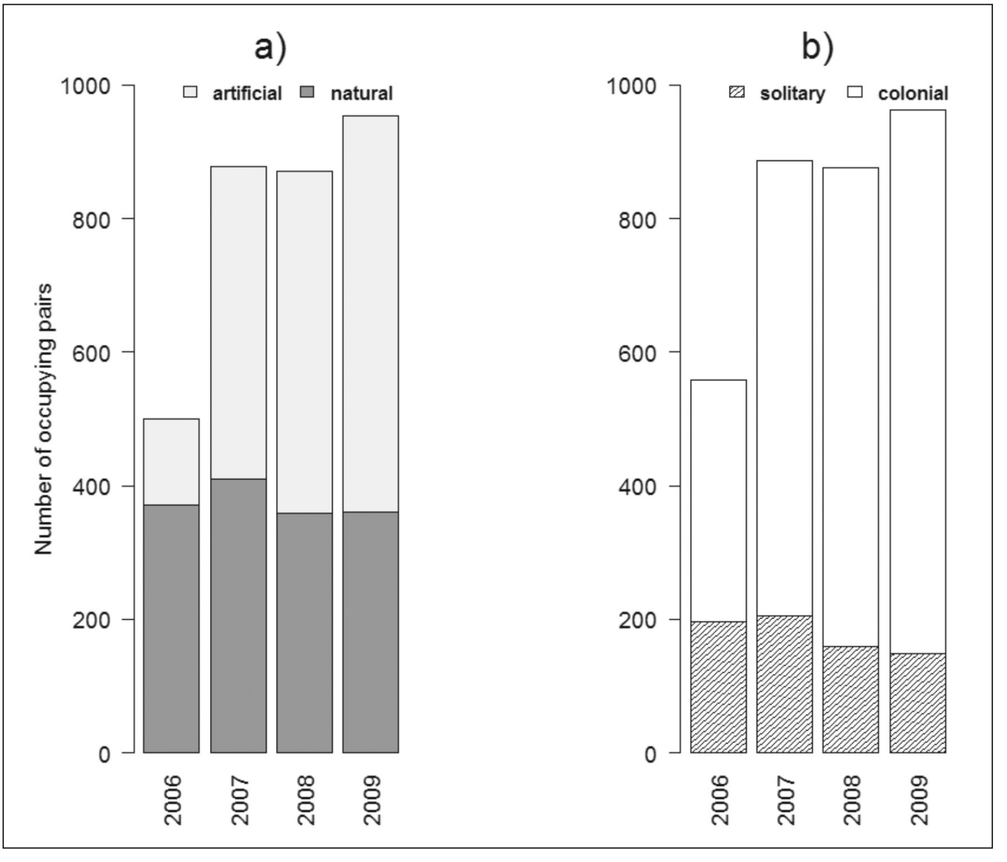

Figure 3. The number of occupying pairs in a) natural vs artificial nests and b) the ratio of solitary vs. colonial pairs in 2006–2009

3. ábra A foglaló kék vércse párok száma a) mesterséges és természetes fészkekben, illetve b) telepes és szoliter párok aránya a 2006–2009 között

p<<0.001) (*Figure 3b).* The ratio of occupying pairs was considerable in the surveyed population and ranged from 17% to 7% decreasing gradually during these 4 years.

Roost sites

We found a total of 105 roost sites, out of which 33 were traditional during the 10 years of the study period. All located roost sites were found within the current breeding range, relatively far from human settlements. The larger traditional roost sites were located close to the centre of the distribution range. The single largest number of birds found was 2000 individuals in the second week of September 2014, near Dévaványa (northern Békés County). Traditional roost sites not necessarily formed in the vicinity of a dense breeding area, in fact the largest ones were in areas with no, or few breeding pairs (*Figure 1)* (northern Békés, southern Heves and north-western Jász-Nagykun-Szolnok Counties). Small scale (i.e. within a 2–3 km) inter-annual roost site displacement was not uncommon. For instance, the roost site in southern Heves County is surrounded by 3 other alternative sites (0.25–2 kms from the

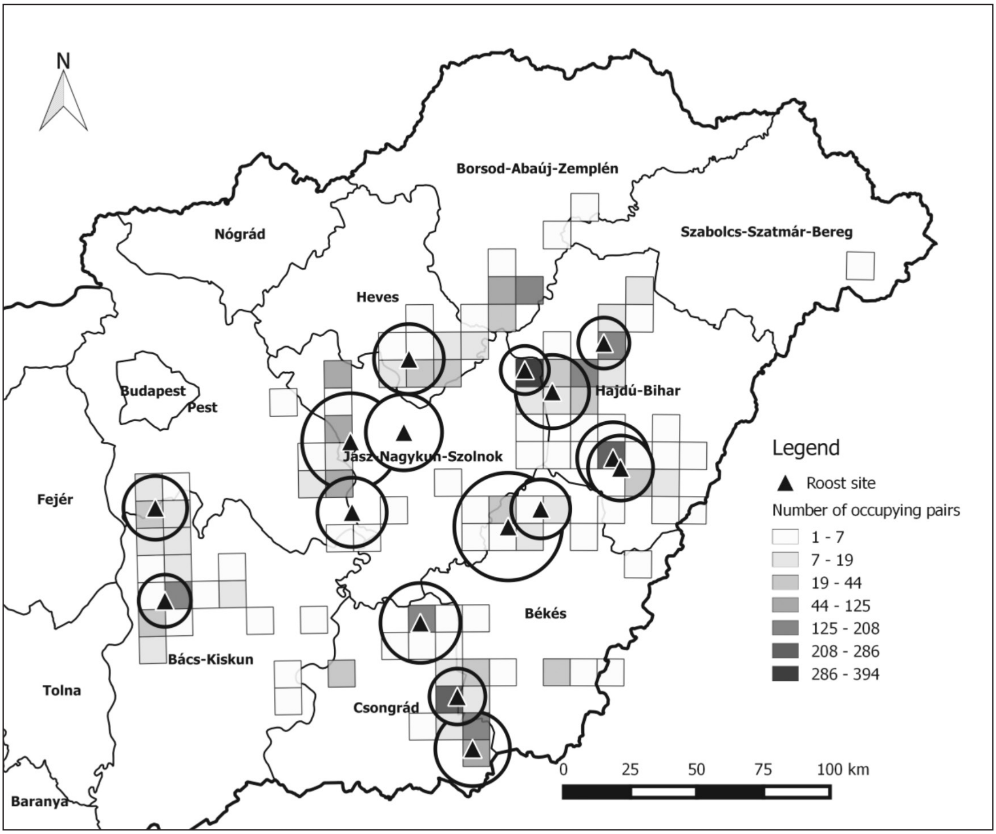

Figure 4. The location of traditional Red-footed Falcon roost sites (i.e. used at least in three years of the study period) where the maximum number of birds reached 400 birds at least once in 2004–2014. The circles around coordinates are proportional to the maximum number of birds observed. The figure depicts two distinct traditional roost sites, 1) formed in areas with high breeding density and 2) roosts formed in areas with no or low breeding density. The three largest roosts are of this later type

4. ábra A tradicionális (a kutatási időszakban legalább 3 évben használt) kék vércse gyülekezőhelyek térbeli elhelyezkedése. Azokat a gyülekező helyeket ábrázoltuk, amelyeken legalább egyszer 400 vagy annál több madarat becsültek. A gyülekezők körüli körök arányosak a maximális megfigyelt példányszámmal. Az ábra alapján két tradicionális gyülekezőhely típust lehet elkülöníteni, 1) amelyek sűrű költőállomány közvetlen közelében alakulnak ki, 2) amelyek a sűrű költő területektől távol találhatók. Az utóbbi típusba tartozik a 3 legnagyobb példányszámot magába foglaló gyülekezőhely

depicted location see *Figure 4*) that the birds have used within the study period. In case of the larger roosts formed in areas with high breeding density, the birds quite often use one of the colonies as roosting sites.

The number of birds gradually increases at roost sites within the pre-migration period up until the second week of September. In the following weeks, the numbers drastically decline, with only a small fraction of the observed birds remaining in the first week of October *(Figure 5, Figure 6)*. In certain years, the weekly increase of the number birds is not gradual. For instance in

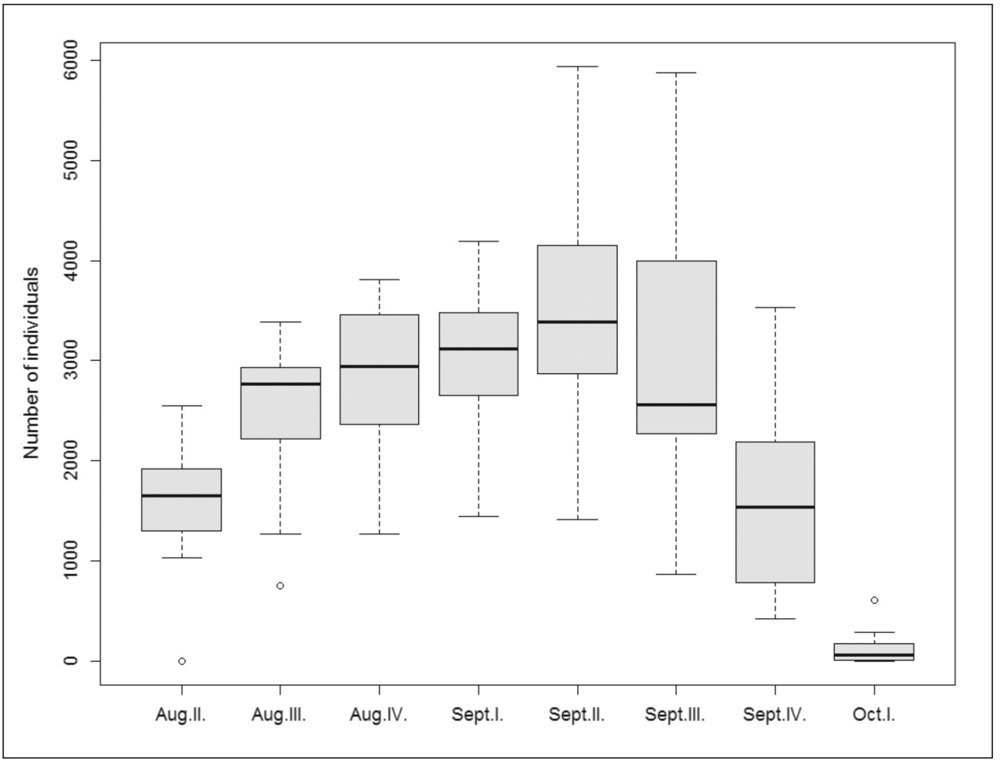

Figure 5. Boxplots of the number of Red-footed Falcons estimated at all roost sites by week of the year in 2004–2014. There is a gradual build up in the number of birds until mid-September, afterwards a steep decline can be observed, with the majority of falcons leaving the roosts within two weeks

5. ábra A gyülekezőhelyeken becsült kék vércsék száma heti bontásban. Graduális növekedés figyelhető meg egészen szeptember közepéig, amikor is a vércsék száma rohamosan fogyni kezd. Szeptember 2. hetét követően a vércsék nagy része 2 hét alatt elhagyja a gyülekezőhelyeket

2009, the maximum number of birds counted showed a peak compared to previous years, however this was caused by a drastic increase in counted birds during the second week of September *(Figure 6)*.

The overall estimated maximum number of roosting birds fluctuated considerably during the study period *(Figure 6)*. This fluctuation however does not correlate significantly with the annual number of breeding pairs (Spearman's rank correlation: S= -122670, δ=-0.08, p=0.45) *(Figure 7)*. We found no evidence of change in the mean number of birds roosting within the country during the study period (linear regression: effect of year=-14.33, SE=47.05, t-value=-0.3, p-value=0.76).

Discussion

Breeding population

Our results show that the considerably declining breeding population reached a minimum in 2006, when only 558 occupying

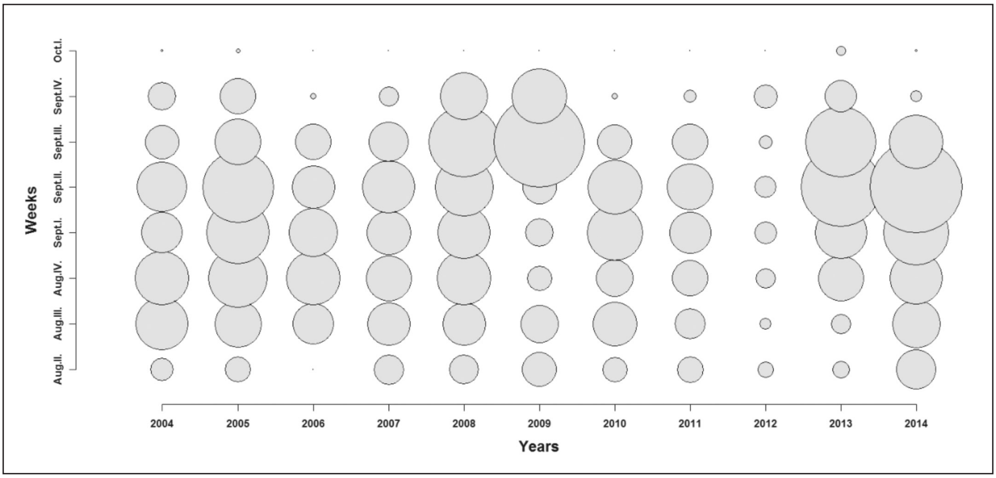

Figure 6. The weekly number of Red-footed Falcons observed during the study period. The area of the circles are proportional to the number of estimated individuals

6. ábra A vizsgált időszakban a gyülekezőhelyeken hetente becsült kék vércse egyedszámok. A körök mérete arányos az összes példányszámmal

pairs were known from Hungary. Considering the fact that single colonies had this order of magnitude pairs in the 1930s and '40s (Schenk 1934, Horváth 1956, Keve & Szijj 1957), this result was indeed alarming. The large scale nest-box programme initiated in the same year, immediately started showing results and gradually increased the number of breeding pairs, while also shifting emphasis on artificial breeding sites. This increase in the whole population simultaneously affected the ratio of colonial and solitary pairs. While the number of colonial pairs breeding in artificial colonies drastically increased, the number of solitary pairs remained relatively constant in 2006–2009. This is largely due to the fact that nest-boxes were placed out predominantly as to mimic rookeries. However, it is yet unclear why a considerable proportion of the Red-footed Falcon pairs choose solitary breeding and that what effect does this altered ratio have an effect on the viability of this population. From a conservation perspective, large aggregation of birds to a small location increases the importance of localized threatening factors. For instance localized pollution sources, disturbance or predation can have detrimental effect on sizeable proportion of the whole population (e.g. Eeva *et al.* 2012). Thus, at least in areas where the density of natural nests is low, supplementing nest-boxes for solitary pairs has to be considered to help dilute local effects. The fact that by 2014 the population increased by approx. 100% and nearly two thirds of the falcons (25–35% of the whole EU population) used nest-boxes for breeding shows how limiting the lack of rookeries was. However, nest-boxes, regardless of materials used, wear of and thus need constant maintenance. This conservation dependency of the bulk of the population causes a previously unanticipated potential threat. Nest-box maintenance is resource consuming and necessitates a continuous effort from conservationists and stakeholders (Palatitz *et al*. 2009). Although we have no exact data on the expected lifetime of the boxes used, but even if it is over 15 years, the majority

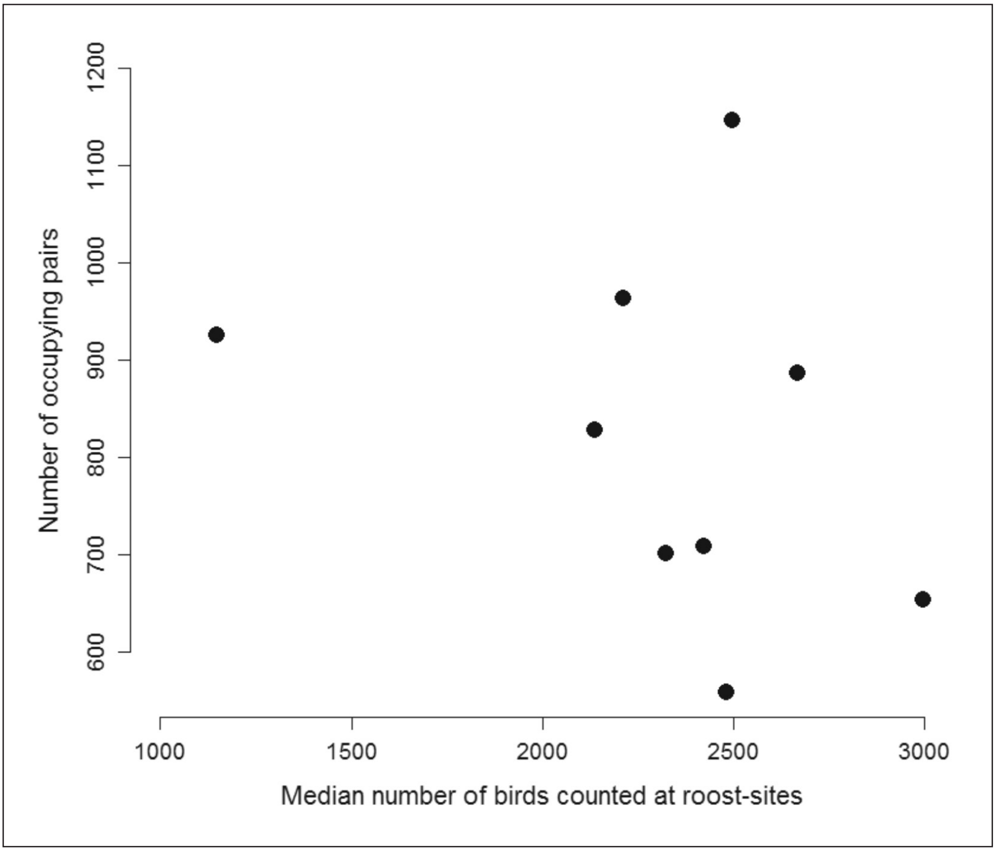

Figure 7. The median number of birds counted at roost sites as a function of the estimated number of breeding pairs in 2004–2014. There is no significant relationship between the two parameters

7. ábra A gyülekezőhelyeken számolt madarak éves mediánja és a becsült foglaló párok száma 2004–2014 között. A két érték között nem volt kimutatható összefüggés

of the now used nests have to be replaced in the following years. If funding is limited or is only regionally distributed, the population size and breeding extent can yet again drastically change in the near future. Artificial colonies, despite their lack of self-sustainability have a clear advantage over rookeries, as their location can be freely chosen given that the surrounding habitats are suitable. Indeed, the majority of artificial colonies today are located in protected areas, reducing potential direct human related threats like illegal felling of nest-box holding trees or disturbance. Rookeries on the other hand, despite the protected status of Rooks, are still subjected to various forms of direct human induced threats. Resolving this conflict is important and initiations have been already implemented (Solt 2008, Horváth *et al*. 2015), however it is unlikely that law enforcement alone can ensure the viability of the Rook population. Changing the reputation of rooks in the local communities is time consuming and is unlikely to occur in the near future. Presumably, the most successful approach for Red-footed Falcon conservation efforts is to simultaneously manage risks associated with both natural and artificial breeding types and to gradually allocate resources to better understanding of factors limiting the re-expansion of rookeries to natural breeding habitats.

Roost sites

Our results show that the large scale spatial distribution of roost sites is within the current breeding range. However, the fact that some of the largest traditional roosts are in areas with low breeding densities suggests that habitat requirements in the pre-migration period may be somewhat different. A previous study on diet and foraging habitat use of birds around a single roost site showed that there may be considerable dietary shift compared to that in the breeding period, with small (<1 cm) insects being the most abundant prey items in the pre-migratory period. Moreover, the birds showed less articulated preference for habitat types as in the breeding period (Széles 2011). These two factors may suggest that the birds shift emphasis to aerial feeding in the pre-migratory period. When analysing the habitat composition of the vicinity of roost sites, we failed to establish models with high predictive power (Széles 2013), while the same was feasible for breeding sites (Fehérvári *et al*. 2009, 2012). The fact that two traditional roost site types can be differentiated based on the breeding density suggests that alternative strategies may exist. Individuals either utilize an alternative roost or only return to a given roost once during the day, as opposed to the breeding period when numerous foraging bouts are made within a day (Palatitz *et al*. 2011, Palatitz *et al*. 2015). This liberates time to allocate into searching resources or other activities, thus the extent of potential habitat use may be orders of magnitude larger than that during breeding (Fehérvári *et al*. 2014). Correlative evidence suggests that the density of larger prey items like voles may be lower around colonies with the progress of the breeding season (Palatitz 2015). Once the juveniles have fledged and individuals are less constrained to a single location the birds may decide to either remain in the vicinity of the breeding grounds and join roosts there or leave to distant areas with lower breeding densities where traditional roost sites are available. In the former case, the advantage might be local knowledge of the surrounding foraging area with the constraint of potential lower prey densities depleted during breeding in the direct vicinity, while roosts with low breeding densities may have higher prey densities or are close to other food sources that are less available or sufficient during or for breeding.

The within season phenology of the cumulative number of birds at roosts shows that after a steady increase in the first 5 weeks (mid-August to mid-September) the majority of the birds leave the area within two weeks. In case of non-gregarious species that migrate individually autumn migration phenology typically follows a normal distribution like pattern (Knudsen *et al*. 2007), however in case of Red-footed Falcons this difference may indicate synchronized individual decisions on timing of migration initiation.

We found large inter annual fluctuation in peak number of falcons that is apparently independent from the number of breeding pairs. It is possible that product of mean reproductive output and the number of breeding pairs would show a higher correlation however, data is insufficient to precisely estimate country-wide breeding success for the whole study period. Nonetheless, our results may indicate that the number of falcons observed during the pre-migration period is not intimately linked to local breeding. Indeed, satellite tagged birds showed that individual decisions on roost site choice are made on a much larger spatial extent than the area of this study (Fehérvári *et al.* 2014). These tagged birds used roost sites in southern Ukraine and eastern Romania, and it is plausible to assume that birds breeding in that area may just as well appear within the Carpathian Basin. For instance, in 2009 the number of individuals peaked a week later than in other years, and the observed number of birds was much higher than expected based on the trend observed in previous weeks of the same year. It is possible that this unexpected result was a massive influx of birds from more eastern regions and that either local prey availability or weather drove these birds to the monitored roost sites.

Recommendations

One of the identified problems is that the developed monitoring protocol is less effective when carried out on a voluntary basis. Therefore, we propose a modification that may allow to assess precise temporal changes in the whole population, while considering bias in survey efforts by participants. As an alternative to conducting annual countrywide complete census point counts, we recommend the designation of at least four 10×10 km UTM sampling units distributed along the major axes of the breeding range. For instance, a sampling unit in the north-eastern region (Hortobágy), in the western region (Kiskunság), central (Jász-Nagykun-Szolnok and Heves Counties) and in the southern regions (see Kotymán *et al.* 2015) would probably cover major spatial effect deviations within the breeding range. The complete protocol would be necessary to be implemented annually, and with constant effort within these units. The results obtained would allow for estimating inter-annual effects and major temporal trends, while regionally reducing the allocated resources into monitoring efforts. To assess spatio-temporal changes we propose that a country-wide large scale census should be carried out every 5 years. The protocol for this census can be that one described here with the modification of recording absence data in surveyed UTM squares. Meanwhile future research should concentrate on assessing detection probability of solitary pairs depending on habitat structure.

Nonetheless, it is paramount to continue annually monitoring areas with large aggregation of breeding birds to ensure early detection of localised threatening factors. However, if our recommendations are considered, there is no need to evaluate the number of pairs, their breeding success and various other parameters that are time and energy consuming to acquire in all of these locations.

In case of roost sites, we emphasize the importance of carrying on with annual surveys as they not only provide intriguing results but are inherently helping the protection of roost sites. Weekly presence of surveyors helps ensuring the protection of the birds, and may contribute to early detection of localized threatening factors.

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History and current status of Red-footed Falcon population size and conservation activities in Voivodina

Krisztián Barna

Krisztián Barna 2015. History and current status of Red-footed Falcon population size and conservation activities in Voivodina. – Ornis Hungarica 23(1): 94–100.

Abstract The Red-footed Falcon population in Voivodina shows a considerable decrease on a large temporal scale, however due to recent conservation measures, it seems to be stable in the past six years. Here I present the history of population estimates and results of partial surveys that have been carried out since 1909. I also show the details and results of conservation efforts recently implemented in the region. Recovery records of individually colour ringed birds indicate that the population breeding in northern Serbia is an integral part of the Carpathian Basin population and thus conservation management should be coordinated within a framework of international cooperation.

Keywords: survey, colour ring, nest-box, Serbia, *Falco vespertinus*

Összefoglalás A vajdasági kék vércse állomány jelentős csökkenést mutat nagy időbeli skálán, azonban, köszönhetően az elmúlt néhány év védelmi intézkedésének, ez a tendencia megállni látszik. Röviden bemutatom az elmúlt közel száz év részletes eredményeit és a közelmúlt természetvédelmi intézkedéseit, amelyek feltehetően segítették megállítani az állománycsökkenést. Színes gyűrűs kék vércse megkerülési adatokkal demonstrálom, hogy a vajdasági költő állomány szerves része a kárpát-medencei állománynak, és így hatékony és hosszú távon sikeres védelme csak nemzetközi együttműködés keretében valósulhat meg.

Kulcsszavak: felmérés, színes gyűrű, költő láda, Szerbia, *Falco vespertinus*

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Introduction

Red-footed Falcons *(Falco vespertinus)* sparked the interest of ornithologists in Serbia as early as the beginning of the 20th century. This attention can partially be attributed to the connection between Red-footed Falcons and Rooks *(Corvus frugilegus)*, the latter being widespread and having large colonies at the time in Voivodina (Tucakov *et al.* 2010). Despite the attention, we only have sporadic data on the distribution and population size of Red-footed Falcons from that time. It was probably a scarce to rare breeder; larger number of birds was typically observed prior to autumn migration (Dimitrijević 1980). The first confirmed breeding data derive from the vicinity Aleksa Šantić (Babapuszta), where Red-footed Falcons were recorded to nest on the Fernbach estate in 1909 (Fernbach 1912). This small colony existed until 1981, when a large storm destroyed it, making it one of the longest operating Red-footed Falcon colony to date (Fülöp & Szlivka 1988). Richárd Csornai took on the survey of Red-footed Fal-

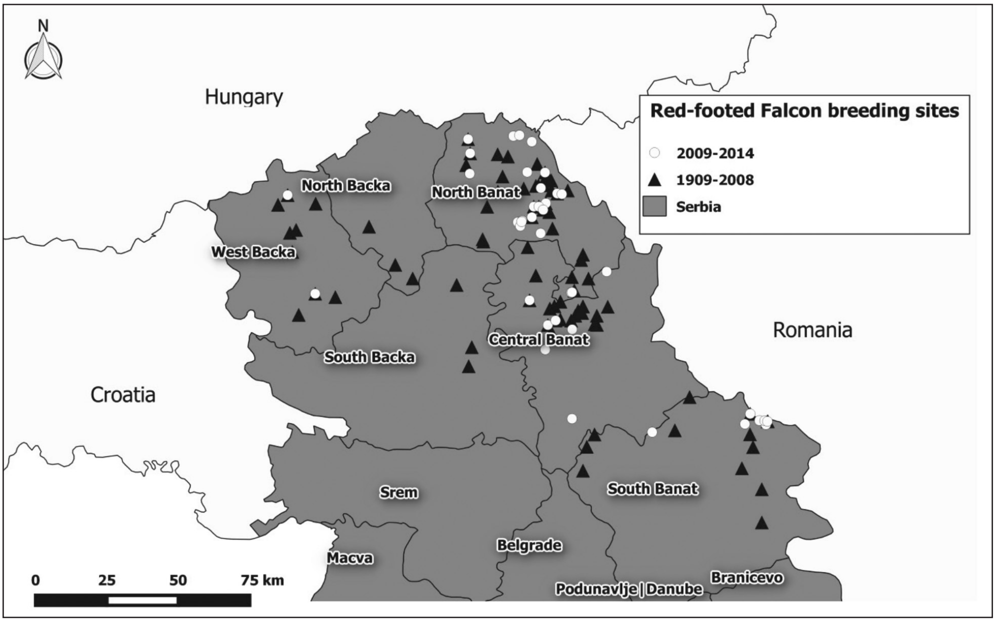

Figure 1. Spatial distribution of the historic and current Red-footed Falcon breeding sites in Voivodina (partially based on the data of Purger 1996, 2008, Žuljević 1998, Đapić 2002). Today, the majority of the population can be found in North and Central Banat

1. ábra A historikus és a jelenlegi ismert kék vércse költőhelyek elhelyezkedése a Vajdaságban (részben Purger 1996, 2008, Žuljević 1998, Đapić 2002 alapján). A populáció jelentős része ma Észak és Közép-Bánátban található

cons from the 1930s (Király 1993), confirming breeding near Senta (over 100 pairs) and Kanjiža (Magyarkanizsa, approx. 50 pairs) in rookeries found in riparian forests along the River Tisza (Gergelj *et al*. 2000). Mikuska (Gergelj & Šite 1989, Gergelj & Šoti 1990, Gergelj *et al.* 2002) regularly observed the species at the Kapetanski rit (Kapitány rét) in the 1960s indicating the probability of Red-footed Falcons breeding in nearby rookeries. Furthermore, Red-footed Falcons were known to breed in south-east Serbia (Šumadija area), near Negotini (Matvejev & Vasić 1973). However, the breeding distribution soon was only restricted to Voivodina. A survey of raptors in Voivodina carried out in 1977–1996 showed that the species was present in 64 UTM squares, and breeding was confirmed in 46 of these. The bulk of the population was found along the river Tisza in northern parts of Banat County. The surveying team concluded that despite probable large inter-annual fluctuations, the population is stable or even slightly increasing and expanding its range (Ham & Rašajski 2000). A specific survey of Voivodina conducted to map Red-footed Falcon colonies recorded 308 pairs in 1990, while only 128 in 1991 (Purger 1995, 1996, Purger & Mužinić 1997). Repeating the survey after 10 years revealed a total of 116 pairs in 2000 and 61 pairs in 2001 (Purger 2008). In agreement with these findings, our previous survey suggests that a drastic population collapse occurred in the 1988–2003 period (Puzović *et al*. 2003). Central Banat County had an estimated 150–200 breeding pairs in the '90s, however only 20–30 pairs

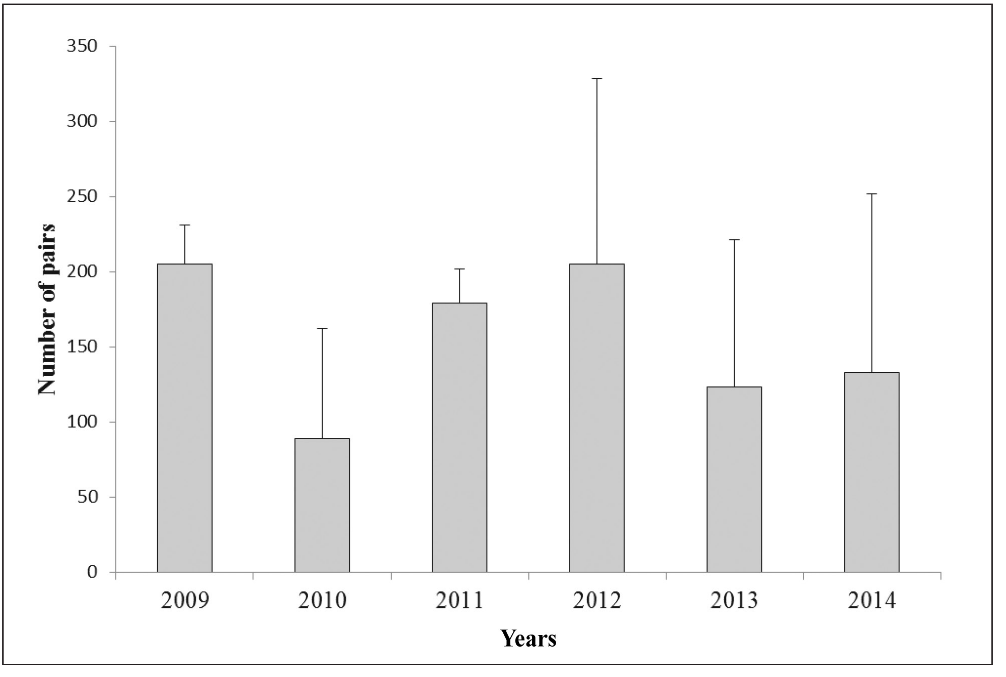

Figure 2. Number of observed (bars) and estimated (whiskers) Red-footed Falcon breeding pairs in Voivodina. Large inter-annual fluctuations occur in the breeding population size

2. ábra A megfigyelt (oszlopok) és a becsült (vonal) kék vércse párok száma a Vajdaságban. A párok számában nagymértékű évek közötti ingadozás figyelhető meg

were present a decade later (Gergelj 2003). The most apparent decrease was observed in the northern Banat, the once stronghold of this species. The number of breeding pairs decreased considerably at the large breeding colonies such as near Jazovo (Hódegyháza), Crna Bara (Feketető) and Banatski Monoštor (Kanizsamonostor) (Ružić *et al.* 2009). In some cases complete colonies disappeared (Gergelj 2003).

In general, based on the above described sporadic data, the population substantially decreased both in numbers and in breeding range *(Figure 1)* in the past 20 years in Voivodina. Sparked by the negative tendency, recent Red-footed Falcon conservation facilitated efforts through reorganizing monitoring activities and active conservation measures in the region. Here we describe the results and activities carried out in these new initiations.

Establishing artificial colonies

Several thousand rook pairs are still breeding in Voivodina, thus, in theory nest site shortage is not a limiting factor for the Red-footed Falcon population. However, as in Hungary, the frequency of rookeries shifting to urban settlements is increasing (Fehérvári *et al.* 2009), making active conservation measures necessary to maintain the falcon population. We have erected over 350 nest-boxes in various locations, primarily choosing sites that had historic breeding records, or were pin-pointed by landscape scale habitat modelling as suitable breeding

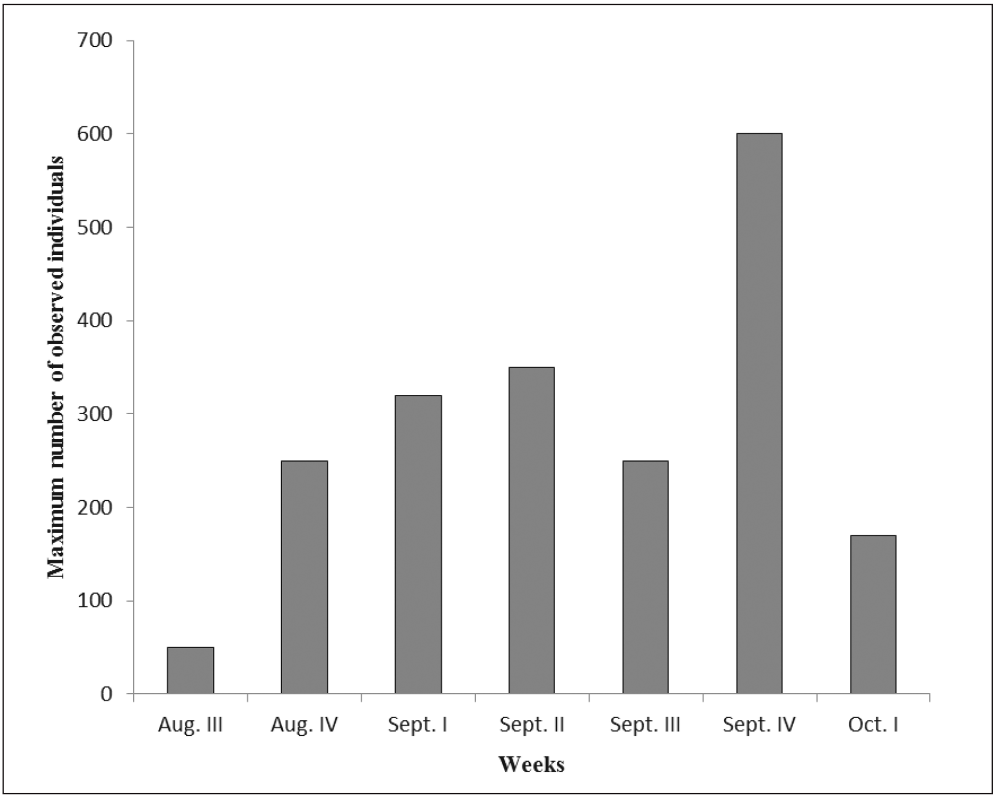

Figure 3. Maximum number of counted birds of weekly surveys carried out at the Mokrin pre-migration roost-site between 2010–2012

3. ábra A maximum kék vércse egyedszám a mokrini kék vércse gyülekezőn 2010–2012 között

sites (Fehérvári *et al.* 2012). Predominantly we used 2 nest-box designs; 1) the box most often used in Hungary (see Kotymán *et al.* 2015): 2.C.B. box, and 2) a relatively large box that in shape resembles the previous type, however with approx. twice the base area and with multiple openings (Tucakov nest-box). Our observations suggest that occupancy rate is similar in the first two box types.

Monitoring activities

We carried out several partial surveys on Red-footed Falcons since 2009 to locate breeding pairs and potential suitable habitats for artificial colonies *(Figure 1)*. Our results reflect high inter-annual fluctuations; however, the population seemed to be overall stable between 2009–2014 *(Figure 2)*. The mean number of observed breeding pairs was 156 ± 47 SD. One of our intriguing findings was that we recorded a small colony (4 pairs, near Jazovo) breeding in natural tree cavities. Csornai (Gergelj 2003) reported that Red-footed Falcons used willow tree cavities on the edges of riparian forests along the River Tisza. We believe that this type of breeding was not uncommon prior to river and forestry control measures along the rivers, when sufficient number of

Birds ringed in Voivodina and recovered elswhere				
Year of ringing	**Year of recovery**	**Place of ringing**	**Place of recovery**	**Type of recovery**
2011	2014	Vrbica (Egyházaskér)	Békéssámson, Hungary	Re-sighted as a breeding individual
2011	2012	Padej (Padé)	Sagu-Hunedoara Timisana, Romania	Re-sighted
2012	2013	Jazovo (Hódegyháza)	Görbeháza, Hungary	Re-sighted as a breeding individual
2011	2011	Vrbica (Egyházaskér)	Kosice, Slovakia	Re-sighted
Birds ringed in foreign countries and recovered in Voivodina				
Year of ringing	**Year of recovery**	**Place of ringing**	**Place of recovery**	**Type of recovery**
2009	2011	Királyhegyes, Hungary	Stanišić (Őrszállás)	Re-sighted as a breeding individual
2011	2014	Sanmartin, Romania	Margita	Re-trapped at the colony
2011	2014	Mezőcsát, Hungary	Vrbica (Egyházaskér)	Re-sighted as a breeding individual
2008	2012	Tiszafüred, Hungary	Mokrin	Re-sighted at roost site
2008	2011	Jászboldogháza, Hungary	Mokrin	Re-sighted at roost site

Table 1. Foreign recoveries of ringed Red-footed Falcons in Voivodina and recovered individuals ringed in elsewhere

1. táblázat Külföldön gyűrűzött és a Vajdaságban megkerült kék vércsék adatai

hollow trees was present. Our monitoring work also discovered the first pre-migration roost site (Fehérvári *et al.* 2014, Palatitz *et al.* 2015) in Serbia, near Mokrin (Agošton 2009, Gergelj *et al.* 2012). Coordinating with the Hungarian annual roost-sites surveys (Palatitz *et al*. 2015) we counted the number of roosting birds in 2010–2012 *(Figure 3)*. In 2013 the birds did not use this site for roosting, and we had no information on other alternative sites in Serbia in that year. In 2014 we discovered a new site near Kanjiža (Magyarkanizsa) where a total of 700 individuals were observed to roost in a small forest-patch at Kapetanski rit (Kapitány rét) on 2015.09.03.

Ringing

Individual marking of Red-footed Falcons has a long history in Voivodina. The first documented records of nestlings ringed derive from 1909, when Mrs. Károly Fernbach marked birds breeding in the colonies found within their estate near Aleksa Šantić. A total of 295 individuals were ringed in the period 1909–1932 (Schenk 1935, Matvejev 1938, Keve and Szijj 1957). Furthermore, Keve & Szijj (1957) estimate 450 ringed individuals between 1933 and 1945; however, only a small proportion of the data survived the Second World War. For instance Richárd Csornai ringed a total 71 clutches and a few adults (277 individuals) from 1933 to 1937 (Csornai 1952). Additional 164 birds were ringed until 1990 in the former Yugoslavia. Ringing was carried out within the scope of the Belgrade Ringing Centre, after the Yugoslav war in the early '90s. Since then a total of 441 individuals were ringed. We started ringing birds with individual coded colour rings in 2010, and since then over 300 individuals received these read-rings. Ring recovery data is available from 2009–2014. We have records of 5 foreign recoveries from Voivodina *(Table 1)*, all birds found in the breeding period within the Carpathian Basin. These records indicate that the Red-footed Falcon population breeding in Voivodina is an integral part of the Carpathian Basin population, and as such successful conservation of the species can only be achieved if stakeholders and professionals closely cooperate in all countries within this region.

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