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A case study on the phylogeny and conservation of Saker Falcon

Krisztián Pomichal[1]*, Balázs Vági[2] & Tibor Csörgő[1]

Abstract The Saker Falcon is a falconid raptor species with Palearctic distribution. It has never been a common bird in Hungary, now there are cc. 220–230 nesting pairs within the country borders. Currently total world population is cc. 19 000–34 000 individuals. Its taxonomic status is complicated. Two subspecies are distinguished (*Falco c. cherrug* and *Falco c. milvipes*); however, molecular data does not support this split. Phylogeny of the species is also not clarified, similarly to closely related raptors. There are many factors threatening the population of the Saker. One of these factors is the occurrence of the hybrid falcons. By molecular investigations more data can be gained, that could be useful in practical conservation, too.

Összefoglalás A kerecsensólyom a sólyomfélék családjába tartozó, palearktikus elterjedésű faj. Magyarországon sosem volt gyakori madár, jelenleg 220–230 pár fészkelhet az országban. A világállomány körülbelül 19 000–34 000 párt tesz ki. A faj taxonómiája nagyon összetett. Jelenleg két alfaját különböztetik meg, molekuláris bizonyítékok azonban nem támasztják alá ezt a felosztást. A faj leszármazási vonala szintén nem tisztázott, ugyanúgy, ahogy a legközelebbi rokon fajoké sem. Számos tényező veszélyeztetei a faj állományait, ezek közül az egyik legfenyegetőbb a hibrid madarak problematikája. A molekuláris vizsgálatok segítségével olyan ismeretek szerezhetőek, melyek haszonnal alkalmazhatóak a gyakorlati természetvédelemben is.

[1] *Department of Anatomy, Cell- and Developmental Biology, Eötvös Loránd University,*
1117 Budapest, Pázmány Péter sétány 1/c, Hungary, e-mail: krisztian.pomichal@gmail.com
[2] *MTA-ATK-NÖVI Lendület Evolutionary Ecology Research Group, 1022 Budapest, Herman Ottó út 15., Hungary*
*corresponding author

Molecular approaches have been gaining increasing importance in every field of biology in the last 60 years since the description of the molecular structure of the DNA. Investigations on nuclear and mitochondrial genomes yielded significant knowledge in several streams of biology, which questioned the relevance of traditional taxonomic categories and this way affected other research fields as well, e.g. practical nature conservation.

On one hand, clarifying taxonomic status and relations of recent species could be fascinating, on the other hand new results may challenge widely accepted taxonomy,

e.g. previously undivided world populations could be split into two or more species. This could change conservation categories when marginal or isolated subpopulations which comprise only a fraction of the world population turn out to be separate species.

Certain species may have evolved by hybridization and this could be important not only on a theoretical base but it could have practical implications as well. In practice of the last decades new hybrids of greater size, robustness and superior hunting skills have been created between falconid species. It is dubious whether these hybrids escaping

to the wild can reproduce with wild specimens; whether they are capable of creating viable offspring, and if so how they affect the gene pool of wild populations.

It is also problematic that there is different legislation affecting trade in hybrids originating from breeding stocks. This poses a threat that captured wild specimens can be traded as hybrids to thwart regulations. Here, we present a case study of such problematic on the Saker Falcon.

Distribution and population size

The Saker Falcon (*Falco cherrug* Gray, 1834) is a palearctic species belonging to the falconid family (Falconidae). The western border of its distribution area is in Central Europe, while its eastern border is near the Amur River (Ragyov *et al*. 2010). The total area of its nesting range and habitats is cc. 10 300 square kilometres (BirdLife International 2012). The world population of the species is decreasing in its whole range, the loss was 32% according to 1991–2010 estimation means (the exact value should be somewhere between 30 and 49 percent). Currently total world population of the species is cc. 19 200–34 000 individuals (BirdLife International 2012), but there are also world population size estimates of 7200–8520 individuals from the year of 2003 (Bagyura *et al*. 2007).

Saker Falcon has never been a common bird in Hungary; but in the 1970s its population reached a critical state. At the beginning of the following decade only 8 breeding attempts were recorded in the 13 known territories. Two of them were successful with 2-2 fledged juveniles. In 1980 the population on country level have not been more than 30 pairs (Bagyura *et al*. 2004). The main cause

of this was that time common nest looting which concerned mainly nests built on cliffs. In several cases nesting failure was caused by human disturbance, and in certain occasion illegal shooting also happened. The species has been preserved due to enormous efforts of nature conservation experts. In 22 years the population grew from 8 breeding pairs to 113–145 pairs (Bagyura *et al*. 2004). According to latest reports the Hungarian populations can be estimated 220–230 pairs (Bagyura *et al*. 2012).

Taxonomy of the Saker Falcon

The Saker Falcon was described by the British zoologist John Edward Gray in Hardwicke's book Illustrations of Indian Zoology in 1834. The description was made on a young raptor wintering in India. As researchers were not aware of its complete distribution area, the Saker was described independently by several taxonomists, thus, its nomenclature has been confused (Ragyov *et al*. 2009). Previously, six subspecies of the questionable species were described as follows: *F. c. cyanopus* (distributed in Central Europe and along the Volga river), *F. c. cherrug* (Russia), *F. c. hendersoni* (Pamir Mountains, Himalaya), *F. c. altaicus* (Altai-Sayan Region), *F. c. milvipes* (Kyrgyzstan and Mongolia), *F. c. coatsi* (from Iran to Tian Shan) (Nittinger et al. 2007). Some authors' work (e.g. Pfeffer 2009) also mention the Siberian Saker *(Falco c. saceroides)* and the Anatolian Saker *(F. c. anatolicus)*. *Falco ch. saceroides* is known as hybrid between the Gyrfalcon and the Saker, while *F. c. anatolicus* is an other subspecies.

Most debated is the population of Central Asian mountains (Altai, Tian Shan) which is considered to be a separate species (the Al-

tai Falcon – *Falco altaicus*) (Moseikin & Ellis 2004). Others claim that the Altai Falcon is a persistent hybrid between the Gyrfalcon and the Saker Falcon. Based on genetic research the Altai Falcon cannot be separated from the other two subspecies of the Saker (Wink *et al.* 2004).

The Saker Falcon is a polytypic species with two accepted subspecies: *F. c. cherrug* and *F. c. milvipes* (Clements *et al.* 2011). While *F. c. cherrug* is distributed in Europe as well as east from the Yenisei River and the Altai Mountains to China, *F. c. milvipes* is restricted to the northern and eastern parts of Central Asia and North-Eastern China (Ferguson-Lees & Christie 2001). This separation is based on phenotypic traits solely. Molecular investigations based on microsatellites and mitochondrial control regions of DNA samples extracted from skin and plumage of museum specimens failed to detect any differences between ssp. *cherrug* and ssp. *milvipes* (Nittinger *et al.* 2007).

Taxonomy of the species is still concerning researchers. Some taxonomists claim that division into two subspecies is oversimplified (Karyakin 2009, Pfander 2011). Pfeffer (2009) propose a separation of further six subspecies, one of which *(F. c. anatolicus)* has been still undescribed. This concept is based on the species' undoubtedly remarkable phenotypic variance, which is underpinned by the authors' observations by traditional methods in nature and captivity; however, it contradicts current phylogenetic results (which are otherwise cited in that paper).

Pfander (2011) suggests the introduction of a currently unused taxonomic concept, the 'semispecies' to the taxonomy of the Saker Falcon. He considers that Saker Falcon is geographically separated and proposes four different semispecies.

Phylogenetics

The first molecular investigations from the 1960s to the middle of the 1980s were based on allozyme variance. Allozymes are different variants of enzymes which are coded at the same locus of the chromosomes. While researchers managed to get information by direct inspection of the DNA this method lost its significance; it has been outcompeted by DNA sequencing with restriction enzymes and later direct sequencing of the DNA. Recently the whole genome of the Saker Falcon has been sequenced.

Certain sources treat the *Hierofalco* group as a subgenus (Wink & Seibold 1996), while others consider it only as collective terminus without any taxonomic relevance (Nittinger *et al.* 2007). Recent species of the *Hierofalco* group originate from Africa and they spread out of that continent in several consecutive waves. This group consists of four species: the Saker Falcon, the Gyrfalcon *(F. rusticolus)*, the Laggar Falcon *(F. jugger)* and the Lanner Falcon *(F. biarmicus)* (Nittinger *et al.* 2007). Based on some research the Black Falcon *(F. subniger)* from Australia is also belonging to this group (Wink *et al.* 2004).

The northern and southern populations had been separated from each other by the formation and expansion of the Sahara Desert. Northern populations begun to spread towards the Mediterranean area and colonized the whole Eurasian continent in three waves during the warmer periods of the Pleistocene. The Laggar Falcon evolved from population spreading towards India through the eastern part of the Mediterranean Basin, while the Gyrfalcon evolved from individuals colonizing the Palearctic. The Saker Falcon came from the Eastern African coast then evolved in Central Asia. At

the end of the last glacial period both the Saker and the Gyrfalcon expanded their area towards north and east respectively, and as a consequence a new contact zone formed somewhere in Central Asia, where the two species could hybridise with each other. The most ancient species of the group is presumably the Lanner Falcon what is supported by fossil records. The oldest *Hierofalco* fossil was discovered in Corsica. It is more than 34 000 years old and has been identified as *F. biarmicus* (Bonifay *et al.* 1998, Nittinger *et al.* 2005). However, African fossils of this species are currently undiscovered.

Nittinger *et al.* (2005) performed research on 56 DNA samples from the *Hierofalco* group, all of them originating from wild birds with only one exception. They identified 31 haplotypes based on mitochondrial control and pseudocontrol regions. They found that none of the species of the *Hierofalco* group were monophyletic. Members of the group are closely related to each other and separated during the last 1 million years, what is underpinned by the similarity of haplotypes, confirming the results of previous investigations based on cyt-b genes (e.g. Wink *et al.* 2004). The observed pattern of haplotypes could be caused by two, not necessarily contradicting phenomenon: (1) incomplete lineage sorting of ancestral polymorphism and (2) interspecific gene flow through hybridization (Nittinger *et al.* 2005).

The Saker Falcon proved to be the most diverse species of the *Hierofalco* group by a genetic research on approximately 200 samples covering the whole distribution area. It can be divided into at least three, well-defined clades which were signed with Roman numerals (I, II, III) in the study. All clades comprise individuals of both recently accepted subspecies, e.g. clade III contained

samples from Hungary as well as Kazakhstan, but neither clade I nor II corresponded to a subspecies or a part of the distribution area (Wink *et al.* 2004).

What causes this high level of morphological and genetic diversity? The researchers hypothesize that the above mentioned clades are the results of hybridization events which happened 100 000–200 000 years ago between the Saker and the Gyrfalcon or rather the Lanner Falcon. Considerable variation observed in the plumage of the Saker Falcon and the fact that that Saker and Gyrfalcon can readily hybridise in captivity gives reasonable proof to this argument (Wink *et al.* 2004).

A more recent study based on mitochondrial control region classified the haplotypes into two major groups (A, B) within the Saker's population. Altogether 186 individuals were investigated from the whole distribution range of the species. In Central Europe and in Northern Kazakhstan haplotype group B was the dominant, while in the populations of Central-Asia and Southern Siberia haplotype group A was more widespread. In Mongolia the frequencies of the two haplotype groups were around the same. Interestingly, only haplotype group A was found within the Gyrfalcon population (Nittinger *et al.* 2007).

The authors presume that the ancient population of the Saker Falcon contained only haplotypes B, while the A haplotypes conquered the genom of the species by introgression. The introgresson was asymmetric, as no Gyrfalcon carrying haplotypes group B have been found until now. However, we should not draw any conclusions as the Gyrfalcon was represented in the study with a low sample size (n=19), although the samples covered the whole distribution area of the species (Nittinger *et al.* 2007). How

could this zonality formed between haplotype groups? The Saker Falcon carrying haplotype group B was spreading from the west to the north-east during its presumptive postglacial expansion. After reaching the grasslands of Kazakhstan it spread into Dzungaria through the mountains of Tian Shan and Altai, and then it reached the areas what are now Eastern Mongolia and the northern regions of China. In the elevated regions of Kazakhstan and Mongolia it could have merged with populations of the Gyrfalcon which carried haplotypes group A. These hybrid birds might have been fitted better to the climatic conditions of these elevated steppe habitats and thus they survived. Haplotypes A might have been introduced from here to the areas which are now called Tibet and Iran. Data gained from mitochondrial DNA is not sufficient to undoubtedly clarify the origin of haplotype distribution patterns within the *Hierofalco* group. This pattern was shaped by several evolutionary processes (hybridization, incomplete lineage sorting) together (Nittinger *et al.* 2007).

To explore phylogenetic relations conserved mitochondrial and intranuclear marker genes are sequenced. Among the most commonly studied mitochondrial genes we can find the cytochrome-b (cyt-b), the NADH-dehydrogenase 2 (ND2) and the cytochrome oxidase c subunit 1 (COI), with which the mitochondrial phylogenetic lineage or haplotype could be reconstructed (Ballard & Rand 2005). If the studied species has populations with a low level of inter-population gene flow even the place of origin can be detected by investigating haplotypes of a captured migrating specimen (Wink 2006).

Former molecular studies (Wink *et al.* 2004, Nittinger *et al.* 2005) failed to unam-

biguously separate the two species based on mitochondrial cytochrome-b and control regions. They are not even isolated reproductively (Eastham & Nichols 2005). The Saker and the Gyrfalcon readily reproduce with each other in captivity, their hybrids representing a remarkable percent of falconry birds in the Middle East (Kenward 2009). Both species are listed on CITES, however, their phylogenetic relationships are unexplained. Their distinction based on phenotypic traits is sometimes doubtful, however, distinction could be refined with the use of morphometrical characteristics (e.g. wing, tail and tarsus length) (Eastham & Nichols 2005). In general, this separation based on genetic markers would yield several benefits. On one hand it would make it possible to track the origins of illegally captured or poached specimens, and on the other hand it would help increasing the efficacy of the preservation of small, isolated units of the two species (Moritz 1994a).

In the study of Dawnay *et al.* (2008) gene of mitochondrial cytochrome oxidase 1 (COI) and nine intranuclear microsatellite marker of the two species were compared. The researchers aimed to refine phylogenetic relations between the two species, moreover they wanted to explore if these DNA sequences would be suitable for undoubtful identification of the species. Samples originated from two Gyrfalcon populations (altogether 39 samples from one captive and one wild population) and three Saker populations (altogether 37 samples, one of the populations was captive). COI region of the DNA is substantially different even among closely related species, thus it is capable for correct species identification (Hebert *et al.* 2004). According to the COI sequences the two species are in a paraphyletic relationship. Paraphyletic relations are common on

phylogenetic trees of bird species based on mitochondrial sequences (Funk & Omland 2003). This could imply that species could not be identified properly. Moreover their application can lead to the construction of incorrect phylogeny. However, McKay and Zink (2010) states that the presumptive paraphyly is often caused by the inherently flawed taxonomy. Incomplete lineage sorting resulted from speciation events in the recent past could also lead to paraphyly. The authors predict that phylogenetic relationships between species can be reconstructed based on mtDNA, but considering the limits of this method these sequences could be also used for distinction between species (McKay & Zink 2010). The most effective would be if researchers first explored phylogeographic patterns by mitochondrial genes from a large sample size covering the whole distribution area, and then fine-tuned their results using nuclear genes and particularly, Z-linked loci. The authors claim that in species with a wide distribution mitochondrial loci are also suitable for constricting phylogenetic trees (Drovetski *et al.* 2014). However, phylogenetic and phylogeographic results based on mitochondrial DNA have always received criticism. Application of mtDNA has been questioned by several, claiming that these results are not relevant in ecological and conservational research. Bazin *et al.* (2006) were led to this conclusion by investigating frequently used mtDNA markers from cc. 3000 various vertebrate and invertebrate species. They explain mtDNA variations found in closely related species or populations within a species by recurrent adaptive evolution. However, they found that intranuclear markers are eligible for phylogenetic reconstructions (Bazin *et al.* 2006). The main point of critical arguments, however, is that mitochond-

rial genes are evolving as a single linkage unit. Thus, there is no effect of studying several genes from the mitochondrial genome, as the resulting gene trees will be the same, which would infer false conclusions. Maternal inheritance of the mitochondrial genome is also necessary to take into consideration, as if a sex-dependent dispersion event happened in the past, the result should be misleading (Zink & Barrowclough 2008). Most migrating bird species of the Palearctic, e.g. the Saker Falcon, colonized its recent nesting area after the last glacial. In that case several marker gene sequences can be so similar between different populations that their investigation would not enable proper differentiation between them (Waits *et al.* 2003, Lovette *et al.* 2004).

Results of Dawnay *et al.* (2008) strengthen the phylogeny established earlier by comparing other mitochondrial regions (e.g. Nittinger *et al.* 2005). However, the authors state that unambiguous distinction is only possible using intranuclear microsatellite markers. Using this method, individuals of the Gyrfalcon and the Saker could be told apart with 98% accuracy. According to the authors (Nittinger *et al.* 2005), the observed allelic differences are caused by recent separation of the species and not geographic distance between populations. As a consequence, the method should give reliable results with a substantially larger sample size, and it was proposed a route use during CITES controls (Dawnay *et al.* 2008).

Some researchers aim to explore taxonomy and ancestry of the species with other than genetic methods. Karyakin (2011) separated three groups (one western Saker and two eastern Sakers) based on spatial analysis of eight phenotypic traits, and these groups were further subdivided into five geographically distinct subspecies. This

analysis was made on the following traits: variations of pale pattern of upper body without wings and tail, colouring of crown, moustache, colouring of upper body, presence and intensity of a bluish-gray shade and degree of its distribution, colouring of breast and belly, dark pattern of underbody and pale pattern of tail, respectively. Karyakin (2011) used not only museum specimens or trapped individuals, but also took photographs in order to get more comprehensive view of phenotypical variances within the population.

Further, Karyakin (2011) drew a more detailed picture on the phylogenetic relationships of the species within the *Hierofalco* group. He based his assumptions on a study which states that there were no geographic isolation between recent area of the Saker and Gyrfalcon during the middle and late Pleistocene (Potapov & Sale 2005). This area was populated by a hypothetic *Protofalco* species. The geographic barrier, i.e. the taiga belt, started to form 9–11 thousand years ago, and it increasingly divided nesting area of the species from the East to the West. However, it is hard to define any geographical barriers in case of excellent flying species like birds.

It is worth mentioning that this isolation was completed faster at the western part of Eurasia, thus, a corridor remained in the East, through which gene flow could be maintained between the populations (Karyakin 2011). The absolute isolation then completed around 6000 years ago. This isolation resulted in the evolution of at least five great falcon species (or subspecies). Of the two Gyrfalcon populations one evolved at the extremely fragmented tundra, while the other one evolved in the high mountains of Central Asia. Two Saker populations, an eastern and a western one (these can cor-

respond for *Falco c. milvipes* and *Falco c. cherrug* as well), furthermore the recent Laggar Falcon could have been isolated this way. The author considers feasible that the eastern population of the Saker hybridised with the western Saker and Gyrfalcons 'captured' in high mountains, which resulted in several hybrid populations. The former could have been a rare hybridization event due to geographic barriers, while the latter could have been a more frequent event, due to the gradual disappearance of those barriers (Karyakin 2011). It is also worth mentioning that some authors propose a distinction between 'eastern' and 'western' form of the Sakers based upon exactly these assumptions (Karyakin 2011, Pfeffer 2012).

The Saker, the Gyrfalcon and the Laggar Falcon hybridize with each other in captivity. Thus, they can only be considered when geography is taken into account. The protofalcon is still separating into four distinct forms. In woody steppes the 'western' Saker's, while in arid mountains the 'eastern' Saker's speciation is happening now. In the mountains of Central Asia hybrids of the 'captured' Gyrfalcons and Sakers are evolving slowly into a new species, and the fourth protofalcon descendants are the Gyrfalcon populations living in the tundra belt. Divergence of the 'eastern' Saker is obvious, but the western population seems to be a lot more homogeneous, in which plumage differences are negligible even between populations in far corners of its area. Although gene flow/transfer/exchange could be implied among these populations, but it must have been ceased with the elimination of populations in the West of the Ural Mountains. And it has a very little chance that vagrant young, western birds could hybridise with Asian specimens (Karyakin 2011).

Hybridization

Hybridization among falcon species is rare in nature; however, there exist some observations. A male Peregrine Falcon *(Falco peregrinus)* and a female Prairie Falcon *(Falco mexicanus)* had a successful breeding in Canada (Oliphant 1991), while in China a nesting of a Saker and a Barbary Falcon *(Falco peregrinoides)* was observed (Angelov *et al.* 2006). In Bulgaria several nesting of Saker and Lanner Falcon mixed pairs were documented (Boev & Dimitrov 1995). In 2005 a hatching of female Peregrine Falcon and a 'tribrid' (Gyrfalcon/Saker × Peregrine) male falcon were noted. The pair was reared at least two chicks, but the offspring died before leaving the nest due to a rock slide and the hybrid individual was shot (Everitt & Franklin 2009).

As keeping captive bred birds spread in falconry, so spread the crossing between different species. One of the first hybrid clutches was a brood between a female Saker and a male Peregrine Falcon at the beginning of the 1970s in Ireland. At first the crossing was viewed as a pure novelty, and then it aimed to create new hunting types for different game species (Kenward 2009). For instance in the Middle East Saker was crossed with the Gyrfalcon to unify Saker's speed with the robust physique of the Gyrfalcon (Kenward 2009). These specimens are also more tolerant to heat and diseases (Fox 1999).

Divergence between the Saker, the Gyrfalcon and the Lanner Falcon is very small, the interspecific genetic distance is only 0.4–2.0%. Interestingly, taxa with a similar degree of relatedness are considered subspecies in several other genera (Wink *et al.* 2004). It is not surprising thus that species of the *Hierofalco* group are easily hybrid-

ise with each other, and the hybrids (supposedly) preserve their reproductive potential several generation down. According to Fox (1999) offspring of *Hierofalco* individuals crossed with Peregrine Falcons are rarely capable to sire, females are often sterile. Contrary, nestings of a Peregrine × Saker male and a Saker female were observed in several years; eggs were usually sterile but their offspring hatched successfully e.g. in 1999 or in 2003 (BirdLife International 2008).

However, it should not be forgotten that birds can hybridise even under natural condition, so it does not necessarily mean an anthropogenic, often disadvantageous effect, rather an important evolutionary mechanism, which takes part in the evolution of individual species (Pierotti & Annett 1993, Easthem & Nichols 2005). Hybridization is more frequent in bird families and subfamilies where males take a large part in raising up offspring, and it is much rarer where males invest only their genetic material into the young. Also remarkable is the phenomenon that there is also a difference in the number of subspecies. In those bird families where males' attendance is significant, there are usually more polytypic species. That implies that reproductive isolation may be rare while local adaptations are more common.

In the Falconidae family intergeneric hybridization was observed in seven out of 57 species (Pierotti & Annett 1993).

Recent hybridization could be excluded between allopatric species pairs: *F. rusticolus/F. jugger* and *F. biarmicus/F. rusticolus*, but not between Saker, Lanner and Laggar Falcons. There are potential hybrid zones in Pakistan and India (in south-western nesting areas of the Laggar Falcon), further in the Balkan Peninsula and Anatolia (nesting areas of the northern popula-

tions of the Lanner Falcon). Certain specimens of the Lanner and the Laggar Falcon get in contact in Southern Iran and Pakistan, while the Saker can get in touch with the Gyrfalcon in Southern Siberia during the nesting season (Moseikin & Ellis 2004, Nittinger *et al.* 2007).

In Europe every year several hundreds of hybrid falcons escape from their owner or released into the wild. In the Middle East frequency of such events are estimated to an order of several thousand each spring (Lindberg 2006). In Great Britain more than 1500 Peregrine Falcons escaped from captivity between 1983 and 2007, around 40% of which were hybrid birds (Fleming *et al.* 2011).

Based on samples from 156 specimens of seven falcon species Nittinger *et al.* (2006) concluded that hybrid birds have a huge impact on the gene pool of Saker Falcons living wild in Europe. According to samples collected between 1970 and 2003, 21% of individuals were a hybrids or descendants of hybrid birds (Nittinger *et al.* 2006). Thus interspecific genetic introgression poses a real threat.

BirdLife International promoted a total ban on keeping and breeding hybrid falcons, although there is no adequate information on the negative effects of hybrid birds getting to the nature. The organization is arguing that there is no serious reason for breeding hybrid birds, as such specimens are unsuitable for *ex situ* conservation programmes, whilst banning would cause disadvantage for only a fistful of economic stakeholder. In six countries of the European Union (including Hungary) falconry use of hybrid birds has been already banned. However, in several other countries even the ringing and registration of hybrid raptors is not mandatory, moreover in the United Kingdom neither hybrid specimens will need a registration in the future according to recent plans (BirdLife International 2008). It poses serious conservational concerns as more than 4000 out of 8000 falcon specimens kept in captivity in the country are hybrid birds, whilst the majority of them (44%) are hybrids of Sakers and Gyrfalcons (Fleming *et al.* 2011).

Applying taxonomic results in practice

Conservation biology can take out several benefits from the results of molecular research. On one hand, it can expand knowledge on the evolution and ecology of species, on the other hand, the acquired knowledge may be used for solving concrete problems. By exploring genetic differentiation of populations we can recognize those populations which are genetically the most different from massive population blocks. These small population fragments which have the greatest genetic variability are the most valuable and most threatened (Friesen 2007). Those populations between which there is no gene exchange, thus which are separated both demographically and evolutionary, are called Evolutionary Significant Units (ESU) (Moritz 1994b in Friesen 2007). These ESUs are present in several conservational directives (e.g. US Endangered Species Act).

For applying appropriate conservation programmes and directives, correct taxonomy of the focal species should be known. For instance, protection of the 'Altai' Falcon would call for different legislation if it was considered a separate species, or only a colour variant of the Saker. Regarding as a separate species may have a further advantage for the Altai Falcon, namely

it draws attention to the Central Asian population, inspiring further research on it (Ferguson-Lees & Christie 2001).

Hybridization has a particular importance from the viewpoint of nature conservation. Hybrid specimens getting into the wild poses a potential threat to natural populations of the species as hybrids may deteriorate gene pool. Several cases of nestings between escaped or released and wild birds have been documented (Fox 1999, Kleinstauber & Seeber 2000). Genetic research also attributes a remarkable effect to hybrid species (Nittinger *et al*. 2006). BirdLife International (2008) regards these birds as one of the main threats to the European Saker population. Without precise legislation and appropriate implements it is extremely troublesome to separate young hybrid and full-blood specimens; by using phenotypic traits it is almost impossible, and even genetic markers not always show a clear picture.

Eastham and Nicholls (2005) studied phenotypic traits of the Gyrfalcon, the Peregrine Falcon, the Saker and the New Zealand Falcon *(Falco novaeseelandiae)* together with their hybrids, and also investigated how this data could be used for the identification of hybrid individuals. All hybrid specimens were born in captivity, thus their descent was clear. The researchers found that phenotypes of the offspring are more similar to the males' phenotypes compared to those of the females. This result is further strengthened by earlier genetic findings that two third of genes linked to sex being carried by the males. This study highlights the problem that discerning full-blood specimens from their hybrids is often difficult (particularly hybrids of the Gyrfalcon and the Saker), and young individuals are especially difficult to discern based on the plumage (Eastham & Nicholls 2005). Accu-

rate identification would require genetic investigations.

An adequate solution would be the introduction of a registration system, although legislative framework is not available in several countries (BirdLife International 2008). Thus there is the possibility that illegally captured pure breed individuals can be sold as hybrids. Apart from the threat of genetic introgression discussed above a further problem may arise when escaped or released hybrids circumvent nesting of wild birds, as it was observed in the case of Peregrine Falcons in the Netherlands (BirdLife International 2008).

Hybridization could have direct conservational risk. For example, the greater Spotted Eagle *(Aquila clanga)* is a rare raptor species of Eastern Europe, which frequently hybridise in nature with its more common relative, the Lesser Spotted Eagle *(Aquila pomarina)*. Researchers studying the genetics of 14 European Greater Spotted Eagle populations found evidence for hybridization or introgression in all of them. In most regions hybrids originating from male Lesser Spotted Eagles and female Grater Spotted Eagles were observed. In those areas where Greater Spotted Eagle maintains a larger population size hybridization was less frequent. The Estonian population is particularly threatened as more Greater Spotted Eagle females were found paired with a Lesser Spotted Eagle male than with a conspecific partner, thus it can be declared that hybridization of species could pose a real danger for populations of certain protected species (Väli *et al.* 2010).

BirdLife International (2008) suggests the following proposal for mitigation of the problem:

– Hybrid offspring should be raised by pairs of species which are not occurring locally

– Hybrids can only be hacked in large conditioning pens
– Hybrids should be only let fly with appropriate telemetric devices
– Every effort should be made to find escaped hybrid birds
– Hybrid specimens should never be wilfully released under any circumstances

Breeders and falconers are on the opinion that crossing species is helping to improve birds' attributes, hence their activity is advantageous and should be supported. However, if individual species are treated as separate biological unit to be protected, we are regarding things from a different point of view. Crossing species is then harmful for their genetic integrity, provoking conservational concerns.

Although breeding of hybrids poses some risks, with an appropriate legislation this technique may have a leading role in the preservation of endangered species (Fox 1999). However, it is worth mentioning that the practice of crossing falconry birds is only 40 years old and thus it is difficult to predict the effects of spreading hybrids on natural populations without any long-term monitoring.

As in other fields of zoology, in ornithology, the results of molecular taxonomy have substantially changed systematics built upon phenotypic traits. Taxonomy of the New World vultures is a prominent example of the essentially conflicting results of the two approaches (Avise *et al.* 1994, Wink 1995). Later research based on mitochondrial and intranuclear genes questioned the monophyly of Old World vultures, too (Lerner & Mindel 2005). By investigating different markers several groups seemed to be far from each other have been finally linked together. Consequences deduced from the results, however, sometimes fundamentally contradict to each other, caused by, for instance, differences in the position of the studied gene sequences within the cell (Bensch *et al.* 2005, Brito 2007). Thus, it is important to emphasize that phylogenetic relationships could be deduced correctly by considering the results of both classical and molecular taxonomy.

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Phylogeny, historical biogeography and the evolution of migration in accipitrid birds of prey (Aves: Accipitriformes)

Jenő Nagy[1] & Jácint Tökölyi[2*]

Abstract Migration plays a fundamental part in the life of most temperate bird species. The regular, large-scale seasonal movements that characterize temperate migration systems appear to have originated in parallel with the postglacial northern expansion of tropical species. Migratoriness is also influenced by a number of ecological factors, such as the ability to survive harsh winters. Hence, understanding the origins and evolution of migration requires integration of the biogeographic history and ecology of birds in a phylogenetic context. We used molecular dating and ancestral state reconstruction to infer the origins and evolutionary changes in migratory behavior and ancestral area reconstruction to investigate historical patterns of range evolution in accipitrid birds of prey (Accipitriformes). Migration evolved multiple times in birds of prey, the earliest of which occurred in true hawks (Accipitrinae), during the middle Miocene period, according to our analyses. In most cases, a tropical ancestral distribution was inferred for the non-migratory ancestors of migratory lineages. Results from directional evolutionary tests indicate that migration evolved in the tropics and then increased the rate of colonization of temperate habitats, suggesting that temperate species might be descendants of tropical ones that dispersed into these seasonal habitats. Finally, we found that diet generalization predicts migratoriness in this group.

Keywords: ancestral area reconstruction, annual cycle, comparative, diet specialization, diurnal birds of prey, molecular dating, seasonality

Összefoglalás A legtöbb mérsékelt övi madárfaj életciklusában alapvető szerepet tölt be a vonulás. A rendszeres, nagy kiterjedésű mozgások, melyek a mérsékelt övi vonulási rendszereket jellemzik, egyes feltételezések szerint a trópusi fajok poszt-glaciális, északi irányú terjeszkedésével párhuzamosan jelentek meg. Ezen felül a vonulás előfordulását számos ökológiai tényező is befolyásolhatja, mint például a környezet szezonalitásának mértéke vagy a téli túlélést befolyásoló tényezők. A vonulás eredete és evolúciója ezért csak úgy érthető meg, ha a madarak biogeográfiai történetiségét és ökológiáját filogenetikai kontextusban tanulmányozzuk. Jelen vizsgálatban a vágómadár-alakúak (Accipitriformes) vonulásának evolúcióját elemeztük komparatív módszerekkel. Első lépésben létrehoztunk egy fosszilis adatok alapján datált molekuláris törzsfát, amelyen jellegrekonstrukciót végeztünk és rekonstruáltuk a fajok ősi elterjedési területét. Az elemzéseink alapján a vonulás többször alakult ki a ragadozók esetében, legkorábban a héjaformákon (Accipitrinae) belül, vélhetően a Miocén közepén. A legtöbb esetben a vonuló leszármazási vonalak nem vonuló őseinél trópusi elterjedésre következtethetünk. A direkcionális evolúciós teszt alapján a vonulás a trópusokon jelent meg és megnövelte a mérsékelt égöv kolonizációjának rátáját. Eszerint tehát a mérsékelt övi ragadozómadár fajok vonuló trópusi fajok leszármazottainak tekinthetők, melyek az erősen szezonális, északi élőhelyek irányába terjeszkedtek. Végezetül negatív kapcsolatot találtunk a vonulás megjelenése és a táplálékspecializáció mértéke között.

Kulcsszavak: éves ciklus, jellegrekonstrukció, komparatív, molekuláris datálás, nappali ragadozómadarak, szezonalitás, táplálékspecializáció

[1] *MTA-ELTE-MTM Ecology Research Group, 1117 Budapest, Pázmány Péter sétány 1/C, Hungary, e-mail: jenonagy.off@gmail.com*
[2] *MTA-DE "Lendület" Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, 4032 Debrecen, Egyetem tér 1., Hungary, jtokolyi@vocs.unideb.hu*
corresponding author

Introduction

Birds originated, according to our current knowledge of the fossil record, about 150-200 million years ago during the geological era of Jurassic (Padian & Chiappe 1998). The appearance of powered flight, probably in combination with several other avian features such as warm-bloodedness and the presence of extensive parental care has fuelled the diversification of this group of vertebrates, which seems to have accelerated around, or shortly after the Cretaceous-Paleogene boundary (Ericson *et al*. 2006, Brown *et al*. 2008, Jetz *et al*. 2012).

The widespread occurrence of birds is greatly facilitated by their excellent dispersal capabilities. This is perhaps most clearly seen in migratory birds, which can travel thousands of kilometres on continental scale within a single year. Migration is a characteristic feature of birds that is extremely common especially in species inhabiting the Northern Hemisphere temperate zone and the Arctic, but it also occurs, although in less extreme forms, in other regions of the globe in the form of intratropical migration systems (Alerstam 1993, Berthold 2001, Newton 2008).

Migration itself profoundly influences the distribution, ecology and diversification of birds (Newton 2008), hence it is not surprising that a great deal of information has accumulated on its internal, proximate determinants and its phenology ever since Hans Christian Mortensen started ringing birds at the very end of the 19th century. These studies revealed that the migratory phenotype is determined by a set of complex and tightly regulated mechanisms (Gwinner 1990), which includes, among others (1) sensory elements underlying orientation and navigation, (2) mechanisms responsible for the regulation of

migratory restlessness ('zugunruhe') during the annual cycle and (3) a range of physiological adaptations that cover the metabolic requirements of long-distance flights during migration. Understanding how such a complex phenotype could have evolved is a major challenge in ornithology.

While a wealth of information has accumulated on the details of the process of migration, comparatively little is known about how migration originated and evolved in birds. This is not surprising, since behavioral traits, such as the migratory habits of a species do not fossilize and hence our current ideas of it are strictly inferred from phylogenetic or biogeographic studies. Current theories of the evolution of migration can be divided into two groups (Rappole & Jones 2002, Bruderer & Salewski 2008). The 'tropical origin' hypothesis proposes that migratory birds derive from species inhabiting regions where environmental factors were constant during the year, so there was no need for migration. These species could have colonized more seasonal, northern habitats, which, during the summer months provided appropriate conditions for reproduction. However, during winter food availability decreased, hence these birds were forced to return to southern latitudes (Rappole & Jones 2002, Bruderer & Salewski 2008). Cox (1985) developed a stepping-stone model of this hypothesis. According to this model, resource-limitation due to competition for food forced certain tropical resident species to expand their range to the subtropics. These birds continued to return to the tropics during the winter, resulting in the formation of partial migrant species. These partial migrants then continued to spread to higher latitudes where they were able to breed successfully while still returning to the original area in the winter

(Stiles 1980, Cox 1985). Thus, this hypothesis predicts that migratory species evolved from tropical ancestors.

Several lines of evidence support the tropical origin of long-distance migrants. Joseph *et al.* (1999), in a study of waders, analyzed the evolution of breeding and wintering distribution of 16 species from the genus *Charadrius* using phylogenetic methods. By reconstructing the hypothesized distribution of the ancestors of these birds, they showed that species that are migratory today derive from ancestors whose breeding and non-breeding ranges were located in the tropical zone. Another similar study investigated the evolution of migration in *Catharus* thrushes (Outlaw *et al.* 2003). This study showed that North American (migratory) thrushes are sister to tropical species, and the ancestral area for the whole lineage was inferred to be in the Neotropics, providing further support for the 'tropical origin' hypothesis. This pattern is not restricted to interspecific comparisons but is also seen among populations differing in migratory status. For instance, in a study of North American Chipping Sparrows *(Spizaella passerina)*, Milá *et al.* (2006) have shown that the northern, long-distance migrant populations descend from non-migratory Mexican populations, which colonized North America after the last glacial maximum 18 000 years ago. Thus, long-distance migration and colonization of temperate regions in this species developed in tandem.

Other hypotheses on the origin of migration emphasize the importance of changes on the breeding territories of birds with a northern distribution ('northern origin' hypothesis) (Bell 2000, 2005, Bruderer & Salewski 2008). According to these suppositions, climatic or other ecological changes (e.g. global cooling) could have led to the evolution of migration by forcing non-migratory temperate and arctic species to leave there home ranges during the winter (Bell 2000, 2005), resulting in migratory strategies which allowed the survival of populations in a strongly seasonal milieu (Bell 2000, 2005). Thus, this hypothesis predicts that migration evolved from temperate resident species, a prediction that has received relatively low support to date. It is clear, however, that migration can evolve without the expansion of the breeding ranges, as examplified by the large number of intra-tropical migrants (e.g. Boyle & Conway 2007, Boyle *et al.* 2011). Comparative studies of the occurrence of migration among some of these tropical taxa, such as the passerine group Tyranni revealed that a number of ecological traits, specifically diet and habitat, predict whether a species is migratory or not in the tropics (Boyle & Conway 2007, Boyle *et al.* 2011). Thus, year-round variation and predictability of food sources (Boyle & Conway 2007, Boyle *et al.* 2011), as well as the ability to exploit these sources (Bell 2011, Boyle *et al.* 2011) appears to predispose some avian taxa for migration.

As the examples above suggest, the evolution of migration in birds is a complex problem that requires an integrative approach combining aspects of the historical biogeography (range expansions), ecology (habitat, food availability) and behavioral ecology (diet specialization) of birds. Yet, phylogenetic studies often target only one of these aspects, while ignoring others. Here, we describe an attempt for such an integrative approach using accipitrid birds of prey (Accipitriformes) as a model group. This taxon is ideal for our purpose because it includes both tropical and temperate species and there is wide variation in migratory behavior, habitat and diet within the group (Ferguson-Lees

& Christie 2001). Specifically, we investigate the following: (1) the phylogeny and historical biogeography of diurnal birds of prey; (2) the evolutionary origins of migration in raptors in a phylogenetic context and (3) the ecological and behavioral traits that are associated with migratoriness in this group. The traits we investigate are body mass, diet and habitat. Body mass influences nearly all aspects of birds' life and could be a crucial factor determining which species can survive periods of food shortage and/or cold wheather (e.g. Newton 2008). Therefore, we hypothesize that larger birds are more likely to become residents (or vice versa: residents might be selected to become larger) (Tökölyi & Barta 2011). Diet can be important for two reasons: first, raptors feeding on warm-blooded prey or carcass are more likely to survive the winter at temperate latitudes and hence be non-migratory. Second, species with a generalist diet should be more likely to subsist during periods of resource shortage by finding alternative food sources, hence we predict that food generalists are more fre-

quent in migrants. Lastly, habitat type was hypothesized to be important in the evolution of tropical-temperate migration systems because it could have determined the availability of suitable corridors for tropical-temperate dispersal routes (Rappole & Jones 2002). Rappole and Jones (2002) noted that the majority of long-distance migrants in the Nearctic spend the winter in forests, whereas almost none of the Palearctic/Asian migrants do so. They proposed that the lack of forested habitats in North Africa could have acted as a dispersal barrier, effectively filtering range expansions from south. Therefore, we tested whether habitat type is associated with migratoriness in birds of prey.

Methods

Phylogenetic reconstruction and molecular dating

The list of genes used to reconstruct the molecular phylogeny of birds of prey for

Gene (Abbreviation)	No species	No. bp	Model
12S ribosomal RNA (12S)	74	900	TIM2+I+G
16S ribosomal RNA (16S)	53	1527	GTR+I+G
ATP synthase F0 subunit 6 (ATP6)	56	684	TrN+I+G
ATP synthase F0 subunit 8 (ATP8)	56	168	TrN+I+G
β-fibronigen intron 7 (BFI7)	69	922	TVM+G
Cytochrome c oxidase subunit 1 (COX1)	86	1551	TIM2+I+G
Cytochrome b (CYTB)	164	1146	TIM3+I+G
NADH-ubiquinone oxidoreductase subunit 2 (ND2)	151	1047	GTR+I+G
NADH-ubiquinone oxidoreductase subunit 2 (ND6)	66	525	GTR+I+G
Recombinase activating gene 1 (RAG1)	87	2872	GTR+I+G

Table 1. Gene sequences used to reconstruct the phylogeny of *Accipitriformes*, their availability, length and the most appropriate evolutionary model of sequence evolution applying to them, as evaluated by jModelTest

1. táblázat A vágómadár-alakúak törzsfa-rekonstrukciójához használt génszekvenciák neve, elérhetősége (fajok száma), hossza és a jModelTest által meghatározott legmegfelelőbb evolúciós modell

which genetic data is available is shown in *Table 1*. All sequences were retrieved from GenBank (http://ncbi.nlm.nih.gov/). Sequences were aligned using MAFFT-LINSI (Katoh *et al.* 2005) with default parameters and alignments were visually checked. Two alignments (12S and 16S) contained multiple indels and were run through Gblocks (Castresana 2000) to remove poorly aligned positions. Sequence management was done in the R statistical environment (R Development Core Team 2012) using functions from libraries *ape* (Paradis *et al.* 2004) and *seqinr* (Charif & Lobry 2007).

Alignments were concatenated and species with few data (<500 nucleotides) were removed. The median sequence length for the remaining 180 species was 1038 base pairs (range 519-2872) *(Table 1)*. This taxonomic sample represents approximately 70% of extant species.

The resulting sparse supermatrix was used to reconstruct the phylogenetic relationships of the 180 species. First, RAxML (Stamatakis 2006) was used to obtain a starting tree for phylogeny estimation. We used a rapid bootstrap analysis with 100 bootstrap replicates followed by a search for the best-scoring maximum likelihood tree, using the GTR+I+G model of evolution. The Secretary Bird *Sagittarius serpentinus* (Sagittariidae) was used as an outgroup in this process; the sister relationship between Sagittariidae and the rest of the Accipitriformes (Pandionidae and Accipitridae) is well supported from molecular phylogenetic studies (e.g. Ericson *et al.* 2006, Brown *et al.* 2008, Hackett *et al.* 2008).

Next, the best-scoring tree obtained from this analysis was used as a starting tree in a Bayesian MCMC analysis (implemented in BEAST; Drummond & Rambaut 2007) to simultaneously reconstruct the phylogeny and divergence times of birds of prey. The ten gene segments were partitioned separately and each gene segment was assigned its own best-fit evolutionary model, as evaluated by Akaike Information Criterion (AIC) in the software jModelTest 2 (Guindon & Gascuel 2003, Darriba *et al.* 2012) *(Table 1)*.

Molecular dating was done using an uncorrelated relaxed molecular clocks approach, which takes into account variation in the rate of molecular evolution among lineages (Drummond *et al.* 2006). Three fossil constraints were used to date the phylogenetic tree (following do Amaral *et al.* 2009 and references therein): (1) the minimum age of divergence between Pandionidae and Accipitridae was set to 37 Mya, based on the oldest known fossil belonging to Pandionidae (Harrison & Walker 1976); (2) the maximum age of divergence for *Buteo galapagoensis* was set to 4 Mya and (3) the maximum age of divergence for *B. solitarius* was set to 5.1 Mya. *B. galapagoensis* and *B. solitarius* are both island species (restricted to the Galapagos Islands and Hawaii, respectively) and the latter two age constraints are based on the assumption that these species cannot be older then the islands which they inhabit (do Amaral *et al.* 2009). Two independent BEAST runs were performed, each allowed to run for 50 000 000 generations with a thinning interval of 5000 generations. Convergence was evaluated by checking effective sample size (ESS) of parameters in Tracer (Rambaut & Drummond 2012). All parameters had ESS values >100 and most were >>200. The two runs were combined (after removing 10% burnin) and resampled at intervals of 10 000 generations to yield 9000 trees that represents a sample of the posterior distribution of phylogenetic trees. A maxi-

mum clade credibility tree was generated from this sample in TreeAnnotator (Rambaut & Drummond 2012).

To visualize diversification rate through time, we created a lineages-through-time plot for 100 trees selected randomly from the posterior sample and the maximum clade credibility tree.

Ancestral area reconstruction

We collected breeding season distribution data on 180 species from Ferguson-Lees and Christie (2001). Species were scored as present/absent in the following biogeographical realms: Nearctic, Palearctic, Neotropical, Afrotropical, Malagasy, Indomalayan, Australasian. The delimitation of these realms is based on Ferguson-Lees and Christie (2001).

We inferred ancestral ranges based on this distribution data by employing probabilistic historical biogeography methods using the BioGeoBEARS R package (Matzke 2013). These methods model geographic range evolution by assuming different forms of anagenetic and cladogenetic changes in geographic distribution during speciation events: dispersal, extinction, vicariance, sympatric speciation and founder-event speciation. We evaluated which of the traditionally used historical biogeographic models best fits range evolution in birds of prey by calculating and comparing six models using Akaike Information Criterion. These models are the Dispersal-Vicariance (DIVA) model (Ronquist 1997), the Dispersal-Extinction-Cladogenesis (DEC) model (Ree *et al*. 2005, Ree & Smith 2008) and the BayArea model (Landis *et al*. 2013), together with the combination of these three with founder-event speciation. The three baseline models all assume dispersal, extinction,

sympatric speciation and vicariance as possible range evolution mechanisms but differ in the way they treat sympatric and vicariant speciation events: the DIVA model allows narrow-scale sympatry but both narrow and widespread vicariance. The DEC model assumes narrow-scale and subset sympatry, but only narrow-scale vicariance whereas BayArea assumes narrow-scale and wide-scale sympatry to occur (Matzke 2013). We used the best fit of these models to estimate the most likely ancient distributions at each node (ancestor state) of the phylogeny. The method also gives a relative probability, ranging from 0 to 1, which gives the probability that the node was in the given state. The higher this value, the higher is our confidence in the actual reconstuction is correct and uncertainty in the ancestral range reconstruction is low. These analyzes were done using the maximum clade credibility tree.

Life history data

All data, with the exception of body mass information, were collected from Ferguson-Lees and Christie (2001), complemented from the Global Raptor Information Network (2013), if necessary. Migratory behavior was categorized based on previous phylogenetic studies (e.g. Kondo & Omland 2007, do Amaral *et al*. 2009) as: (1) non-migratory (no seasonal movements present), (2) partially migratory (part of the populations, or part of the individuals within the species perform regular seasonal movements) and (3) completely migratory (all populations and individuals migratory). We used this variable to infer rates of evolution to and from complete migration (see below). However, the number of completely migratory species was relatively low in our

sample (N=13), therefore, migration was binarized in all other analyzes as either migratory or non-migratory.

Information on body mass was obtained from Dunning (2008), and in a few cases from Ferguson-Lees and Christie (2001). We used the average of male and female body masses (log-transformed) when they were available; however, in 8 cases data on male or female body mass was available only. For 29 species no reliable body mass data could be found.

Diet (winter diet) was categorized following Roulin and Wink (2004). These authors assigned a relative importance value ranging from 1 to 9 to each of nine food categories (live birds, mammals, reptiles, fish, amphibians, crustaceans, insects, worms and carrion) based on descriptions of individual species' diet in Ferguson-Lees and Christie (2001). Food types that do not appear in the diet of a species received a score of 9, whereas the most important food type received a score of 1. From these values, we calculated reliance on warm-blooded prey and carrion as the minimum of the importance scores received for bird or mammal prey or carrion. Diet specificity was estimated by counting the number of food types in the diet of a given species that received a score <9.

Finally we classified habitat type as open or closed based on descriptions in Ferguson-Lees and Christie (2001).

Comparative analyzes

We performed Bayesian ancestral state reconstruction in BEAST (Drummond & Rambaut 2007) to infer the migratory behavior at ancestral nodes in the phylogeny of birds of prey. Migratory behavior was recoded as a binary variable for this analysis (as either migratory or non-migratory, thus complete and partial migrants were collated). Bayesian ancestral state reconstruction takes into account phylogenetic uncertainty and calculates the probability that a given node was migratory or non-migratory, based on the trait values of its ancestor and descendants. By taking into account uncertainty in phylogenetic reconstruction, this method is substantially better than parsimony-based reconstructions, whose outcome is conditional on a single (possibly erroneous) topology. In addition, Bayesian ancestral state reconstruction also takes into account differences in branch lengths, which makes them more realistic than parsimony-based methods.

Next, we investigated how changes in migratory behavior occurred on the phylogeny by estimating transition rates between the three levels of migratory behavior (i.e. the rate of transition from migratory to partial or complete migrant and vice versa, and the rate of transition from partial to complete migrant and vice versa). This analysis was done using the MultiState module of BayesTraits 1.0 (Pagel *et al.* 2004).

We determined whether body size (log-transformed), habitat type, diet breadth, reliance on warm-blooded prey and geographical location (Old vs. New World) affects migratory behavior by constructing a multivariate phylogenetic generalized linear mixed models as implemented in the MCMCglmm package in R (Hadfield & Nakagawa 2010), with these traits as dependent variables. We also included the interaction between habitat and geographical occurrence to model the differences in habitat use among Old World and New World migrants.

Lastly, we tested the correlated evolution among migration and explanatory variables found to be significant in the multiva-

riate analyses using the Discrete module of BayesTraits 1.0 (Pagel & Meade 2006). This method evaluates transition rates among pairs of binary traits on a phylogeny revealing details of correlated evolution among traits. For example, when analyzing the correlated evolution between migration and diet specificity one can ask whether migration is more likely evolve in generalist (or specialist) lineages or vice versa: does a generalist (or specialist) diet evolve more likely in migrants? Since this analysis can handle only binary traits we dichotomized diet specificity as specialist (<5 food types consumed) or generalist (at least 5 food types consumed).

Results

Phylogeny and diversification of Accipitriformes

Figure 1 shows the relationship between major lineages of raptors. Our analysis recovered the relationships among major lineages of birds of prey described in previous molecular phylogenetic studies (Wink & Sauer-Gürth 2004, Lerner & Mindell 2005, Griffiths *et al.* 2007). Crown group Accipitriformes (i.e. the split between *Sagittarius* and the rest of the species) is inferred to have originated ~44 million years ago (95% highest posterior density interval: 56.4 – 37.4), during the Eocene period. The
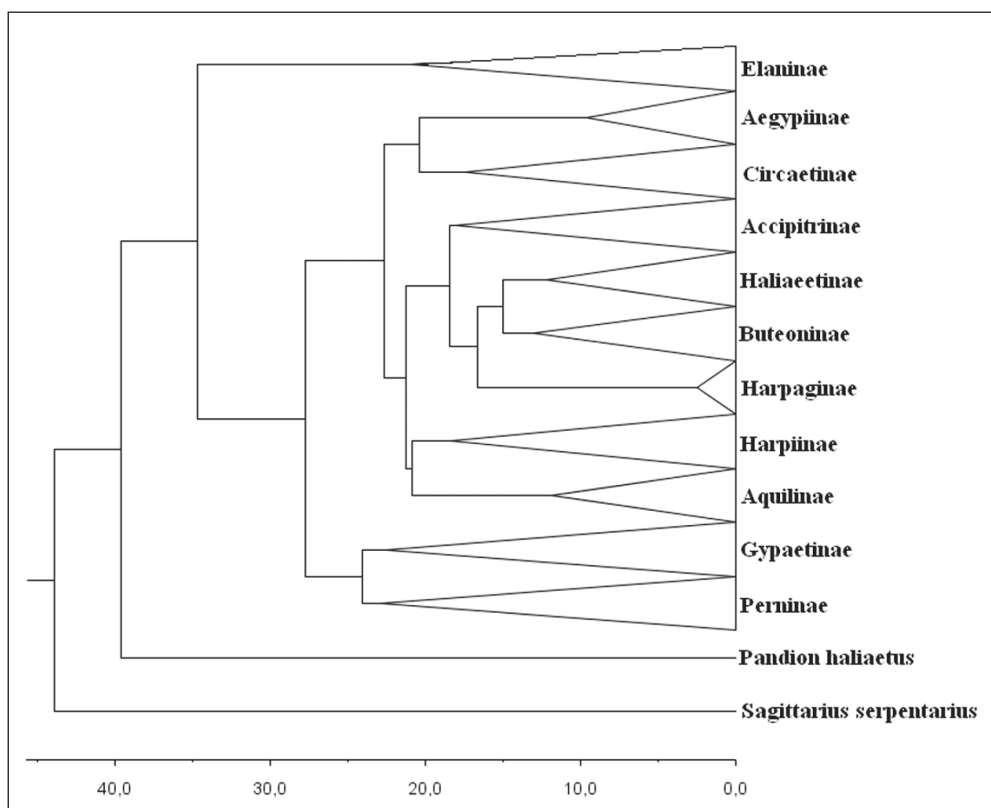

Figure 1. Simplified phylogeny showing major sublineages of Accipitriformes
1. ábra Egyszerűsített törzsfa a vágómadár-alakúak főbb csoportjainak filogenetikai viszonyairól
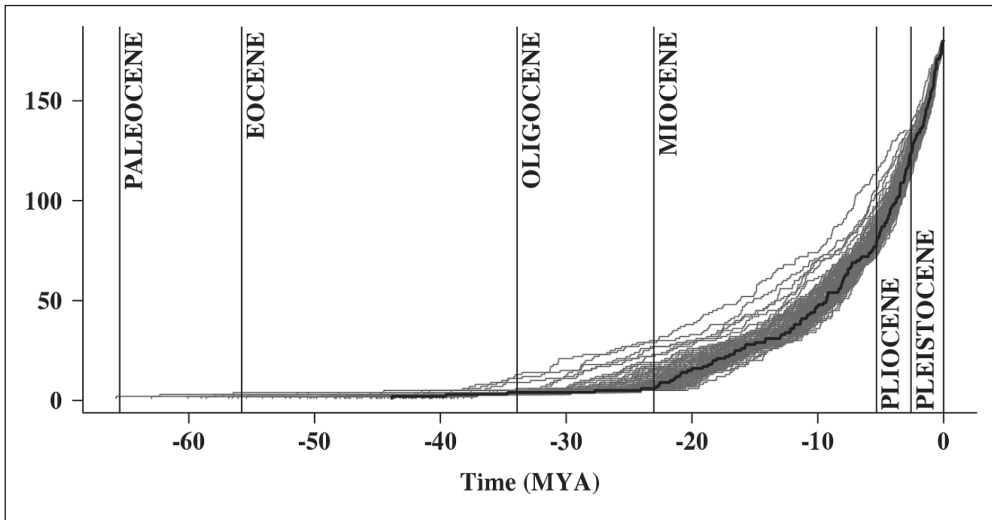
Figure 2. Lineages-through-time plot showing the pattern of diversification and accumulation of raptor species through time as reconstructed by our multi-gene relaxed molecular dating analysis. Grey lines show random trees (N=100) from the posterior sample of dated ultrametric trees obtained from BEAST; the black line denotes the maximum clade credibility tree

2. ábra A vágómadár-alakúak diverzifikációja a molekuláris datálás alapján. A szürke vonalak a törzsfa-rekonstrukció során létrehozott poszterior mintából 100 véletlenszerűen kiválasztott ultrametrikus fa, a fekete vonal pedig az összegzett mintából számolt ultrametrikus fa ágainak számát mutatja az idő függvényében

split between *Pandion* and the rest of Accipitriformes occurred ~39.5 million years ago (95% highest posterior density interval: 49.5–37). The two earliest branchings within Accipitridae resulted in the appearance of elanid kites (Elaninae) ~34.7 million years ago (95% highest posterior density interval: 44.3–29.4) and the group containing Gypaetinae and Perninae (~27.7 million years ago; 95% highest posterior density interval: 35.3–23.2). Then, around the start of the Miocene period the diversification of raptors accelerated and continued at a high rate until recent times *(Figure 2)*.

Ancestral area reconstruction

The best model describing range evolution in birds of prey was the DEC model containing founder-event speciation. Based on this model, a southern origin was inferred for all raptor subfamilies. These analyses suggest that Accipitrinae, Aegypiinae and Gypaetinae have an Afrotropical origin, whereas Elaninae and Perninae derive from the Neotropics. Buteoninae and Harpiinae had a joint Afrotropical/Neotropical distribution according to our reconstruction, whereas Aquilinae have an Afrotropical/ Neotropical and Indomalayan origin, although we note that the accuracy of these reconstructions is quite low (<0.3) *(Table 2)*. Circeatinae were assigned an Indomalayan origin with relatively high probability (0.87) *(Table 2)*. Lastly, the most likely ancestral distribution of Haliaeetinae was Australasia.

Subfamily	Genera	Node age (Mya; 95% HPD interval)	Ancestral distribution	Prob.
Accipitrinae	*Accipiter, Circus, Kaupifalco, Melierax, Urotriorchis*	15.1; 23.0	At	0.79
Aegypiinae	*Aegypius, Gyps, Necrosyrtes, Sarcogyps, Torgos, Trigonoceps*	7.4; 12.6	At	0.78
Aquilinae	*Aquila, Hieraaetus, Ictinaetus, Lophaetus, Nisaetus, Oroaetus, Polemaetus, Spizaetus, Spizastur, Stephanoaetus*	9.8; 15.4	NtAtIm	0.26
Buteoninae	*Busarellus, Butastur, Buteo, Buteogallus, Geranoaetus, Geranospiza, Harpyhaliaetus, Ictinia, Leucopternis, Parabuteo, Rostrhamus*	10.3; 16.7	NtAt	0.24
Circaetinae	*Circaetus, Dryotriorchis, Pithecophaga, Spilornis, Terathopius*	13.8; 22.5	Im	0.87
Elaninae	*Elanus, Gampsonyx*	14.4; 29.4	Nt	0.15
Gypaetinae	*Gypaetus, Gypohierax, Neophron, Polyboroides*	18.5; 29.0	At	0.99
Haliaeetinae	*Haliaeetus, Haliastur, Ichthyophaga, Milvus*	9.8; 15.7	Au	0.30
Harpiinae	*Harpia, Harpyopsis, Macheiramphus, Morphnus*	13.6; 24.4	NtAt	0,20
Perninae	*Aviceda, Chondrohierax, Elanoides, Eutriorchis, Hamirostra, Leptodon, Lophoictinia, Pernis*	18.7; 29.4	Nt	0.15

Table 2.   Geographic origin of major sublineages of Accipitriformes as inferred from the ancestral area reconstruction following a dispersal-extinction-cladogenesis-founder-event speciation (DEC+J) model of geographic area evolution. This table lists the major subfamilies of Accipitriformes, the genera they contain, the inferred age of these groups (age of the crown group, i.e. the most recent common ancestor of all extant species), shown as 95% highest posterior density interval (HPD) and the most likely ancestral area inferred for the crown group, along with the probability that the node was in the given state. Geographic distribution is abbreviated as: Pa – Palaearctic; Na – Nearctic; At – Afrotropical; Nt – Neotropical; Im – Indomalayan; Au – Australasian

2. táblázat A vágómadár-alakúak főbb csoportjainak rekonstruált ősi elterjedési területe. A táblázat a főbb alcsaládok nevét, az ezekbe sorolt génuszokat, az alcsaládok molekuláris datálás által becsült korát, a legvalószínűbb ősi elterjedési területet, illetve ennek a valószínűségét mutatja. A földrajzi elterjedések rövidítése: Pa – Palearktisz; Na – Nearktisz; At – Afrotropisz; Nt – Neotropisz; Im – Indomaláj; Au – Ausztrálázsiai

Table/táblázat 3a

Species	Distribution	Ancestor's age (Mya; 95% HPD interval)	Ancestor's posterior node support	Prob. of ancestor being non-migratory	Ancestor's distribution	Prob.
Accipiter gularis	Pa	0; 0.5	0.95	0.98	Palm	0.56
Accipiter nisus	PaAtIm	2.4; 5.2	0.42	0.84	NtPaAtIm	0.21
Accipiter soloensis	Palm	6.3; 13.3	0.92	0.96	ImAu	0.18
Accipiter striatus	NaNt	1.3; 3.3	0.53	0.84	NaNtAt	0.51
Aegypius monachus	PaAt	2; 4	1.00	0.98	At	0.46
Aquila chrysaetos	NaPaAt	3.6; 6.2	1.00	0.99	At	0.91
Aquila heliaca	Pa	0.5; 1.6	0.94	0.99	Pa	1.00
Aquila nipalensis	Pa	1.6; 3.5	1.00	0.97	Pa	0.99
Hieraaetus wahlbergi	At	3.8; 6.6	1.00	0.59	At	1.00
Butastur indicus	Palm	2.1; 5.1	0.83	0.56	Im	0.32
Butastur rufipennis	At	2.9; 6.4	1.00	0.57	At	0.29
Buteogallus anthracinus	NaNt	0; 0.1	1.00	1.00	Nt	0.95
Buteogallus meridionalis	Nt	2.7; 4.5	1.00	1.00	Nt	1.00
Buteo lineatus	Na	1.1; 2.1	1.00	0.79	NaNt	0.38
Buteo nitidus	NaNt	3; 4.8	0.32	0.66	Na	0.71
Buteo platypterus	NaNt	2.8; 4.5	0.99	0.70	Na	0.72
Buteo polyosoma	Nt	0.4; 1.1	1.00	0.99	Nt	1.00
Buteo swainsoni	Na	0.2; 0.4	1.00	0.99	Nt	0.44
Circaetus fasciolatus	At	1.5; 3.9	1.00	0.91	At	1.00
Circaetus gallicus	PaAtIm	2.8; 6.1	1.00	0.78	At	0.78
Circaetus pectoralis	At	4.7; 8.8	1.00	0.79	At	0.99
Elanoides forficatus	NaNt	15.5; 25.1	0.53	0.84	NtPa	0.22
Gypohierax angolensis	At	18; 27.8	0.43	0.88	At	0.90
Gyps coprotheres	At	0.3; 0.8	0.35	1.00	At	0.40
Gyps fulvus	PaAt	0.3; 0.9	0.66	1.00	At	0.96
Haliaeetus leucogaster	ImAu	0; 0.3	1.00	0.89	Au	0.87
Haliaeetus vocifer	At	0.7; 1.9	1.00	0.91	At	1.00
Haliastur sphenurus	Au	2.3; 4.8	1.00	0.70	Au	0.37
Hieraaetus ayresii	At	2.4; 4.7	1.00	0.51	At	0.88
Hieraaetus pennatus	PaAt	0.7; 1.7	1.00	0.53	PaAtAu	0.28
Macheiramphus alcinus	At	13.6; 24.4	0.99	1.00	NtAt	0.20
Neophron percnopterus	PaAtIm	14.4; 24.7	1.00	0.87	At	0.42
Pandion haliaetus	NaNtPaAtImAu	37; 49.5	1.00	0.91	At	0.37
Parabuteo unicinctus	NaNt	4.5; 7.5	1.00	0.98	Nt	0.95
Polyboroides typus	At	18.5; 29	0.95	0.91	At	0.99
Rostrhamus sociabilis	NaNt	7.5; 12	0.96	0.99	Nt	0,96

Table/táblázat 3b

Node number	Distribution	Ancestor's age (Mya; 95% HPD interval)	Ancestor's posterior node support	Prob. of ancestor being non-migratory	Ancestor's distribution	Prob.
185	NaNtPaAtImAu	14.4; 29.4	1.00	0.77	Nt	0.15
217	Nt	11.7; 18.2	1.00	0.63	Nt	0.71
251	NaPa	7.1; 11.9	1.00	0.93	Im	0.10
255	PaAtImAu	5.3; 9.3	1.00	0.69	Au	0.38
261	NaNt	9.5; 14.5	0.90	0.99	Nt	0.93
344	Pa	2.1; 4.4	0.98	1.00	Pa	0.81
359	Pa	15.5; 25.1	0.84	0.53	NtPa	0.22

Table 3. Possible cases of independent appearance of migration in Accipitriformes. This table lists migratory species (a) or nodes that were inferred to be migratory with a probability >0.8 (b) with non-migratory ancestors. The probability that the ancestor was non-migratory, as inferred from ancestral character estimation, is shown along each possible case. Note that only those cases are listed where this probability is >0.5, i.e. the node is more likely to be non-migratory than migratory. The greater this value, the higher is our confidence that migration appeared on this branch. Also shown are the ancestral nodes' posterior support, the 95% highest posterior density (HPD) interval of the nodes' age, along with the most likely distribution of these nodes and the probability that the node was in this state, as inferred in the ancestral area reconstruction. Geographic distribution is abbreviated as: Pa – Palaearctic; Na – Nearctic; At – Afrotropical; Nt – Neotropical; Im – Indomalayan; Au – Australasian. Node numbers appearing in (b) are shown in *Figure 3*

3. táblázat A vágómadár-alakúak törzsfejlődése során a vonulás egymástól függetlenül többször megjelent. Ez a táblázat azokat a vonuló fajokat (a) vagy közös ősöket (b) mutatja, amelyek nagy valószínűséggel vonulók voltak (>0.8 valószínűséggel). Mindegyik esetben fel van tüntetve: (i) a vonuló faj (ős) jelenlegi (becsült) előfordulása, (ii) a közvetlen ősük becsült kora, (iii) a közvetlen ős filogenetikai helyzetének pontossága, (iv) annak a valószínűsége, hogy a közvetlen ős nem-vonuló volt, (v) a közvetlen ős rekonstruált ősi elterjedési területe, illetve (vi) annak a valószínűsége, hogy az ősi elterjedés ténylegesen ebben az állapotban volt. Csak azok az esetek szerepelnek, ahol a közvetlen ős legalább 0.5 valószínűséggel helytülő volt. Minél nagyobb ez az érték, annál bizonyosabb, hogy a vonulás ténylegesen ezen az ágon alakulhatott ki. A földrajzi elterjedések rövidítése: Pa – Palearktisz; Na – Nearktisz; At – Afrotropisz; Nt – Neotropisz; Im – Indomaláj; Au – Ausztrálázsiai. A (b)-ben szereplő számok közös ősöket jelölnek, amelyeknek helyzete a *3. ábrán* látható

Figure 3. Bayesian ancestral state reconstruction of migratory behavior in Accipitriformes. Tip labels show migratory behavior in extant species (white: non-migratory; black: partial or complete migrant). Pie charts labelling the nodes show the probability that the given species was migratory (black) or non-migratory (white). A completely black chart indicates that the ancestor was migratory with high posterior probability. The size of the charts is proportional to the posterior support of specific nodes: small charts indicate high uncertainty in phylogenetic reconstruction

3. ábra Vonulási viselkedés rekonstrukciója a vágómadár-alakúak törzsfáján. A fajnevek melletti négyzetek színe az illető fajok vonulási viselkedését jelöli (fehér – helytülő; fekete – részleges vagy teljes vonuló). A közös ősöket jelölő kördiagrammok mutatják annak a valószínűségét, hogy az illető faj vonuló volt (fekete). A kördiagrammok mérete egyenesen arányos az illető csomópontok rekonstrukciójának pontosságával

Evolution of migration in Accipitriformes

Table 3 shows possible cases of independent appearance of migratory behavior in Accipitriformes. Since the presence of migration is quite variable among species, our reconstruction of ancestral states involves considerable uncertainty in some nodes. On the other hand, in several cases (e.g. *Buteo* hawks, *Accipiter* hawks or *Haliaeetus* eagles), closely related species are all migratory, with the consequence that the most likely state for the ancestor of these species is being migratory.

Two important patterns can be seen from this list of evolutionary events. First, most of
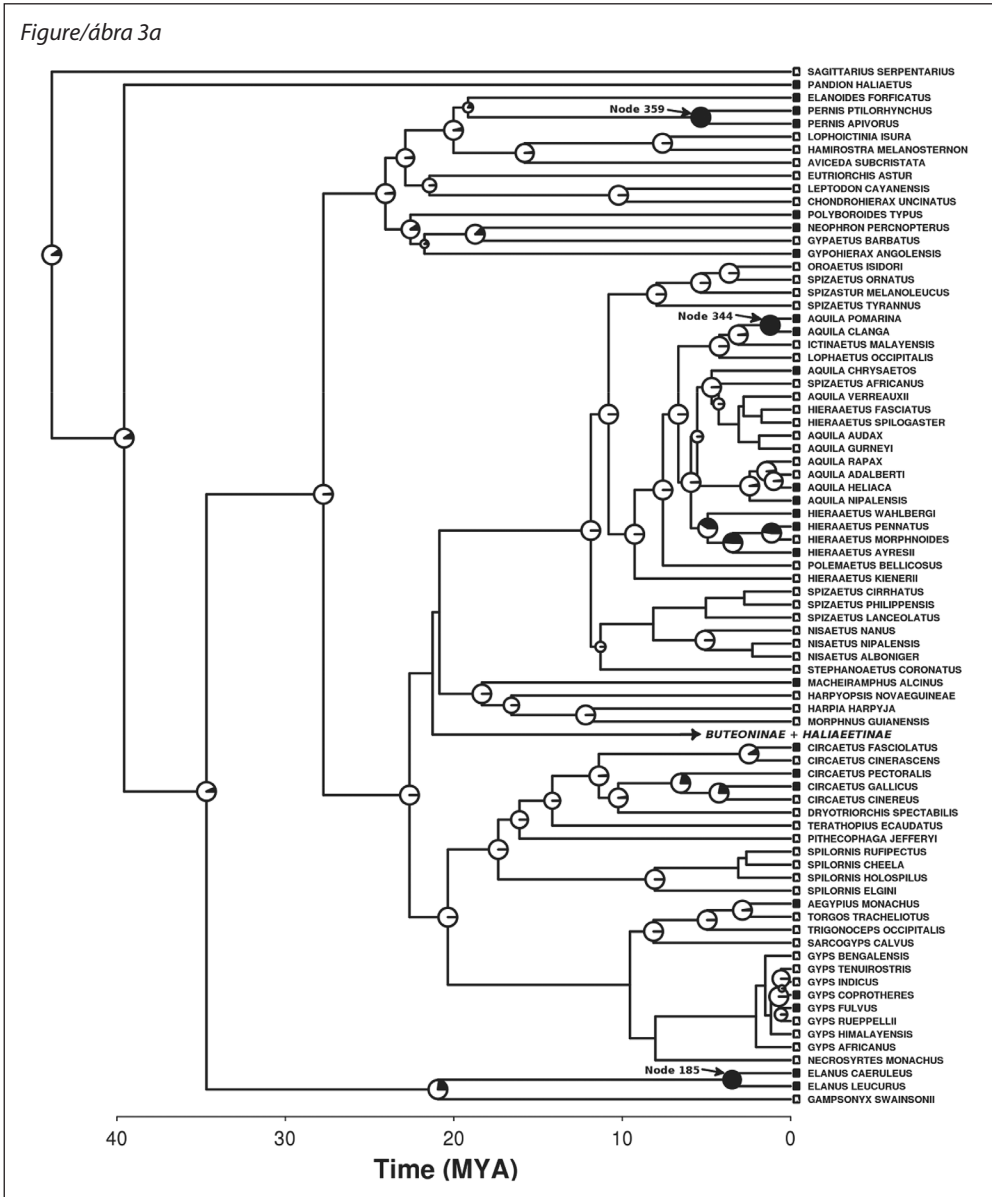
Figure/ábra 3a

Figure/ábra 3b
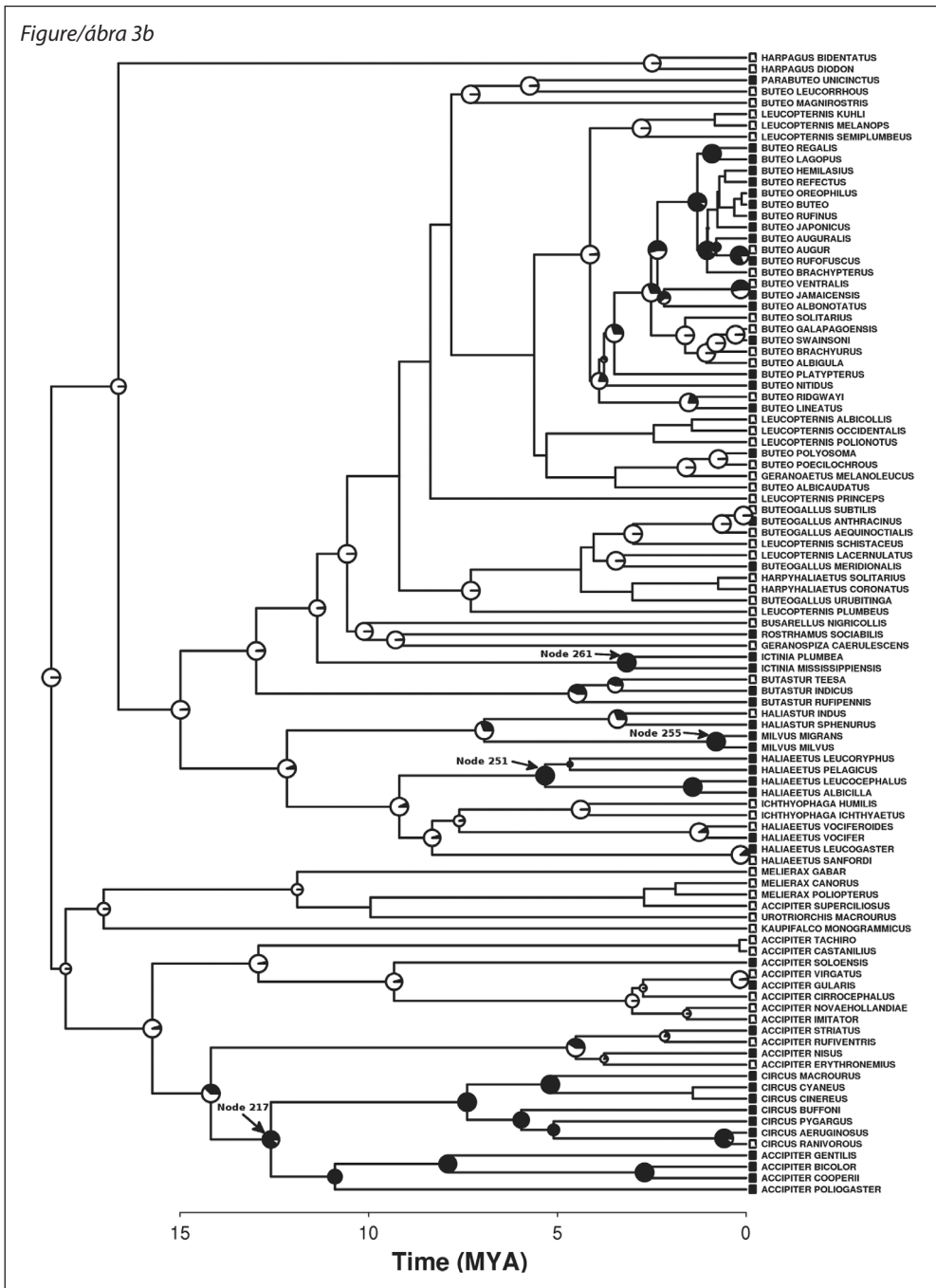
Figure 4. Evolutionary transition rates between levels of migratoriness in birds of prey

4. ábra Vonulási stratégiák közötti evolúciós tranzíciós ráták
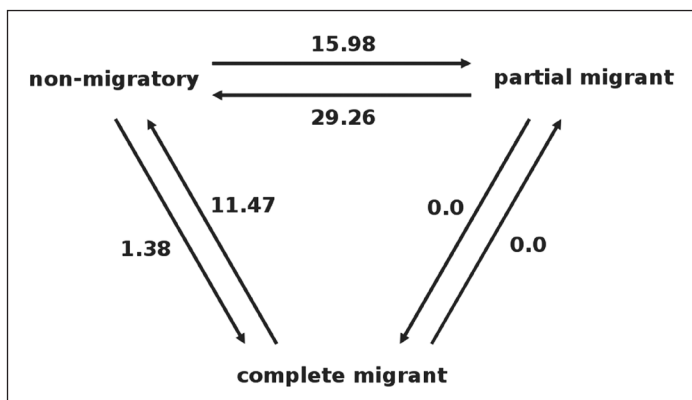
the independent events leading to the appearance of migration involve single species *(Table 3a)*. In these situations, the upper bound for the time of appearance of migration is the age of that particular species (i.e. when it split off from its ancestor). Hence, migration could have appeared in these lineages recently; this possibility is supported by the observation that most of these upper bounds are not older than the beginning of the Pliocene epoch (~5.3 Mya). On the other hand, nodes that are reconstructed as migratory provide lower estimates for the origin of migration *(Table 3b)*. The oldest of these nodes is the common ancestor of the Goshawk and the harriers, with an estimated age of 12.9 Mya (95% highest posterior density interval: 16.3–10.1 Mya).

Second, a tropical or partly tropical ancestral area was inferred for the ancestor of most migratory lineages. There are very few exceptions from this pattern. For instance, our results suggest that *Aquila heliaca* and *A. nipalensis* (both migratory) evolved within the Palearctic from non-migratory ancestors. Similarly, two migratory *Buteo* hawks (*B. platypterus* and *B. nitidus*) seem to have evolved in the Nearctic from non-migratory ancestors, although in these latter cases posterior support for the phylogenetic reconstruction is quite low (0.32 for the ancestor

of *B. nitidus*). In sum, our results provide broad support for a tropical origin of migratory species.

Comparative analyzes

Analysis of the transition rates using BayesTraits Multistate module revealed that both complete and partial migrations evolved from a non-migratory state, but evolutionary transitions between partial and complete migration or vice versa are very low *(Figure 4)*, suggesting that partial migration is not a transitional state between complete migration or lack of migration.

Multivariate analysis of the ecological factors influencing migration suggests that only diet breadth and habitat are associated with migration *(Table 4)*. However, when this multivariate model is simplified by backward elimination of nonsignificant parameters, habitat type does not remain significant. Hence, the only ecological factor associated significantly with migration was winter diet breadth: species with a more generalist winter diet are more likely to be migratory.

Finally, we performed directional tests between migratory behavior on one hand and geographic distribution and diet breadth, respectively, on the other. In the first case, we found that evolutionary transitions to

	Parameter estimate	lower 95% confidence interval	upper 95% confidence interval	P-value
Habitat (Forest/Open)	1.30	0.13	2.27	0.02
Old/New World	0.78	-0.75	1.75	0.16
log(body mass)	-0.06	-0.51	0.33	0.78
Diet generalism	0.44	0.21	0.75	<0.01
Reliance on warm-blooded prey or carcass	0.00	-0.21	0.23	0.99
Habitat : Old/New World interaction	-1.39	-3.35	0.40	0.18

Table 4. Factors affecting the occurrence of migration in diurnal birds of prey (N=151 species); parameter estimates, their 95% confidence intervals and P-values from a multivariate mixed effect models controlling for phylogeny

4. táblázat A vonulás előfordulását befolyásoló tényezők vágómadár-alakúaknál (N=151 faj); filogenetikai viszonyokra kontrollált többváltozós kevert lineáris modellből származó becsült értékek, azok 95%-os konfidenciaintervalluma és a P-értékek

migration occured with a higher rate in lineages with a tropical distribution (9.08 vs. 0.73 in lineages with a non-tropical distribution) *(Figure 5a)*. Furthermore, transitions to a non-tropical distribution are much more likely in migratory (30.01) than in non-migratory lineages (0.15). The transition rates also revealed that switches in the geographic distribution from a tropical to a non-tropical distribution or vice versa are virtually lacking in non-migratory lineages, whereas they occur at a relatively high rate in migrants *(Figure 5a)*. In the second case, transition rates indicate that migration
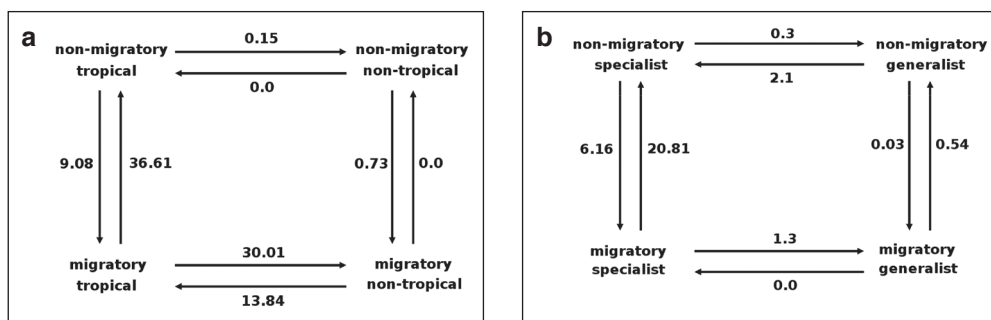

Figure 5. Results from pairwise directional test between migratory behavior (migratory or non-migratory) and (a) geographic distribution: tropical (species not present in the Nearctic or the Palearctic) or non-tropical (species present in the Nearctic or the Palearctic); (b) diet specificity: specialist (consumes <5 types of food) or generalist (at least 5 food types consumed). The graph show transition rates among pairs of traits indicating the rate with which these evolutionary changes are inferred to have occurred on the phylogeny

5. ábra A vonulási viselkedés és a földrajzi elterjedés (a) illetve a táplálékspecializáció (b) közötti direkcionális tesztek eredményei. A vonulási viselkedés kódolása: vonuló (részlegesen vagy teljesen) vagy nem vonuló. A földrajzi elterjedés kódolása: trópusi (nem fordul elő sem a Palearktiszban sem a Nearktiszban) vagy nem trópusi (az előző ellentettje). A táplálékspecializáció kódolása: specialista (<5 tápláléktípust fogyaszt) vagy generalista (az előző ellentettje). Az ábra a különböző jellegpárok közötti evolúciós tranzíciós rátákat mutatja

is more likely to arise in specialist lineages and that a generalist diet is more likely to evolve in migrants than in non-migrants. Hence, it appears that diet breadth evolves as in response to the selective environments imposed by migratoriness, rather than predisposing species for migration.

Discussion

Phylogeny of Accipitriformes

The phylogenetic relationships among and within major lineages of Accipitriformes have been extensively studied before (e.g. Wink & Sauer-Gürth 2004, Helbig *et al*. 2005, Lerner & Mindell 2005, Griffths *et al*. 2007, do Amaral *et al*. 2009). Here, we combined all available genetic information to produce a multi-gene phylogeny of Accipitriformes with a broad taxonomic sampling, including approximately two-thirds of extant species of accipitrid birds of prey. The phylogenetic hypothesis obtained from this analysis is broadly congruent with previous reports showing that several traditionally established clades are in fact polyphyletic or paraphyletic. For instance, Old World vultures form a polyphyletic clade comprised of: (1) Gypaetinae which is monophyletic with Perninae and includes the Bearded Vulture *Gypaetus barbatus* and the Egyptian Vulture *Neophron percnopterus* and (2) Aegypiinae which contains all remaining Old World vultures and is the sister clade of Circaetinae. *Accipiter* hawks are paraphyletic and should include harriers (*Circus* spp.), which are closely related to the clade containing goshawks (see also Breman *et al*. 2013 for a more detailed analysis). In addition, we also observed widespread paraphyly in aquiline eagles and buteonine hawks, as

reported previously (Helbig *et al*. 2005, do Amaral *et al*. 2009).

On the other hand, we also observed several discrepancies in the higher level relationships of Accipitridae between our reconstructions and those of obtained from previous studies (e.g. Lerner & Mindell 2005, Griffths *et al*. 2007). For instance, we recovered Aquilinae and Harpiinae as sister clades, albeit with relatively low support (posterior probability: 0.45). *Harpagus* kites were inferred as the sister group of the clade containing Buteoninae and Haliaeetinae with relatively high support (posterior probability: 0.83). Lastly, the sister relationship between the clade containing Aquilinae and Harpiinae on one hand and Buteoninae, Haliaeetinae and Accipitrinae on the other was strongly supported (posterior probability: 1).

Historical biogeography and evolution of migration in Accipitriformes

Our ancestral state reconstruction suggests that migratory behavior in birds of prey evolved multiple times. Most of these appear to be relatively recent events (occurring during the Pliocene or Pleistocene, i.e. <5 million years ago). In one case however, migratory behavior appears to be much more ancient. In true hawks (Accipitrinae) migration appears to have evolved approximately 14-12 million years ago, during the middle of the Miocene period. By comparison, do Amaral *et al*. (2009) reconstructed the origin of migration in one *Buteo* clade at approximately 5 million years ago, a result that is supportedby our analyses *(Figure 3b)*. More direct estimates based on the age distribution of fossilized individuals (specifically, the lack of juveniles) found at Olduvai Gorge, in Tanzania, suggest that this site was a wintering location of shorebirds belon-

ging to Charadriidae 1.9-1.74 million years ago, implying that migration was present at this time (Louchart 2008). Hence, our estimate for the origin of migration in accipitrid hawks appears to be one of the oldest dates published so far. Such estimates are important (yet remarkably lacking) if we are to understand the evolution of migration in a constantly changing spatiotemporal context at a global scale (Louchart 2008).

The middle of the Miocene period saw a series of global cooling events (Zachos *et al*. 2001), which resulted in the expansion of grasslands and contraction of forest habitats, possibly opening new niches for birds of prey. Our analyses suggest that accipitrid hawks appeared shortly before this period, probably in the Afrotropical realm and colonized other parts of the world shortly thereafter. Since most extant species belonging to this lineage are at least partly migratory today, it is likely that their ancestor also performed seasonal migratory movements. Alternatively, migration could have evolved separately in these lineages due to similar selective environments (i.e. as a consequence of convergent evolution rather than shared phylogenetic background). Since migration is a phylogenetically labile trait that can evolve very quickly (see e.g. Zink 2011), independent evolution in multiple lineages experiencing similar selective environments is a plausible scenario for the occurrence of migratory behavior in clusters of closely related species. However, this explanation is clearly less parsimonious in explaining the evolution of migration in true hawks, since this group contains both temperate-tropical and intra-tropical migrants on different continents, which would imply simultaneous, independent selection for migration in a wide variety of different environments on different parts of the world.

Joint reconstruction of ancestral distribution and migratory behavior suggests that in raptors, migration appeared mostly in species with a southern origin. This is further strengthened by our directional analyses, which suggest that migration is more likely to evolve in tropical species and that migratory raptors are more likely to switch to a non-tropical breeding range, hence suggesting that migratory behavior and range expansions are evolving in parallel. Interestingly, we also found that the transition rate from a tropical to non-tropical distribution (and vice versa) is very low in non-migratory raptors, but not in migrants, suggesting that migration greatly enhanced range expansions in this group of birds.

The southern origin of migratory raptors is in line with previous studies obtaining similar results in a variety of taxonomic groups (Joseph *et al*. 1999, Outlaw *et al*. 2003, Milá *et al*. 2006). We have to emphasize, however, that this result helps little in understanding the evolution of migration in birds of prey. As we have shown, all major lineages within Accipitridae trace back their origin to one of the southern biogeographic realms. Hence, both migratory and non-migratory species currently inhabiting the temperate zone descend from the tropics. Our analyses do suggest, however, that migration is more likely to emerge in the tropics than in the temperate zone, and that migratory birds are more likely to disperse and switch from a tropical distribution to a non-tropical one. Hence, the relationship between colonization of the temperate zone and the evolution of migration could be the reverse of what traditionally is assumed, i.e. migratory birds (intratropical migrants) more likely to colonize novel habitats and expand to North. This hypothesis could be tested in the future by investigating the ecological and behavioral traits pro-

moting the colonization of temperate habitats in a broader sample of birds.

Since all birds of prey are of tropical ancestry, their ancestors must have undergone range expansions to the temperate region. Yet, not all of these species became migratory. We found that winter diet specialization predicts the occurrence of migration in accipitrid birds of prey, with migratory species relying on more variable diets. The ability to feed on a wide source of food types could greatly enhance the probability that a species survives the winter in the temperate zone where food availability is much lower during the winter (Newton 2008). Hence, this could at least partly explain interspecific differences in migratoriness. Interestingly, we found no association between migration and reliance on warm-blooded prey or carcass, suggesting that these food sources alone might not be enough to sustain most species in the temperate zone during winter. For instance, two of the four vulture species that occur in Europe (the Griffon Vulture *Gyps fulvus*, and the Egyptian Vulture) are migratory, despite the fact that their major food source – carcass – is most likely available year-round. However, these food sources might also show sea-sonal fluctuations (e.g. Kendall *et al.* 2012). Alternatively, other factors, such as selection for early breeding or extended breeding season could generate differences in migratoriness between populations or species (e.g. Tökölyi & Barta 2011, Camacho 2013). Further work is required to clarify ecological determinants of migration in birds of prey.

Acknowledgements

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Pre-migration roost site use and timing of post-nuptial migration of Red-footed Falcons *(Falco vespertinus)* revealed by satellite tracking

Péter Fehérvári[1*], Bence Lázár[2], Péter Palatitz[3], Szabolcs Solt[3], Attila Nagy[4], Mátyás Prommer[3], Károly Nagy[3] & Andrea Harnos[2]

Abstract Red-footed Falcons are gregarious trans-equatorial migrants, forming up to several thousand strong roost sites after the breeding season and before commencing migration. This pre-migration period is presumed to play a major role in defining the survival of long-range migrants. Here we investigate the autumn movements of 8 individuals caught and satellite-tagged within the Carpathian Basin. We found that birds may use multiple roost sites that can be separated by large distances. A single individual's home range was 88 km² (80% kernel home range) and was near concentrical to the roost site. Two individuals travelled to southern Ukraine soon after tag-deployment. Our results demonstrate that even a small number of satellite tagged birds show behavioural plasticity in terms of roost site selection indicating that post-breeding foraging habitat choice decisions may have substantial variability. The night localization points of birds marked out 2 and 5 yet unknown potential roost sites in Hungary and in the Ukraine, respectively. Using the data of an international weekly survey (2006–2011) carried out in the Carpathian Basin, we cross-referenced the departure dates of tagged individuals with the 6 year means of counted individuals. The tagged birds initiated migration with the first 25% percent of the surveyed population.

Keywords: *Falco vespertinus*, post-nuptial migration, Platform Terminal Transmitter, gregarious behaviour, home range extent

Összefoglalás A transzekvatoriális vonuló kék vércsék a fészkelési időszak után, a vonulást megelőző időszakban csoportos éjszakázó, úgynevezett gyülekezőhelyet alakítanak ki. Ez a periódus feltehetően igen fontos a hosszú távú vonulók túlélése szempontjából. Ebben az időszakban a Kárpát-medence különböző területein 8, műholdas nyomkövetővel felszerelt madár őszi mozgásmintázatát vizsgáltuk. Eredményeink szerint a madarak akár több, egymástól nagy távolságra lévő gyülekezőhelyet is használhatnak. Az egyik egyed mozgáskörzete 88 km² volt (80% Kernel home range becslés), és közel koncentrikusan helyezkedett el a gyülekezőhelyhez viszonyítva. Két egyed Dél-Ukrajnába repült nem sokkal a jeladó felhelyezése után. Eredményeink azt mutatják, hogy még a kisszámú, műholdas jeladóval felszerelt madár viselkedése is nagyban különbözött. Az éjszakai adatok alapján 2 magyarországi, valamint 6 dél-ukrajnai lehetséges új gyülekezőhelyet határoltunk be. A Kárpát-medencében 2006 és 2011 között hetenként végzett nemzetközi felmérés adatait felhasználva összevetettük a jelölt madarak indulási adatait a populáció 6 éves átlagaival. A jelölt madarak a felmért populáció első 25%-ával együtt kezdték a vonulást.

Kulcsszavak: *Falco vespertinus,* őszi vonulás, műholdas jeladó, pre-migráció, mozgáskörzet, gyülekezőhely

[1] *Department of Zoology, Hungarian Natural History Museum, 1088 Budapest, Baross utca 13., Hungary, e-mail: fpeter17@gmail.com*
[2] *Department of Biomathematics and Informatics, Faculty of Veterinary Sciences, Szent István University, 1078 Budapest, István utca 2., Hungary*
[3]*Red-footed Falcon Conservation Working Group, MME/BirdLife Hungary, 1121 Budapest, Költő utca 21., Hungary*
[4] *Milvus Group, Bird and Nature Conservation Association, 540343, Crinului St. 22, Tirgu Mures, Romania*
*corresponding author

Introduction

Long-range migrant birds have precisely timed annual cycles that can be categorized into discrete periods, each having a considerable impact on individual life history (Alerstam 1990). Despite its presumable influence on survival, the pre-migration period – i.e. the period after breeding and before the commencement of autumn migration (Rivera *et al.* 1998, 1999, Pagen *et al.* 2000) – has been scarcely studied, mainly due to methodological restraints (de Frutos 2008). Basically, this period may be utilized to optimize individual condition for migration, to select future breeding habitats and aid spring navigation (Mitchell *et al.* 2010). Several markedly differing behavioural patterns have evolved to achieve this goal. Dispersal from the natal breeding grounds is typical, but the magnitude of dispersion may be different amongst age and sex groups (Morton 1992). Forming of large foraging flocks (e.g. Caccamise *et al.* 1983, Eiserer 1984, Metcalfe & Furness 1984) is not uncommon, and several species may also form common large roost sites (Newton 1998, Kruckenberg & Borbach-Jaene 2004, de Frutos *et al.* 2007, Lambertucci *et al.* 2008, Catry *et al.* 2010). Intriguingly, only a handful of raptors breeding in the Western Palaearctic are known to form pre-migratory and wintering roost sites (Ferguson-Lees & Christie 2001). One of these is the Red-footed Falcon – a trans-equatorial migrant – of high nature conservation concern ('near-threatened' in IUCN Red List, ANNEX I of EC Birds directive 79/409/EEC, Annex I of the Bonn Convention). The core of the EU population breeds in the Carpathian Basin (Eastern Austria, Hungary, Western Romania and Northern Serbia) forming the western border of the range

(Palatitz *et al.* 2009). Although they have long been recognized as facultative colonial breeders (Horváth 1956, Fehérvári *et al.* 2009, Fehérvári *et al.* 2012), their autumn roosting behaviour has only recently been described in detail (Borbáth & Zalai 2005). Today, a total of 20 stable roost sites (i.e. with birds present in every year since the discovery of the roost site) and 37 occasional (i.e. used in at least one year for more than one week in the period between 2004-2011) are known within the Carpathian Basin. These sites have been surveyed weekly (from mid August to early October) since 2006 in Hungary, Northern Serbia and Western Romania (Palatitz *et al.* 2010). Despite the extensive data on the spatial and temporal patterns on the number of birds present, little is known on the turnover rates and individual roost site selection. A single, second calendar year male marked with a VHF radio telemetry tag was shown to appear at several distinct roost sites in 2006 (Palatitz *et al.* 2011). This bird was the first to show the possibility of individual within-in-season movements between roosts (Fehérvári *et al.* 2007). However, there is no knowledge on the temporal and spatial dynamics of individual roost site use.

From a conservation perspective, being a gregarious in the post fledgling period makes large number of birds vulnerable to even small scale and/or local threats. The roost sites are often highly localized, found in a small group of trees, or even a single tree may suffice. In many cases, dirt roads are in the vicinity making unintentional disturbance probable. Other typical threats may be agricultural works, or felling of trees in the pre-migration period, but poaching has also been documented (Palatitz *et al.* 2009). Where the general protection against killing of the species is resolved, the roost sites can

be conserved with relative ease. Active protection against disturbance and other threatening factors is needed only in short time period, and as these sites are highly localised, their protection hardly restrains large scale agricultural works or other human activities. Therefore, the knowledge of the location of roost sites is essential and often adequate for effective protection. Despite the fact that large, up to several thousand strong flocks may occur at a single site, it is remarkably challenging to find the exact location of the roost. Birds will approach the roosts in low light conditions often close to ground level and are less vocal compared to the breeding period (Fehérvári *et al.* in prep).

With agricultural intensification pacing up in Central and Eastern Europe, the conservation management of foraging areas surrounding the roost sites may also become important. However, effective measures can only be implemented if the spatial extent of foraging area and the habitat preferences are well established. Knowing the size of the hunting area may help understand the post-fledging biology and could aid designing specific large scale conservation measures (de Frutos 2008).

In the current paper we used the data of 8 satellite tagged Red-footed Falcons to shed light on individual roost site selection patterns, the extent of individual foraging area and to locate new possible roost sites. The initial aim of deploying the tags was to reveal the autumn migratory routes and wintering grounds (Fehérvári *et al.* in prep), however the data cumulated in the pre-migratory period will hopefully help in both elaborating direct conservation measures and reveal certain aspects of an important yet hardly known time period of an enigmatic raptor species.

Materials and Methods

Platform Terminal Transmitter

We mist-netted 8 adult female-above average weighed Red-footed Falcons and fitted them with 5 g solar Argos Platform Terminal Transmitters (PTT-100, Microwave Telemetry Inc.) during the breeding season of 2009. The PTTs were harnessed on the back of the birds with a 5 millimetre Teflon ribbon (Kenward 2001, Steenhof *et al.* 2006, Gschweng *et al.* 2008). At the time of harnessing, the 5 g PTT was before mass production phase and it had not been widely tested. Initially, we observed that the tiny PTT may sink under the feathers and may cover the solar panels. We overcame the issue by applying small plastic 'slippers' to lift the PTT out of the cover of the feathers. The whole mounting procedure was usually less than 45 minutes including all measurements and regular ringing activity. When possible, birds were revisited and followed for several days after tag deployment to ensure that the harness and the device is not altering their behaviour or flying capabilities. All birds were tagged at different breeding sites within the Carpathian Basin, seven in Hungary, and one in Western Romania.

The PTTs transmitted for 10 hours with 48 hour gaps in between two periods. When not transmitting, the device charged itself from the small solar panel on the surface. The transmitted signal was received via the ARGOS system and only location classes 3,2,1,0 were considered, A,B,Z were excluded due to low level of accuracy (Gschweng *et al.* 2008, López-López *et al.* 2009, Strandberg *et al.* 2009) In general, the reception of the signals by the Argos system is poor in Central Europe (in a circle of 1600 km radius around the Central Balkan with an approxi-

mately 1600 km radius), presumably due to the considerable background noise created by the numerous radio signal emitting devices like radars (Microwave Telemetry Inc. pers. comm.). Thus, bulk of the signals (79%) had to be excluded from the analyses, despite the fact that the pre-migration period is relatively long (mid-August to late September).

Extent of foraging area around roost sites

We applied kernel home range estimate (Worton 1989) on localization points that were obtained between 8 am and 6 pm during the whole pre-migration period. The smoothing parameter was calculated using the Least Square Cross Validation Technique (Seaman *et al.* 1999). Only a single individual provided sufficient number of high quality points (n=28) to allow home-range estimation. We report a conservative (80%) kernel estimate of foraging area to avoid overestimating and to surely exclude data points that may derive from days when a neighbouring roost site was visited.

It has to be noted that only a single individual's data was used in the analyses, thus the results are hardly representative of the population. We hypothesize that our results underestimate the extent of the true mean foraging area. Nonetheless the results presented rely on the best available data and allow to at least give a vague estimate that can be later used to fundament further studies (e.g. habitat use analyses) and active conservation measures.

Locating potentially new roost sites

To identify yet unknown potential roost sites used by the tagged individuals we initially selected all localization points obtained be-

tween 9 pm and 6 am. We then applied a minimum convex polygon (MCP) in case of multiple data points close (<10 km) to each other. Plotting these MCPs against known roost sites where tagged birds have been verified to spend the night allowed to estimate the general accuracy of obtained data. In some cases, the fitted MCPs did not cover the location of the known roost sites, therefore we visually estimated the potential extent of an error buffer of 5 km around the fitted MCPs. This error buffer seems to be relatively large, however the location of roost sites may slightly vary between years (Borbáth & Zalai 2005). Our aim was to identify an area from where observers will have a good chance of spotting low flying birds towards the roosts, instead of trying to pin-point the exact location of a potential new roost site. All buffered locations were then cross-referenced with the coordinates of all known roost sites. These coordinates derived from two separate sources; for roosts within the Carpathian Basin we used all roost locations that were found in 2006-2011, during the weekly pre-migration roost site surveys carried out in Hungary (Palatitz *et al.* 2010). We also used the data of a recent, yet unpublished country-wide breeding population survey carried out in the Ukraine (Kostenko 2009).

Assessing the frequency of roost site changes

When possible, we used the evening locations described above to calculate the number of sites visited, and the number of times roost sites were changed by the tracked individuals. However, the large gap in transmission of the PTTs probably hindered the discovery of all roost sites used. To at least partially overcome this bias, we also consi-

ID	Number of roost sites used	Number of roost site changes	Latitude range difference	Longitude range difference
Indiv. A	2	3	62 km	101 km
Indiv. B	1	0	38 km	56 km
Indiv. C	2	1	22 km	110 km
Indiv. D*	6	7	367 km	214 km
Indiv. E*	6	6	324 km	609 km

* Tagged Red-footed Falcons spending the pre-migration period in southern Ukraine.

Table 1. Number of roost sites used, number of times roost sites have been changed and the range difference of latitude and longitude of all coordinates obtained with PTTs of the 5 tracked birds. The first two parameters were calculated based on evening (between 9 pm and 6 am) locations, while the coordinate range differences were calculated based on all localization points. Birds spending their pre-migration period in the Ukraine seem to change roost sites more often, and utilize a larger area compared to individuals staying within the Carpathian Basin

1. táblázat A nyomonkövetett madarak (n=5) által használt gyülekezők száma, a gyülekezőhely váltások száma és a szélességi és hosszúsági eltérés terjedelme a pre-migrációs időszakban kapott lokalizációs pontok alapján. Az első két paramétert az éjszakai pontok alapján (este 9 és reggel 6 óra között helyi idő szerint) kaptuk. Az Ukrajnában tartozkodó madarak többször váltottak gyülekező helyet, illetve nagyobb területet jártak be Kárpát-medencében maradó társaikhoz képest

dered the location points obtained during the day. In case an individual had a valid location point after 15 p.m. over ~200 km from the previous roost site, we considered that it spent the night at a different location.

Migration timing

We defined the commencement of migration when the tracked individuals initiated a non-returning southward movement. As the tracked birds are hardly representative of the whole population, we cross-referenced the timing of migration to that observed during the pre-migration roost site surveys. These surveys are carried out by professionals and volunteers on a weekly (32nd-40th week of the year) basis at all known roost sites in Hungary and at most known roost sites in Western Romania. Participants positioned in look-out spots estimate the number of birds entering the roost site. Less often early morning counts are also made.

All analyses were carried out using QGIS 1.7.3 'Wroclaw' (Quantum GIS Development Team 2011) and R 2.13.1 (Calenge 2006, R Development Core Team 2011).

Results

A total of 5 of the 8 tagged individuals provided high quality localization points during the pre-migration period of 2009. In general we could show that most of the tracked individuals moved in between sites, only a single individual stayed in the vicinity of a single roost site *(Table 1)*. The 80% kernel home range estimate of a single individual (indiv. A) was 88 km^2 and was near concentrical around the roost site *(Figure 1)*.

Two tagged birds (indiv. D, indiv. E, see *Table 1* and *Figure 2*) left the Carpathian Basin and moved to southern Ukraine within days after PTT deployment, staying in the region until the onset of migration. The dis-
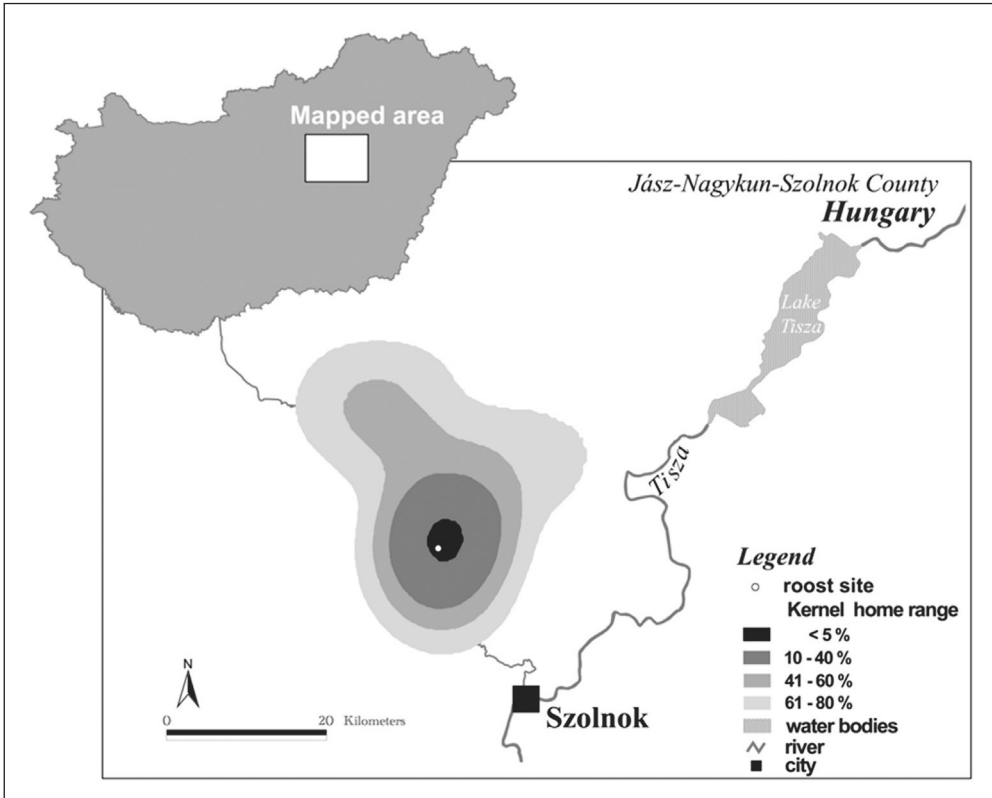
Figure 1. Kernel home-range estimate of pre-migration foraging area extent of a single individual (individual. A) based on satellite localization points during the day. The 80% Kernel home-range (88 km²) is highlighted and reported to allow conservative estimate of a foraging area extent and to exclude localization points deriving from days when the individual utilized a neighbouring roost site. The home-range is near concentrical, centring the roost site

1. ábra Nappali lokalizációs pontok alapján számított kernel home range becslés az A egyed esetében. A 80% kernel becslést használtuk, amely meglehetősen konzervatív, azonban ezzel elkerülhető azon pontok bevétele a becslésbe, amikor a madár egy szomszédos gyülekezőn aludt. A mérések alapján a madár mintegy 88 km²-es területet használt vadászterületként, ami szinte koncentrikusan helyezkedik el a gyülekezőhelyez képest

tance from the original trapping site to the first known roost site was 582 km, and 657 km for indiv. D and indiv. E, respectively. These two birds seemed to have changed roost sites more often, than those staying within the Carpathian Basin, and they have also moved in a larger area *(Table 1)*. Only one of the seven known roosting sites in the Ukraine was used by these birds, however we were able to identify 5 new poten-

tial roost sites *(Table 2, Figure 2)*. We were also able to locate two new potential roost sites in Hungary *(Table 2)*.

The timing of autumn migration of all tagged birds fell between the 37th and 38th week of the year *(Figure 3)*. When considering the change in the number of birds at the roost sites in the period between 2006-2011, the well visible decline (i.e. commencement of migration) fell between the

Country	Region/County	Latitude	Longitude
Hungary	Bács-Kiskun	19.927	46.724
Hungary	Hajdú-Bihar	21.128	47.392
Ukraine	Tatarbunarskyi	29.986	45.815
Ukraine	Ovidiopolskyi	30.484	46.160
Ukraine	Berezivskyi	30.883	47.415
Ukraine	Novoodeskyi	32.013	47.258
Ukraine	Berislavskyi	33.178	46.848

Table 1.   Coordinates of buffer polygon centroids of new potential Red-footed Falcon pre-migra-
              tion roost sites in Hungary and in the Ukraine
1. táblázat Az éjszakai lokalizációs pontok köré húzott pufferzónak súlyponti koordinátái. Ezek köze-
              lében feltehetően eddig ismeretlen gyülekezőhelyek vannak
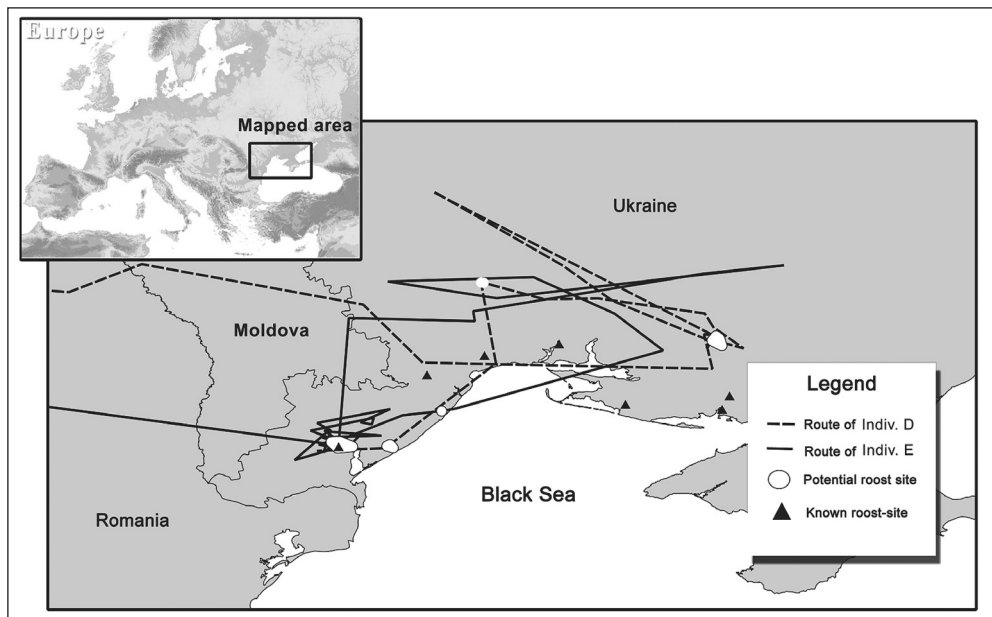
Figure 2. Movement patterns and roost site usage of two tagged Red-footed Falcons spending the
            pre-migration period in the southern Ukraine. These two individuals seemed to be more
            prone to change roost sites compared to the individuals remaining in the Carpathian Basin,
            and also moved in a larger area. Their localization points also helped identify 5 new poten-
            tial roost sites in the Ukraine
2. ábra   A pre-migrációs időszakban Ukrajnában tartózkodó madarak mozgásmintázata. Ez a két
            egyed többször váltott gyülekezőhelyet, és nagyobb területen is mozogtak. A tőlük szár-
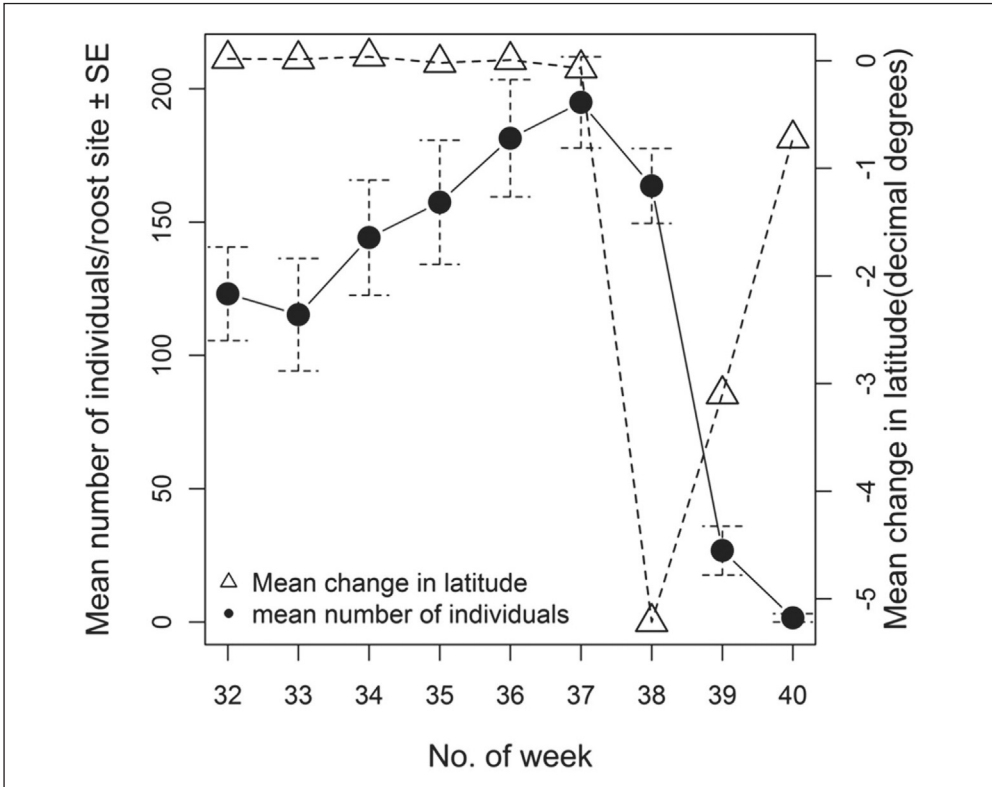   mazó pontok alapján 5 új gyülekezőhelyet sikerült azonosítani

Figure 3. Departure timing of satellite tagged Red-footed Falcons and temporal dynamics of the number of roost site using Red-footed Falcons. The first vertical axis refers to the mean number of individuals at the roost sites within the Carpathian Basin (2006–2011). The second vertical axis scales the relative change in mean latitude of consecutive localization points of the tagged individuals. The PTT tagged birds departed together with the earlier half of the population in between the 37th and 38th week of the year. Autumn migration is rapid, with the bulk of the population leaving the pre-migration roosts in a single week

3. ábra A jelölt kék vércsék vonulási időzítése és a szinkronszámlálások alapján becsült indulási idők. Az első függőleges tengelyen a szinkron számlálások alatt becsült madarak átlagai szerepelnek 2006 és 2011 között. A második függőleges tengelyen a relatív szélességi elmozdulás mértéke (két egymást követő pont közötti észak-déli távolság) látható. A jelölt madarak a korai indulókkal együtt kezdték meg vonulásukat a 37. és a 38. héten. Összességében a gyülekezők gyorsan ürülnek ki, a populáció vonulási időzítése meglepően konzervatív

38th and the 39th week, however a smaller proportion of the population is presumed to leave the pre-migration period a week earlier *(Figure 3)*. Roughly, the tagged birds departed together with the earliest individuals in the 38th week of the year.

Discussion

Our results suggest that Red-footed Falcon individuals may use multiple roost sites and that these roost sites may be separated by large distances. Intriguingly, birds may disperse to distant pre-migration sites – in our case to the northern Black Sea coastal region – even if

potential barriers, like the Eastern Carpathians, stand in their way. Moreover, tracked birds have been shown to change roost sites multiple times during the pre-migration period. The reasons of such a high mobility is yet unknown, we hypothesize that local weather and potential prey abundance may play a vital role in large scale movement decisions of these individuals. Red-footed Falcons often forage in flocks outside the breeding season, thus it might be possible that birds may get attracted to alter their roost site by joining a novel flock during the day.

Colour-ringed Red-footed Falcons from the Carpathian Basin have been re-sighted in Western and Northern Europe in autumn (Palatitz et al. 2009), however easterly movements have seldom been documented (Haraszthy & Palatitz 2009). For yet unknown reason the southern Ukraine seems to attract large number of Red-footed Falcons (Kostenko 2009), including two of the tagged birds. These Red-footed Falcons may originate from the local breeding population and/or from birds of the Russian and Kazakh plains, and as our example shows there is a connection with the Carpathian Basin population. The tracked birds showed a somewhat different behaviour in the Ukraine, with more frequent roost site changes separated by larger distances. This seldom documented plasticity in pre-migration strategies may derive from individual differences or from different prey composition and habitat usage compared to that in Hungary.

It is important to note that the species is not protected in the Ukraine (Palatitz et al. 2009), making large number of birds vulnerable to hunting (e.g. BirdLife International 2007). The lack of legislative background has recently been resolved as the Red-footed Falcon has been listed in Appendix I of the Bonn Convention (CMS) in November 2011. Thus, the Ukraine, as a full member of the CMS, is obliged to change the protection status of the species by 2014. However, the protection of roost sites is not so straightforward as they are most likely overlooked and their importance underestimated. An effective conservation measure against potential threats may be to encourage NGOs to maintain a constant monitoring of these sites. The participants monitoring may inform locals on the importance of the roost sites and report any potential threats. Our results may be used as reference points as the identified 5 new potential roost sites provide valuable information on the target areas worth searching.

Lesser Kestrels (Falco naumanni) are close relatives of Red-footed Falcons and have similar life history traits (Cramp & Simmons 1980). In Spain, the former species has been shown to use a mean of 350 ha of foraging area surrounding the roost sites (de Frutos 2008), which is similar in extent to that used in the breeding period (Donázar et al. 1993, Tella et al. 1998, Franco et al. 2004). However, the foraging area extent estimated in our study was an order of magnitude larger compared to that in the breeding period (Palatitz et al. 2011). Moreover, Lesser Kestrels had high within-season roost fidelity, whereas the tagged Red-footed Falcons seem to be less constrained to a single site. All this may indicate that albeit these species are close relatives and are both highly gregarious throughout their life-cycle, the mechanisms driving the individual selection of a roosting site may well be different. Red-footed Falcons leave the roosts at dawn and do not return until around dusk, therefore are less confined to the vicinity as in case of breeding. The reasons of a larger foraging area may be explained by increased intraspecific competition, as the number of individuals is larger at roost sites than in breeding colonies. Birds also lack the ne-

cessity to return to the site of origin after each successful hunt, thus can use larger foraging areas. A further plausible explanation may be that Red-footed Falcons alter their main prey source and/or their foraging habitat preference in the pre-migration period resulting in the observed pattern.

Our tracked birds have initiated their southward movements relatively early compared to the population. As the tagged individuals were chosen to be heavy, experienced adult females, this result is hardly surprising. However, interpreting the results has to be done with caution as two of the 6 departing individuals started their migration from southern Ukraine, from where no temporal data is available on the number of roosting birds. Nonetheless, all tagged falcons departed within the same week showing that global processes like photoperiod (Berthold 1996) and/or regional weather (Shamoun-Baranes *et al.* 2006) may dictate their departure timing. Seemingly, the whole initiation of autumn migration is rapid, as over 90% of the birds disappear from the roost sites of the Carpathian Basin in two weeks, with the majority departing on the same week. Apart from potential foraging and anti-predatory advantages (Weatherhead 1983), roosting may also be effective information sources to time departure for inexperienced juvenile birds. Cuing on conspecifics is not uncommon in social birds (Danchin *et al.* 2004, Ahlering *et al.* 2010) as public information may enhance the perception of resource quality of an individual. Red-footed Falcon roost sites may act as public information centres that allow assessing local mean foraging efficiency, predation risks and may also aid inexperienced migrants to adjust their departure decisions. Further suggesting this hypothesis is that most of the observations of Red-footed Falcons on migration are of small flocks instead of single individuals (Forsman

1999). These birds migrate on a broad front (Ferguson-Lees & Christie 2001) may utilize soaring, flapping flight (Shirihai *et al.* 2000) and may also migrate at night (Fehérvári *et. al,* unpublished data). Therefore, in theory are less confined to adjust departure decisions to weather, as in case of larger, soaring migrants. Thus, the gregarious behaviour en route may be deriving from common departure decisions at the roost site.

In conclusion, satellite telemetry of birds may not only provide insights on migration routes and wintering grounds, but may also help shed light on less known albeit important periods of individual life cycles. We present that even a small number of satellite tagged birds show behavioural plasticity in terms of roost site selection. Our results may help localize new potential roost sites, future conservation measures, and raise intriguing questions on individual decisions in the pre-migratory period.

Acknowledgements

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Numerical response of the Common Buzzard *Buteo buteo* to the changes in abundance of small mammals

László Tóth

László Tóth 2014. Numerical response of the Common Buzzard *Buteo buteo* to the changes in abundance of small mammals. – Ornis Hungarica 22(1): 48–56.

Abstract I investigated the numerical response of the Common Buzzard to variations in density of small mammals. The study was carried out at the Hortobágy region in 2000-2001. During nest visiting periods clutch size, number of hatched and fledged young were recorded. Population of small mammals were also monitored by live-trapping. Effect of weather on the survival of overwintering rodents was also investigated. There was significant difference in clutch size between 2000 and 2001 (means 2.3 and 3.1). It can be explained by the remarkable differences in abundance of small mammal populations between the two years. The density of rodents was very low (9 specimen/ha) in 2000. During 2001 the amount of small mammals has increased more than eightfold (76 specimen/ha). In February and March, 2000 there were 4 short mild periods alternating with 4 freezing periods, when distribution of significant precipitation (6-8 mm rainfall in each) coincided with the mild periods. Thus the overwintering population almost extincted from the area because the tunnel complexes of voles are repeatedly flooded and huge part of the animals died, resulting very low density during the breeding season. In 2001 there was no such alternating periods, mild weather started 3 weeks earlier, thus voles overwintered successfully and their numbers increased rapidly producing a peak during the breeding season.

Keywords: Common Vole, effect of weather, prey density, reproductive success, resident raptor

Összefoglalás A kisemlősök denzitás változásainak az egerészölyv reprodukciójára gyakorolt hatását (un. numerikus választ) vizsgáltam a Hortobágyon, 2000-2001-ben. A fészekellenőrzések során regisztráltam a lerakott tojások, valamint a kikelt és a kirepült fiókák számát. Az egyik legfontosabb zsákmánycsoport, a kisemlősök állomány változásait élvefogó csapdázással monitoroztam. Vizsgáltam az időjárásnak az áttelelő kisemlősök túlélésére gyakorolt hatását is. Az ölyvek átlagos fészekalja a két évben szignifikánsan különbözött: 2000-ben 2,3, míg 2001-ben 3,1 tojás volt. Ez a kisemlősök – 2000-ről 2001-re bekövetkezett – jelentős mértékű állománynövekedésével magyarázható. 2000-ben nagyon alacsony volt a kisemlősök egyedszáma (9 példány/ha), míg 2001-ben ennek nyolcszorosát regisztráltam (76 példány/ha). A kisemlősök egyedszámában tapasztalt óriási eltéréseket a vizsgált két év tél végi-tavasz eleji időjárási különbségei okozhatták. 2000 február-márciusában, a napi minimum hőmérsékleteket tekintetve, 4 rövid, enyhe periódus váltakozott 4 fagypont alattival, ugyanakkor az enyhe időszakokban jelentős mennyiségű (6-8 mm) eső is hullott. Ekkor az áttelelő kisemlősök járatai ismételten beáztak, az állatok megfáztak, kihűltek, szinte kipusztultak a területről, ezért létszámuk a költési időszakban is rendkívül alacsony volt. 2001-ben a tél vége sokkal enyhébb volt, 3 héttel korábban emelkedtek fagypont fölé a napi minimum hőmérsékletek, mint 2000-ben, nem alakultak ki váltakozó hideg-meleg időszakok sem. Ez kedvezően hatott az áttelelő kisemlősökre, létszámuk gyorsan emelkedett és nyár elejére mezei pocok gradáció alakult ki.

Kulcsszavak: időjárás hatása, mezei pocok, ragadozó madár, reprodukciós siker, zsákmány sűrűség

Institute of Agricultural and Environmental Sciences, Károly Róbert College, 3200 Gyöngyös, Mátrai út 36.
e-mail: ltoth@karolyrobert.hu

Introduction

The relationships between predators and variations in prey density can be separated into two types, numerical and functional responses, with the former describing how the per-capita reproductive rate changes with resource density and the latter how the consumption rate of individual consumers changes with respect to resource density (Solomon 1949). Numerical response may result by two different mechanism: i) increased rate of predator reproduction when prey is abundant or ii) attraction of predators to prey aggregations. The latter, the aggregational response of nomadic specialist predators usually occures without time lags, as their numerical responses are based on mobility, tracking changes in prey density without a time lag (Korpimäki & Norrdahl 1991). Delayed numerical response of resident generalist predators to increase in prey abundance is characterized by a time lag through higher natality and lower mortality (Goszczynski 1977). Delayed numerical response has been documented in resident mammalian predators (Korpimäki *et al*. 1991, Korpimäki & Krebs 1996, Krebs 1996, O'Donoghue *et al*. 1997), and in birds of prey as well (Keith *et al*. 1977, Doyle & Smith 1994, 2001, Rohner 1995, Nielsen 1999, 1996, Rohner *et al*. 2001). Three types of functional responses – linear, convex and sigmoid – are distinguished according to the nature of relationship between predation rate and prey density (Holling 1959). The functional response is mostly determined by foraging and behavior of the predator (Andersson & Erlinge 1977, Korpimäki & Norrdahl 1991). Numerical and functional responses have been shown in the same species as well (Luttich *et al*. 1971, Village 1987). Most studies of generalist predators have focussed on their functional response to only one prey species (Salamolard *et al*. 2000), however consumption by a generalist predator is expected to depend on the densities of all its major prey species (Yodzis 1994, Smout *et al*. 2010).

In this paper I investigate the response of a resident raptor, the Common Buzzard to variations in density of its main prey in the Hortobágy region, Hungary with the comparison of breeding performance of 2000 and 2001. There was great difference in density of rodents – which is the most important prey type of the species in the Great Hungarian Plain (Palatitz & Tóth 2003) – between the two years. Moreover, my aim was to investigate the effect of weather on population dynamics of small mammals – i.e. the role of winter/spring temperature and precipitation in the survival/abundance of overwintering animals which determines the population size of rodents later, during the breeding season.

Material and methods

Study area and species

The study was carried out in the Great Hungarian Plain at Hortobágy region during 2000-2001. The study area covers about 200 km^2 and is dominated by intensively cultivated fields, arable lands, grasslands and pastures. The region is one of the least forested part of Hungary. Buzzards bred in planted tree lines and forest patches with few hectare extension. There is only one large natural forest (200 hectares) in the study area near Ohat village.

The Common Buzzard is the most common raptor species in Hungary. The multi-

plication of the breeding populations since the 1980s is the result of the decrease of human persecution, the good adaptability of the species and the previous wood plantation programmes in the plains that enabled the species to spread in the lowlands (Tóth 2009). The number of breeding pairs exceeds 20000 (Ecsedi & Sándor 2004).

Breeding performance and small mammal abundance

In March when birds reconstructed old nest or built new ones the study area was eximaned to find the occupied nests each year. The founded nests were visited by climbing 5-7 times during the breeding season to record clutch size, number of hatched and fledged young.

Main food supply i.e. the population size and changes of small mammals were also monitored in one hectare large sampling area of a grassland in the centre of the study area. At the sampling area a 1 hectare (100×100 m) live-trapping grid was established, consisting of 121 livetraps in a 11×11 configuration with 10 m spacing. The trapping session was in June and it lasted 4 days. Traps were checked three times per day – in the morning, at noon and in the evening (traps were opened overnight as well). Individuals were uniquely marked with claw cutting applying a code table to distinguish the recaptured animals individually. Captured animales were identifed on species level. To assess population size I used the Minimum Number Alive (MNA) method introduced by Krebs (1966) for capture-mark-recapture data.

Data on weather conditions and statistical analysis

To study the effect of weather on the overwintering population of small mammals, data on weather conditions (from 1st February to 30th April in 2000 and 2001) were analysed. Daily minimum temperature values (in °C) and daily amount of precipitation (in mm) come from the nearest meteorological station of the Hungarian Meteorological Service in Debrecen, 45-50 km away from the center of the study area (available from the web site – under the code 128820 99999 DEBRECEN – in both years: ftp://ftp.ncdc. noaa.gov/pub/data/gsod/).

Comparing the clutch size, number of hatchlings and fledglings between 2000 and 2001. I used generalized linear model (GLM) with quasipoisson error distribution (Venables 2002). The statistical analysis was carried out in R 3.0.2 (R Core Team 2013). Completed first clutches were involved only, when mean values of clutch size were calculated. Moreover, mean number of hatchlings and fledglings were calculated based on those nests where one young hatched from eggs at least.

Results

Breeding success

There was considerable difference regarding the number of breeding pairs between 2000 and 2001. In 2000, 7 buzzard pairs started to breed on the study area, while during 2001 there were 13 breeding attempts. In 2000, 1 breeding attempt out of 7 failed during the incubation period, it was exluded from the analysis because the final number of laid eggs was unknown *(Table 1)*. In

Year	2000			2001			
	$\bar{x}$	SD	N	$\bar{x}$	SD	N	P-value
Number of laid eggs	2.3	0.52	6	3.1	0.86	11	0.0124
Number of hatched young	2.3	0.52	6	2.7	1.41	9	0.3355
Number of fledged young	1.8	0.98	6	2.0	1.33	9	0.4236

Table 1.   Breeding results of the Common Buzzard at Hortobágy region in 2000 and 2001 ($\bar{x}$ = mean, SD = standard deviaton, N = sample size, P-value from GLM)

1. táblázat Az egerészölyv költési eredményei 2000-ben és 2001-ben a Hortobágy térségében. Az adatok fészkenkénti átlagok ($\bar{x}$ = átlag, SD = szórás, N = fészkek száma, P-érték GLM-ből)

2001, 2 breeding attempts out of 13 were exluded when mean clutch size was calculated due to similar reason and another 2 nests with completed clutches were exluded from the analyses regarding mean values of hatched and fledged young due to nest failure during the incubation period *(Table 1)*. Mean values of the investigated three breeding parameters were greater in 2001 than in 2000, however significant difference was found in the mean number of laid eggs only (P=0.01242), buzzards laid approximately one more egg on average in 2001 *(Table 1)*.

Abundance of small mammal community

In 2000, the species diversity and the abundance of small mammal community were very low in the study area. Estimated population size (MNA) of small mammals was less than 10 specimen which belonged to three different species: 6 Common Voles *(Microtus*
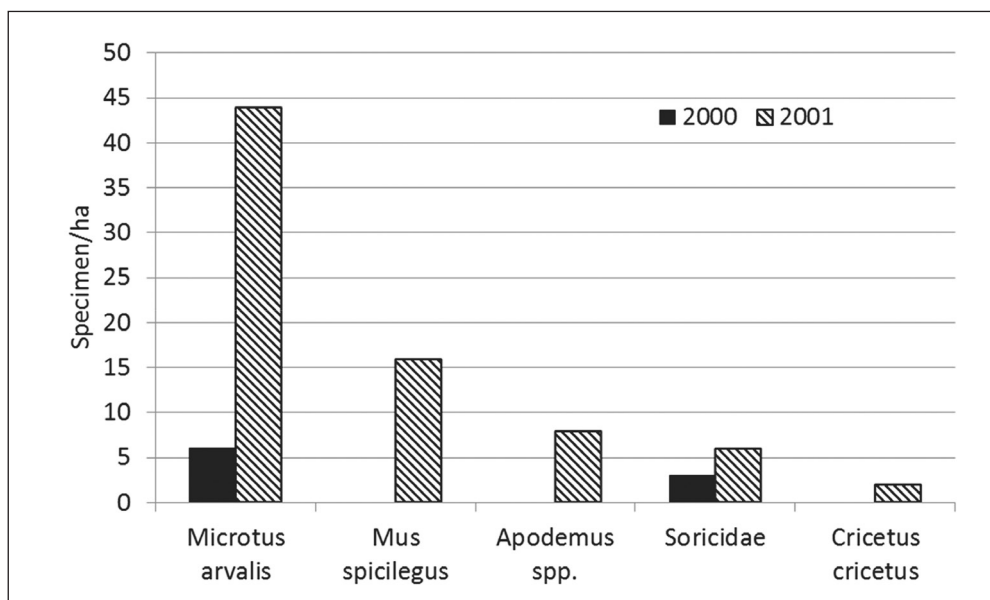

Figure 1. Density of small mammals during the breeding season in 2000 and 2001
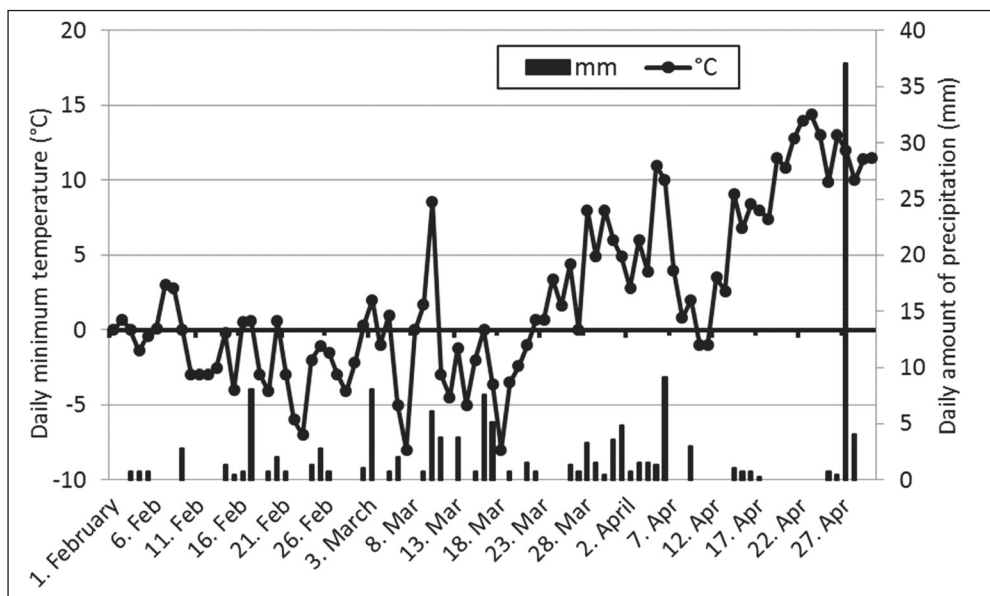*1. ábra*   A kisemlősök egyedsűrűsége a költési időszakban 2000-2001-ben

Figure 2. Daily minimum temperature and daily amount of precipitation in 2000, from February to April
2. ábra A napi minimum hőmérsékletek és a napi csapadék mennyisége 2000-ben, februártól áprilisig

arvalis), 2 Common Shrews *(Sorex araneus)* and 1 Bi-coloured White-toothed Shrew *(Crocidure leucodon)* were trapped *(Figure 1)*. In 2001 there were considerable changes in species composition and abundance of small mammals. During the breeding season the amount of small mammals increased eightfold comparing to previous year, the total number of trapped animals (MNA) was 76 specimen *(Figure 1)*. Captured species were Common Vole, Steppe Mouse *(Mus spicilegus)*, Striped Field Mouse *(Apodemus agrarius)*, Wood Mouse *(A. sylvaticus)*, Yellow-necked Mouse *(A. flavicollis)*, Pygmy Field Mouse *(A. uralensis)*, Common Shrew, Bi-coloured White-toothed Shrew, Pygmy Shrew *(S. minutus)* and Common Hamster *(Cricetus cricetus)*. However, Common Vole and Steppe Mouse dominated the food supply, these two species accounted for 79% of trapped animals (44 and 16 specimen, respectively), while proportion of the other 8 species altogether was 21% *(Figure 1)*.

Weather conditions

There were some differences in weather conditions from February to April between 2000 and 2001. Average (±SD) monthly minimum temperature was similar in February (in 2000: -1.6±2.4 °C, in 2001: -2.0±3.5 °C), while in March and April these values differed considerably. Regarding the minimum values, March was colder in 2000 by 3.1 °C than in 2001 (average minimum: 0.0±4.3 °C and 3.1±3.3 °C, respectively). In April, the year of 2000 was warmer than 2001 (average minimum: 7.8±4.6 °C and 5.1±3.1 °C, respectively). Important difference can be observed in changes of daily minimum values. In 2000 the minimum temperature stayed below zero till 21th, March, however there were 5 short periods (7-8., 16-17. February, 2-3., 9-10., 16. March) when values exceeded zero *(Figure 2)*. In 2001 the last decade of February was rather cold, but from the 2nd of March daily
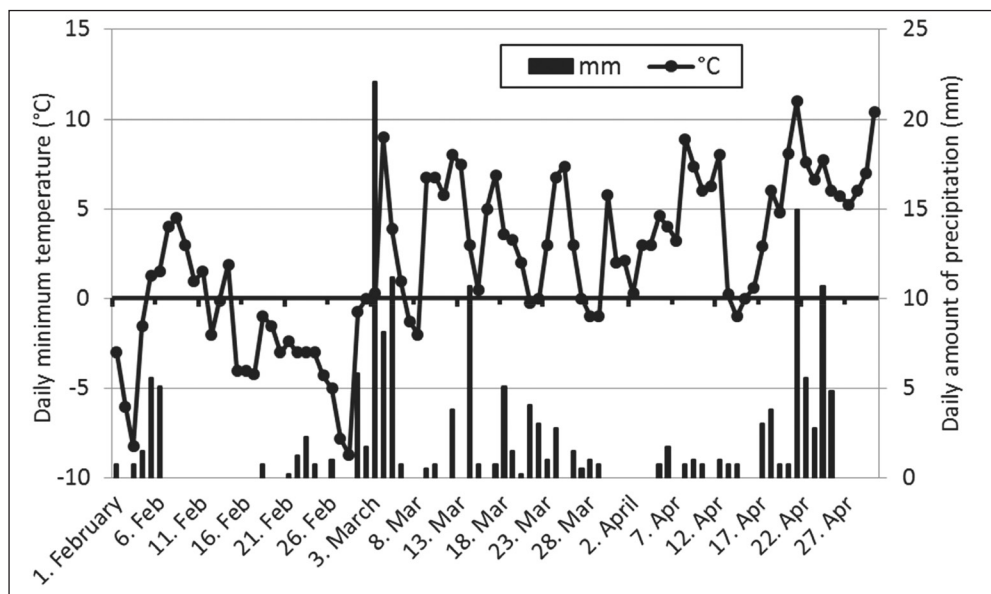
Figure 3. Daily minimum temperature and daily amount of precipitation in 2001, from February to April
3. ábra   A napi minimum hőmérsékletek és a napi csapadék mennyisége 2001-ben, februártól áprilisig

minimum temperature exceeded zero – almost permanently – i.e. mild weather started 3 weeks earlier than in the previous year *(Figure 3)*.

Monthly amounts of precipitation were similar during February in 2000 and 2001 (24 and 20 mm, respectively), during March and April there were differences between the two years (2000: 54, 67 mm, 2001: 89, 55 mm). Distribution of precipitation differed considerably during February and March between the two years: in 2000 there were 4 days (17. February, 3., 10., 16. March) when the amount of precipitation was significant (exceeded 6 mm), while in 2001 there were 2 occasions (3-5., 14. March) only *(Figure 2, 3)*.

Discussion

Breeding population size and reproductive success of raptors are determined by the availability of nesting sites, food supp-

ly and weather conditions (Korpimäki 1985, Kostrzewa & Kostrzewa 1990, Korpimäki & Norrdahl 1991, Butet & Leroux 1993, Jędrzejewski *et al.* 1994, Korpimäki 1994, Salamolard *et al.* 2000, Reif *et al.* 2001, Tóth & Palatitz 2003, Millon & Bretagnolle 2008, Millon *et al.* 2008, also see a review in Csörgő *et al.* 2012). Nest predation can also play an important role regarding breeding success in fragmented habitats, as well (Chalfoun *et al.* 2002). I found considerable differences in the number of breeding pairs and their breeding success of the studied buzzard population between 2000 and 2001. In 2001 the number of breeding pairs increased twofold comparing to the previous year (from 7 to 13 pairs). There was significant difference in clutch size – mean number of laid eggs was greater in 2001 than in 2000. These changes can be explained by the remarkable differences in abundance of small mammal population between the two years. The density of rodents

was very low in 2000 (9 specimen/ha). During 2001 the amount of small mammals has increased more than eightfold (76 specimen/ha). Particularly the population change of the Common Vole was drastic, their density has increased from 6 to 44 specimen/ha. However, there were no significant differences regarding the number of hatchlings and fledglings between the two years. This can be resulted by the higher predation rate in 2001. That year 4 out of 13 nests failed (31%) due to predation in contrast with 14% of 2000. As a result, success of chick raising decreased (there were no hatched young in four nests), thus predation could mask the positive effect of high vole density on reproduction in 2001.

Weather can affect reproductive success either directly – failure of eggs and young due to heavy rainfall and low temperature – or indirectly, e.g. decreasing food availability. Weather conditions during winter and spring determine the overwintering success of small mammal populations. In this respect the most important factors are the changes of temperature and precipitation at the end of winter and the beginning of spring. Overwintering population faces the highest risk when short periods of temperature below and above zero alternates and there is significant rainfall during the mild periods. The tunnel complexes of voles are flooded and huge part of the overwintering animals may die by the cold. During 2000 (in February and March) there were 4 short periods (16-17. February, 2-3., 9-10., 16. March)

when mimimum temperature exceeded zero alternating with 4 freezing periods 3-4 degree below zero and lasted 12-14 days. The distribution of significant precipitation (6-8 mm rainfall) coincided with the 4 mild periods, thus the overwintering population almost extincted from the area resulting very low density of small mammals during the breeding season. In 2001 the above mentioned conditions were much more favourable for the small mammal population. There was no alternating mild and freezing periods, mild weather started 3 weeks earlier than in the previous year (March was extraordinaly cold in 2000). Thus voles overwintered successfully and their numbers increased rapidly producing a peak during the breeding season.

Acknowledgement

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Simultaneous effect of habitat and age on reproductive success of Imperial Eagles *(Aquila heliaca)* in Hungary

Márton Horváth[1*], Tamás Szitta[1], János Bagyura[1], Imre Fatér[1], Gábor Firmánszky[1] & Csaba Moskát[2]

Abstract An unexpected expansion of the Eastern Imperial Eagle *(Aquila heliaca)* population was observed in East Hungary from mountainous habitat into lowlands from 1989 onwards. Here the population markedly increased from 2 to 59 breeding pairs by 2006, while the mountainous population remained more or less stable with 12-17 breeding pairs. At the beginning of the expansion process the nearest neighbour distances between breeding pairs was lower in the mountains than in the lowlands, but presently they are similar, indicating a saturation process in the lowland areas, but no density dependence was revealed on breeding success. During the study period a higher ratio of non-adult pairs was observed in the lowland territories (49%) than in the mountains (22%). We found that both age and habitat influenced breeding success. We also found that age-effect was significant on success rate (i.e. the ratio of pairs that produce at least one chick), while habitat-effect was more evident on fledging success (i.e. the number of fledglings per productive pair). The overall productivity (i.e. number of fledglings per breeding pair) was affected primarily by the age of the pairs, but the interaction term of age x habitat also was significant. We suppose that better feeding possibilities (closer foraging areas and larger prey density) could explain the higher fledging success in the lowlands. We also predicted that pairs inhabiting agricultural areas in the lowlands will have a reduced success rate due to higher human disturbance, together with an age effect of the breeding pairs. Therefore adult pairs probably can habituate to disturbance even if it happens in the close vicinity of their nesting sites.

Keywords: population dynamics, breeding success, territory, raptor

Összefoglalás A parlagi sas kelet-magyarországi elterjedési területe jelentős mértékben kiterjedt az Alföld irányá-ba 1989-től 2006-ig, amely során az alföldi állomány 2-ről 59 párra emelkedett, míg a hegyvidéki állomány vi-szonylag stabil maradt, és 12-17 pár között változott. A terjeszkedési folyamat elején, a hegyvidéki élőhelyeken kisebb volt a párok közötti legközelebbi szomszéd távolság, mint síkvidéken, azonban ez 2006-ra kiegyenlítődött. Denzitásfüggő hatást egyelőre nem lehet megfigyelni az átlagos költési siker alakulásában. A vizsgálati időszak-ban, a síkvidéki territóriumokban magasabb volt az átszíneződő fiatal madarak aránya (49%), mint a hegyvidéki-ekben (22%). A költő madarak korának és az élőhelynek a költési sikerre gyakorolt együttes hatását vizsgáltuk. Azt találtuk, hogy a költő madarak kora inkább a költések sikerességi arányát (sikeres párok/összes költő pár) be-folyásolta, míg az élőhely inkább a kirepülési sikerre (kirepült fiókák száma/sikeres pár) volt hatással. Összessé-gében a produktivitást (kirepült fiókák száma/összes költő pár) alapvetően a madarak kora befolyásolta, de a kor és az élőhely interakciója is szignifikáns hatással volt. Az adatok alátámasztják azt a predikciónkat, miszerint a síkvidéki területek jobb táplálkozási lehetőségei (közelebbi táplálkozó területek és nagyobb zsákmány-denzitás) magasabb költési sikert eredményezhetnek. A másik predikciónk, miszerint a síkvidéki párok sikerességi aránya alacsonyabb a jelentősebb emberi zavarás miatt, csak részben igazolódott. Bár ez a trend megfigyelhető volt az adatokban, de csak a párok korával interakcióban volt szignifikáns a különbség. Ezért úgy gondoljuk, hogy a ta-pasztalt öreg madarak megfelelő mértékben hozzá tudnak szokni az emberi jelenléthez a fészkek közvetlen kör-nyezetében is.

Kulcsszavak: populációdinamika, költési siker, territórium, ragadozómadár

[1] *Magyar Madártani és Természetvédelmi Egyesület (MME BirdLife Hungary), 1121 Budapest, Költő utca 21., Hungary, e-mail: horvath.marton@mme.hu*
[2] *MTA-ELTE-MTM Ecology Research Group, c/o Biological Institute, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/C., Hungary and Hungarian Natural History Museum, 1088 Budapest, Baross utca 13., Hungary*
*corresponding author

Introduction

Biotic and abiotic environmental variables, like topography, vegetation, prey availability, predators, and competitors, influence habitat selection in birds (Hildén 1965, Cody 1985, Wiens 1989). Habitat selection of larger-sized raptor species typically depends on the availability of nesting sites and feeding areas (Janes 1985, Tapia *et al.* 2008). If raptors choose an optimal nesting habitat, they increase their reproductive success by decreasing the risk of predation (Sergio *et al.* 2007), avoiding competitors (Katzner *et al.* 2003), or human disturbance (López-López *et al.* 2007). Another important component, which is connected to habitat quality and has main effects on raptors' reproductive success, is prey-availability in feeding areas, like density and quality of prey (Penteriani *et al.* 2006, Sergio *et al.* 2006) and distance of foraging areas from nesting sites. Distance between nests and feeding areas play a key role when birds optimize their energy expenditure for maximizing their fitness (Cowie 1977). The quality of nesting sites and feeding areas seems to be important factors, which mainly affect the viability of raptor populations (Krüger *et al.* 2002). Besides the direct and indirect effects of habitat quality, density dependence (Ferrer & Donazar 1996, Ferrer *et al.* 2006, Ferrer & Penteriani 2008) and age of breeding birds (Steenhof *et al.* 1983, Balbontín *et al.* 2003, Ferrer & Bisson 2003, Penteriani *et al.* 2003, Margalida *et al.* 2007) are known to have crucial effects on breeding success. The effect of age can be especial-

ly important in instable populations, where the relative frequency of non-adult breeders increases, due to lack of adult breeders in comparison to available habitats (Ferrer *et al.* 2004).

Many of the large-sized raptors are among the threatened birds in the world (Del Hoyo *et al.* 1995). The Eastern Imperial Eagle *(Aquila heliaca)* has a wide distribution area in the forest-steppe zone of the Palearctic region, it breeds from western Austria, Czech Republic, Slovakia and Hungary throughout eastern Europe and Siberia to the Baikal Lake in Russia. Nevertheless its distribution is scattered and the species is globally threatened, as its world population consists only a few thousand breeding pairs (Del Hoyo *et al.* 1995, BirdLife International 2013).

Throughout its distribution area Imperial Eagles are connected to open foraging habitats, where its medium-sized mammal or bird preys are available (Del Hoyo *et al.* 1995). In several regions they are breeding in forested mountains, mostly due to persecution or the lack of suitable trees in the nearby open plain habitats (Petrov *et al.* 1996, Karyakin *et al.* 2008). We have no reliable data about the breeding distribution of Imperial Eagles in Hungary prior to the 1970's, although all early literature since the end of the 19th century mention it as a rare breeder of the Hungarian mountains, and only scarce observations are available from the Great Hungarian Plain (Vasvári 1938). The Hungarian population of the Eastern Imperial Eagle presumably reached its historical minimum with only 15-25 breeding pairs in mountainous forests by

the 1980's. During the last two decades an unexpected increase of the population was observed and by 2009 the Hungarian population already exceeded 100 pairs (Horváth *et al.* 2011). In parallel the species also expanded its breeding range from mountain forests to lowland agricultural areas. Two-thirds of Hungary consists of such agricultural habitats, so there is a chance for further area expansion of Imperial Eagles in the near future.

In the present study we investigated the factors affecting reproductive success of the largest subpopulation of Imperial Eagles in Central Europe during its area expansion. As the population is still exponentially increasing and probably is under the saturation point, we predicted that recently there is no significant density dependent effect on productivity. We also hypothesized that both age of the breeding birds and habitat type affect the reproductive success of Imperial Eagles. On one hand we predicted that the probability of successful breeding in the lowland areas is lower than in the mountains, due to a higher level of human disturbance connected to intensive agriculture and higher density of urbanized areas and infrastructure. On the other hand we also predicted that fledging success is higher in lowland areas where Brown Hares *(Lepus europaeus)*, the main prey species of Imperial Eagles (Horváth *et al.* 2010), are more abundant and open foraging areas are closer to the nesting sites.

Methods

Study area

The study was conducted in the central part of the Great Hungarian Plain and adjacent low mountains (46°30'-48°30'N 19°50'-21°40'E, 20 000 km^2). Most parts of the study area are lowlands between 80-100 m a.s.l., like the Jászság, Heves, Borsod, Nagykunság and Békés Plains, which lie in the wide valley of the Tisza River and its tributaries. The Plain is mostly covered by intensive agricultural fields and small remnants of grasslands, which are scattered by small groups of poplars (*Populus* spp.) and black locust trees *(Robinia pseudoacacia)*. The northern border of the Plain is formed by the Mátra, Bükk and Zemplén Mountains (200-1014 m a.s.l.) which are predominantly covered by oak *(Quercus petraea, Q. cerris, Q. pubescens)*, beech *(Fagus sylvatica)* and introduced pine *(Pinus silvestris, P. nigra, Larix decidua)* forests.

Data collection

Breeding territories of the Eastern Imperial Eagle were monitored by a well-trained network of observers, organised by MME BirdLife Hungary and Hungarian national park directorates since 1980 (Haraszthy *et al.* 1996, Bagyura *et al.* 2002, Horváth *et al.* 2011). In the present study we analysed data collected between 1989 and 2006, when monitoring covered all potential breeding territories. At the beginning of each breeding season (February-March) all previously identified territories and their surroundings up to 10 km were visited in order to locate active nests of Imperial Eagle pairs. Afterwards, during the whole breeding season (from April to August) all active nests were controlled for at least once per month to determine breeding success or failure in each breeding stage (incubation, small-, medium- and large-chick and fledging periods). Observations were carried out by spotting scopes (20–60×) from a distance of 0.5-1.5 km to avoid unnecessary disturbance of the

birds (González *et al.* 2006a). We checked nest content once during the breeding season to monitor the exact number of alive or dead offspring, when the chicks were 4-7 weeks old (mostly between 10-25 June), or when the breeding failed. Locations of the nests were identified with GPS and stored in a GIS database together with other breeding parameters.

During this 18-year study 645 breeding attempts were monitored in 89 breeding territories. By definition two nests belonged to the same territory if they were closer than 7.3 km to each other (the average nearest neighbour distance in 2006) and not more than one territorial pair used them within the same year (Ferrer & Bisson 2003). Two different breeding habitat types were used by the species in the study area, such as mountainous forests and small patches of trees in open agricultural landscape of the lowlands. The breeding attempts were classified into the two breeding habitat types based on the 200 m contour line. This contour line also separated the open and forested nest sites without any notable overlap, as all (100%) of the 262 'mountainous', but only eight (2.1%) out of the 383 'lowland' breeding attempts were in forested habitats. Subsequent breeding attempts of the same territory were usually within the same habitat type (15 pure mountainous and 67 pure lowland territories). However, in seven territories the pairs switched between the two habitat types. These mixed territories were also classified into that habitat type where more breeding attempts occurred and only the average of these breeding attempts were used for territorial comparisons.

Members of the breeding pairs were categorised during the population monitoring as '*adult*' or '*non-adult*' birds, as these two age classes can be distinguished relative-

ly easily in the field based on plumage characteristics. Similarly to the Spanish Imperial Eagle (Ferrer *et al.* 2004, González *et al.* 2006b) and other large eagles (Steenhof *et al.* 1983, Balbontín *et al.* 2003), Eastern Imperial Eagles regularly breed already in their 3rd-5th calendar year, before they accomplish their moult to the dark brown adult plumage (Katzner *et al.* 2006, authors own data). Nonetheless, the exact age determination of non-adult eagles needs substantial experience (Forsman 1999). A breeding pair was classified as '*non-adult*' if at least one member of the pair was in non-adult plumage, and as '*adult*' if both members were in adult plumage. In 25 cases (4% of breeding attempts) the age class of both birds could not be identified, therefore these were typically excluded from calculations.

Statistical analyses

To avoid pseudoreplication that would arise if each breeding attempt would be included separately, we used territories as sampling units in the comparative analyses (c.f. Steenhof 1987, Ferrer & Bisson 2003, Penteriani *et al.* 2003, Sergio & Newton 2003, Margalida *et al.* 2007), and annual mean values for analysing temporal trends during the study period (Balbontín *et al.* 2003, Ferrer & Bisson 2003). Breeding success was measured with three variables (Steenhof 1987, Balbontín *et al.* 2003), such as the number of fledglings per nesting pair (referred to as *productivity* in the followings), the frequency of nesting pairs that fledged at least one chick (referred to as *success rate* in the followings), and the number of fledglings per successful nesting pairs (referred to as *fledging success* in the followings). For the calculation of mean values for territories we controlled for year effect by subtracting

annual means from the original breeding success data (Ferrer & Bisson 2003, Penteriani *et al*. 2003). We excluded those territories from the analyses where less than three breeding attempts occurred. Density dependence was estimated by nearest neighbour distances (NND) (Newton *et al.* 1977, Penteriani *et al.* 2003).

Normal distribution of variables was tested prior applying parametric tests, and in case to significant deviation non-parametric tests were used. Generalized Linear Models were used to test simultaneous effect of habitat type and age of birds on breeding success variables, and the interaction of the two factors were removed from the model, if it had no significant effect. All statistical tests were two-tailed and significance level was set at $P < 0.05$. Data are presented as mean ± SD. Distances were measured by ArcMap© software (ESRI Inc., version 9.0). Analyses were executed by the SPSS programmes package (SPSS Co., ver. 17).

Results

Temporal variation of population parameters

Altogether 79 new territory occupancies (i.e. when a breeding pair appeared in a territory where no breeding attempt was recorded in the previous year) were observed during the study period, with only 12 (15%) located in the mountains, while the rest of the new territories (85%) appeared in the lowland. We identified the age of both breeding birds in 70 cases, from which 57 (81%) new territories were occupied by non-adults. This frequency was significantly different from the 24% value of non-adults, which was observed among the

other 550 breeding attempts ($\chi^2 = 123.416$, $P < 0.001$).

Population size increased markedly in the lowland (annually increased by 25%; $F = 281.401$, $df = 1,16$, $P < 0.001$), and also in the mountains, although here the trend was not so sharp and not constant (annually increased by 5%; $F = 5.859$, $df = 1,16$, $P = 0.033$) *(Figure 1a)*. In parallel with the increasing population size the NND decreased in the lowland ($F = 22.445$, $df = 1,16$, $P < 0.001$), but did not change significantly in the mountains ($F = 2.747$, $df = 1,16$, $P = 0.117$) *(Figure 1b)*. The frequency of non-adult pairs in the breeding population increased in the lowlands ($F = 7.401$, $df = 1,16$, $P = 0.015$) and decreased in the mountains ($F = 5.379$, $df = 1,16$, $P = 0.034$) *(Figure 1c)*. None of the breeding success variables showed significant trends in the two habitat types during the study period (productivity: $F = 0.148$, $df = 1,16$, $P = 0.705$ for mountains and $F = 0.108$, $df = 1,16$, $P = 0.747$ for the lowland) *(Figure 2a)*; success rate: $F = 0.401$, $df = 1,16$, $P = 0.535$ for the mountains and $F = 0.613$, $df = 1,16$, $P = 0.445$ for the lowland, *(Figure 2b)*; fledgling success: $F = 0.041$, $df = 1,16$, $P = 0.842$ for the mountains and $F = 0.718$, $df = 1,16$, $P = 0.409$ for the lowland) *(Figure 2c)*.

Density dependence

Territory averages of NND was significantly lower in mountainous than in lowland territories (6.6 ± 3.2 km and 12.7 ± 14.5 km, respectively; Mann-Whitney U-test, $Z = -2.728$, $P = 0.006$), although the difference became non-significant, or even reversed by the last years of the study period (8.4 ± 4.8 km and 7.1 ± 4.3 km in 2006, respectively; Mann-Whitney U-test, $Z = -0.722$, $P = 0.470$). We did not find any sig-
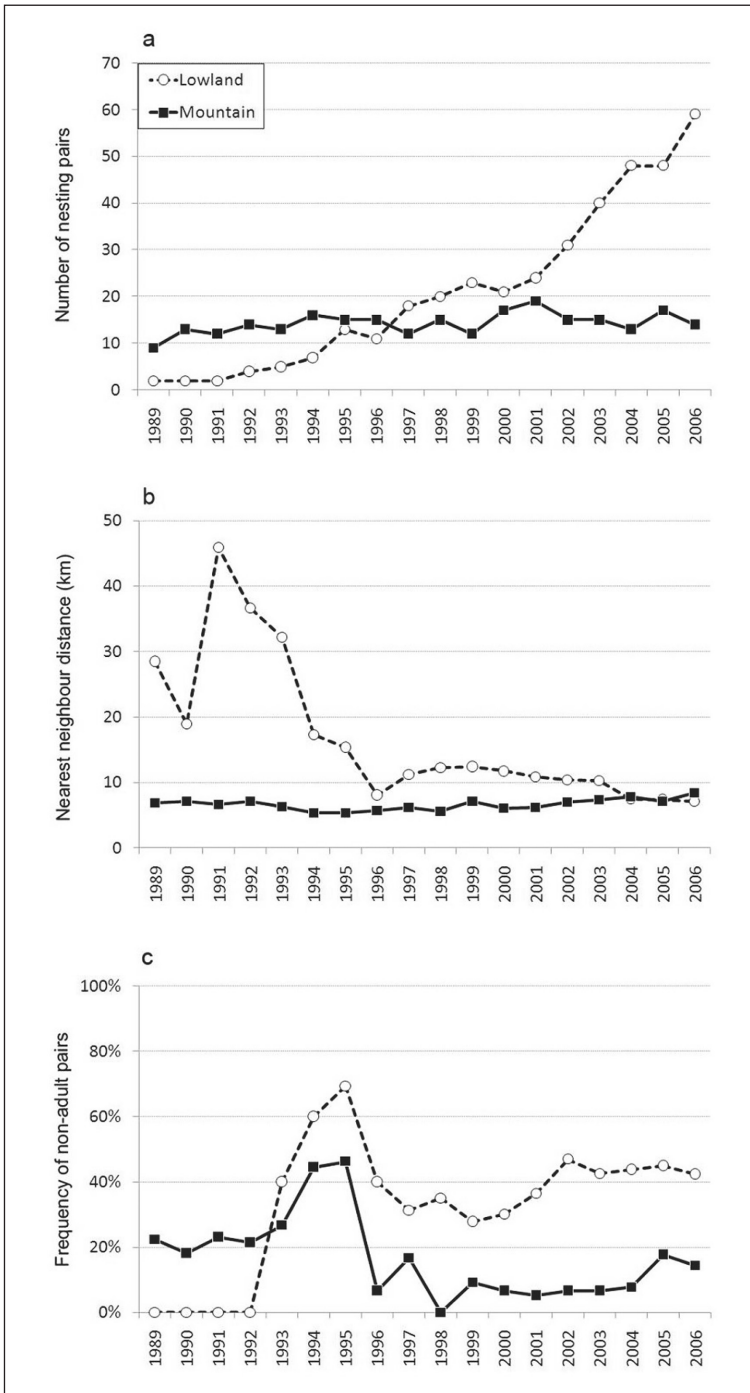
Figure 1. Changes in number of nesting pairs (a), nearest neighbour distance (b) and frequency of non-adult pairs (c) of Eastern Imperial Eagles in lowland and mountain habitats of East-Hungary between 1989 and 2006

1. ábra   A fészkelő párok számának (a), a legközelebbi szomszéd távolságnak (b) és a nem-adult párok gyakoriságának (c) változása a kelet-magyarországi parlagi sas állományban a hegyvidéki (fekete négyzet) és síkvidéki (fehér kör) élőhelyeken 1989 és 2006 között
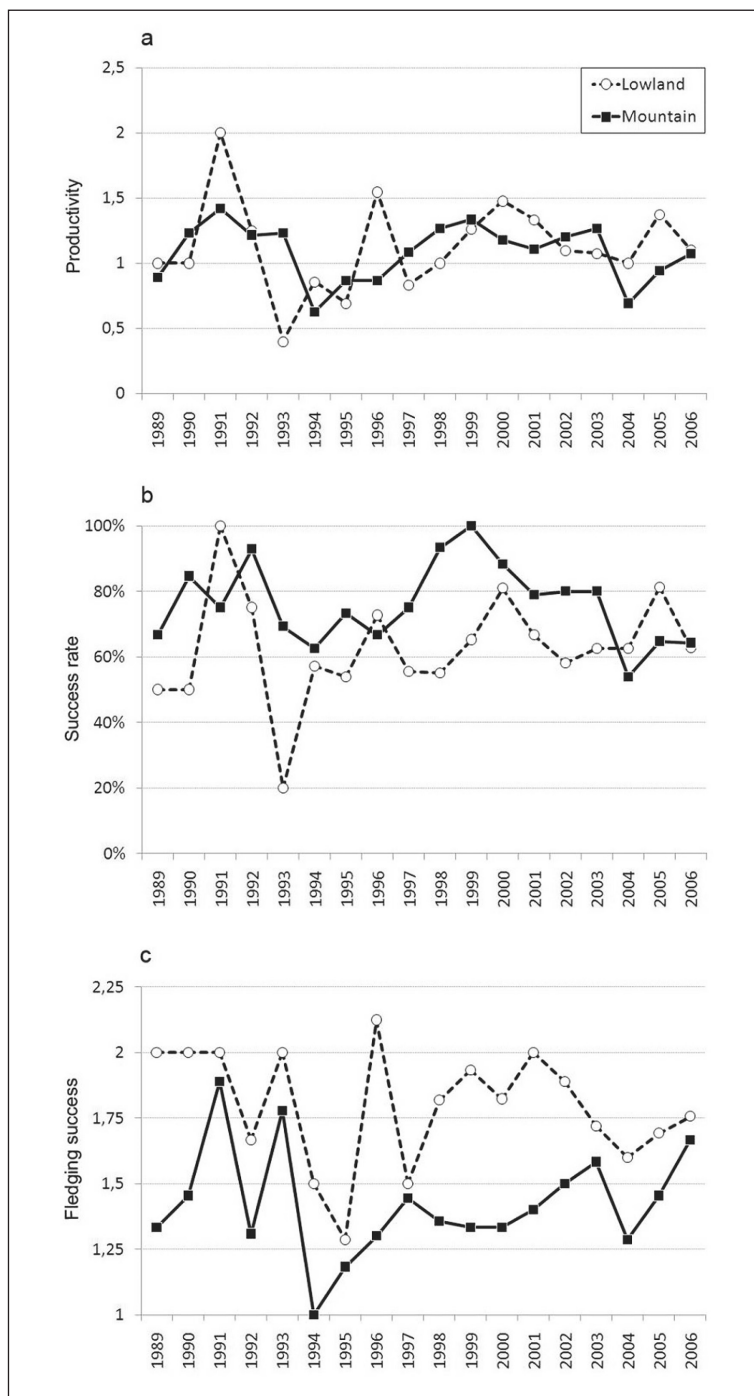
Figure 2. Changes in productivity (a), success rate (b) and fledging success (c) of Eastern Imperial Eagles in lowland and mountain habitats of East-Hungary between 1989 and 2006

2. ábra A produktivitás (a), a sikerességi arány (b) és a kirepülési siker (c) változása a kelet-magyarországi parlagi sas állományban a hegyvidéki (fekete négyzet) és síkvidéki (fehér kör) élőhelyeken 1989 és 2006 között

	Mountain		Lowland			
	n	mean ± SD	n	mean ± SD	t	P
Productivity	20	-0.098 ± 0.371	51	-0.005 ± 0.466	0.805	0.424
Success rate	20	0.006 ± 0.233	51	-0.043 ± 0.210	-0.851	0.398
Fledging success	19	-0.162 ± 0.306	50	0.086 ± 0.390	2.494	0.015*

* significant at P = 0.05 level

Table 1.   Comparison of breeding success variables between the territories of the two habitat types. (Productivity = the number of fledglings per a nesting pair; Success rate = the frequency of nesting pairs that fledged at least one chick; Fledging success = the number of fledglings per successful nesting pairs)

1. táblázat A költési siker változók összehasonlítása a két élőhelyen. (Produktivitás = kirepült fiókák száma / fészkelő párok száma; Sikerességi arány = azon fészkelő párok aránya, amelyek legalább egy fiókát sikeresen kireptettek; Kirepülési siker = kirepült fiókák száma / sikeres párok száma)

	Adult		Non-adult			
	n	mean ± SD	n	mean ± SD	t	P
Productivity	46	0.107 ± 0.602	46	-0.162 ± 0.756	-1.995	0.052
Success rate	46	0.104 ± 0.279	46	-0.115 ± 0.387	-3.257	0.002*
Fledging success	35	-0.079 ± 0.448	35	0.009 ± 0.435	0.903	0.373

* significant at P = 0.05 level

Table 2.   Pairwise comparison of breeding success variables of adult and non-adult pairs within the same territories. (Productivity = the number of fledglings per a nesting pair; Success rate = the frequency of nesting pairs that fledged at least one chick; Fledging success = the number of fledglings per successful nesting pairs)

2. táblázat A költési siker változók páros összehasonlítása az „adult" (két kiszíneződött madárból álló) és „nem-adult" (legalább egy átszíneződő madarat tartalmazó) párok között. (Produktivitás = kirepült fiókák száma / fészkelő párok száma; Sikerességi arány = azon fészkelő párok aránya, amelyek legalább egy fiókát sikeresen kireptettek; Kirepülési siker = kirepült fiókák száma / sikeres párok száma)

nificant correlation between NND and any of the breeding success variables (productivity: r_s = -0.022, P = 0.842; success rate: r_s = -0.056, P = 0.601; fledgling success: r_s = 0.113, P = 0.338). Moreover, as density increased in the lowland habitats during the study period, no changes were observed in any of the breeding success variables (see above). Therefore we assumed that there was no significant density-dependent effect of the studied parameters in the study period.

Simultaneous effect of age and habitat

Breeding success variables showed some difference both regarding habitat type and age of breeding birds in univariate comparisons without considering the possible simultaneous effects (*Table 1* and *Table 2*). We also found significant rank correlations between the frequency of non-adult pairs and each of two breeding success variables of the territories (productivity: r_s = -0.354, P = 0.002; success rate: r_s = -0.337, P = 0.004), although fledgling success did not correlate significantly (r_s = -1.102, P = 0.406). Never-

	Type III Sum of Squares	Mean Square	F	P
Productivity				
Corrected Model	2.447	0.816	4.895	0.004 *
Intercept	0.617	0.617	3.702	0.059
Habitat	0.002	0.002	0.01	0.922
Age	2.308	2.308	13.853	< 0.001 *
Habitat × Age	0.810	0.81	4.859	0.031 *
Success rate				
Corrected Model	0.767	0.256	6.856	< 0.001 *
Intercept	0.207	0.207	5.547	0.021 *
Habitat	0.152	0.152	4.074	0.048 *
Age	0.725	0.725	19.449	< 0.001 *
Habitat × Age	0.383	0.383	10.275	0.002 *
Fledging success				
Corrected Model	1.379	0.690	5.289	0.007 *
Intercept	0.090	0.090	0.692	0.409
Age	0.531	0.531	4.071	0.048 *
Habitat	1.285	1.285	9.856	0.003 *
**Habitat × Age ** **	-	-	-	-

* significant at P = 0.05 level   ** interaction was not significant, therefore it was removed from the model

Table 3.   Results of the Generalized Linear Models analysing the effects of habitat type and age of
          the breeding birds on breeding success variables
3. táblázat Az Általánosított Lineáris Modell (GLM) eredménye, amely az élőhely-típus és a költő
          madarak korának hatását mutatja a költési siker változókra

theless, the frequency of non-adult pairs differed significantly between the two habitat types (22.1 ± 26.3% in the mountains and 49.5 ± 35.1% in lowlands; Mann-Whitney U-test, Z = -2.964, P = 0.003), therefore the possible simultaneous effects were tested in a generalized linear model.

The linear models showed different results for the three breeding success variables *(Table 3)*. We found that overall productivity was affected primarily by the age of the breeding pairs, but also by the interaction between habitat and age effects. Success rate was also primarily affected by the age of the pairs, although the habitat and interaction between the two effects were al-

so significant. Finally habitat showed stronger effect on fledging success, but age of the pairs also had a significant effect.

Discussion

Our results revealed that habitat selection of Imperial Eagles in Hungary changed in the last two decades, causing an unexpected population growth and breeding area expansion. From their mountainous refugees Imperial Eagles expanded their original breeding areas in Hungary to the lowlands, which were most probably abandoned for at least one hundred years. Although presently

the new breeding area, the Hungarian Great Plain, with its developed agriculture and dense system of settlements, seems to be suffering from high human disturbances, the reproductive success parameters suggested that this new breeding area offer high-quality breeding sites for the eagles.

Similarly to other studies (Steenhof 1983, Balbontín *et al.* 2003, Ferrer *et al.* 2003) we found a strong effect of age of breeding birds on reproductive success variables, i.e. non-adult pairs bred less successfully. Not surprisingly, in the newly-occupied areas non-adult eagles were more frequent than in the traditional mountainous areas and we found that age and habitat type had simultaneous effects on breeding success variables, as it was also shown on Bonelli's Eagles *(Aquila fasciata)* in Spain (Penteriani *et al.* 2003). We found that age-effect is more significant on success rate (i.e. the ratio of pairs that produce at least one chick), while habitat-effect was more evident on fledging success (i.e. the number of fledglings per productive pair). The overall productivity (i.e. number of fledglings per breeding pair) was affected primarily by the age of the pairs, but the interaction of age and habitat type had also significant effect. We suppose that better feeding possibilities (closer foraging areas and larger prey density) could explain the higher fledging success in the lowlands. We also predicted that pairs inhabiting lowland agricultural areas suffer more from human disturbance resulting in a lower success rate, but even if this trend was observable it had significant effect only in interaction with the age of the pairs. This interaction is probably caused by inexperienced non-adult pairs, which are threatened by the higher level of lowland disturbance, while experienced adult pairs can breed with similar success as in the undisturbed mountains.

Although the exact causes, which started the population expansion in the Imperial Eagles in Hungary are not known, our study revealed that freshly occupied lowland habitats can be more productive than traditional mountainous ones. Such a process is surprising in an expanding population as most studies report that if a population is not saturated the best habitats are occupied first (Newton 1979, Sergio & Newton 2003). Moreover the population size of Brown Hare *(Lepus europaeus)*, the main prey species of Imperial Eagles is Hungary (Horváth *et al.* 2010), has been continuously declining since the 1960's in parallel with the intensification of agriculture (Báldi & Faragó 2007). Therefore the colonization of the lowlands is most probably not caused by any recent increased availability of food supply, but by an increasing population size in the original habitats. After the population in the mountains started to increase and the level of persecution decreased in the lowlands, some eagles tried to settle in these new habitats. The appearance of these first inventory pairs was probably the most important step in the expansion, as the high natal philopatry of the species (González *et al.* 2006b) hinders the sudden colonization of habitats far from the original breeding distribution area. The huge and well visible nests and territorial behaviour of conspecifics indicate, that lowland agricultural areas can be also suitable habitats for them (Newton 1979). During the last two decades these freshly colonized habitats proved to be even more suitable for the species, than the traditional mountainous forests, and since large agricultural regions of the Hungarian Plain are still not inhabited by the species we expect further expansion in the near future.

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Breeding distribution and nest site diversity of Barn Owl *(Tyto alba)* in the context of restoration of agricultural sector in Central South Bulgaria

Boyan Milchev[1*] & Gradimir Gruychev[1]

Boyan Milchev & Gradimir Gruychev 2014. Breeding distribution and nest site diversity of Barn Owl *(Tyto alba)* in the context of restoration of agricultural sector in Central South Bulgaria. – Ornis Hungarica 22(1): 69–75.

Abstract The Barn Owl *(Tyto alba)* bred in 15 UTM squares (75%, n = 20) of the Kazanlak Valley (central south Bulgaria) at 33 localities (55% confirmed, 12% probable and 33% possible breeding). Its distribution in the Valley was found to be five times larger and its population size ten times greater during our study period than previously thought. Evidence of one to five breeding localities (mean 2.2±1.3) was detected in each occupied UTM square. A breeding density of 4.1 bp/100 km^2 was close to the average in Central Europe. Nests inside or on metal frames and ducts were typical in the region and gave possibility for its successful breeding in most of the habitable buildings. The Barn Owls were breeding mainly in poorly maintained and abandoned buildings whose supply has not decreased markedly since the agricultural restoration started in Bulgaria after it joined the European Union and intensive industrial agriculture has resumed with EU support. Currently, it appears that Barn Owl is not threatened by a 'housing shortage' over the next decade.

Keywords: Barn Owl, *Tyto alba*, breeding density, nest site selection, conservation

Összefoglalás A gyöngybagoly *(Tyto alba)* a Kazanlak-völgy 15 UTM négyzetében költött (75%, n = 20) (Dél-Közép Bulgária) 33 helyen (55% bizonyított, 12% valószínű és 33% lehetséges költés). Az elterjedési területe a völgyben ötször, állománynagysága pedig tízszer magasabb a korábbiakban véltnél. Minden elfoglalt UTM négyzetben 1-5 költőhelyet találtak (átlag: 2,2±1,3). A Közép-Európára jellemző költőállomány sűrűségéhez (4,1 pár/100 km^2) közelít ez az érték. Jellemzően a fémszerkezeteken vagy azok belsejében és a szellőzőjáratokban épültek a fészkek, ezek a szerkezetek biztosítottak sikeres fészkelési lehetőséget a legtöbb gyöngybagoly lakta épületben. Elsősorban elhanyagolt vagy elhagyatott épületekben fészkeltek, ezek mennyisége nem csökkent jelentősen, mióta Bulgária csatlakozott az Európai Unióhoz, és EU támogatással megindult a mezőgazdaság intenzifikálása. Úgy tűnik, hogy a gyöngybagoly nem fog fészkelőhely-hiánnyal szembesülni a következő évtizedben.

Kulcsszavak: gyöngybagoly, *Tyto alba*, állománysűrűség, fészkelőhely-választás, természetvédelem

[1] *Department of Wildlife Management, University of Forestry, 10 K. Ohridski Blvd, 1765 Sofia, Bulgaria, e-mail: boyan.m@abv.bg*, *gradi.val@gmail.com*
*corresponding author

Introduction

The Barn Owl *(Tyto alba)* has a stable cosmopolitan population, and the IUCN (2013) assigned it into the 'least concern' category for global protection. But, it probably has undergone a moderate decline (>10%) in Europe and was evaluated as 'declining', thus it has got an unfavorable conservation status there (BirdLife International 2004). The main negative factors in Europe and North America are related to industrialized agriculture with mechanization and use of chemicals, loss of suitable roosting and nes-

ting sites and increased mortality with the expansion of the road network and increased traffic speed (Taylor 1994, Mebs & Scherzinger 2000, Golawski *et al*. 2003, Martínez & Zuberogoitia 2004, Martin *et al*. 2010, Hindmarch *et al*. 2012, Borda-de-Águaa *et al*. 2014). In Bulgaria, the Barn Owl population has been reported to be stable but, in fact, the species is poorly studied. Gaps in good information may explain the great differences in the range intervals of population estimates over the last decade, i.e. from 150-500 pairs (BirdLife International 2004) to as many as 1300-1700 pairs (Nankinov 2004).

The Barn Owl inhabits open agricultural landscapes where modernization of agricultural machinery, renovation of the agricultural buildings, and recultivation of abandoned lands has been underway since Bulgaria joined the European Union in 2007. This study aims to determine its present breeding distribution and types of nest sites in the context of the restoration of agricultural sector in the Kazanlak Valley in central south Bulgaria. The Barn Owl has been recently reported as a breeding bird in three localities in the Valley (Iankov 2007). It has not been included among 'other important species' in the Natura 2000 protected sites there (MOSW 2013). This must be changed in order to its protection as 'vulnerable' bird in the Bulgarian Red Data Book (Golemanski 2011).

Materials and methods

The Kazanlak Valley lies between the Stara Planina Mountains (highest local peak Triglav 2276 m a.s.l.) on the north and the Sredna Gora Mountains (peak Bratan 1236 m a.s.l.) on the south and it encompasses an area around 800 km². Its western border is the transverse Krastetz Hill (N 42°35` E 25°00`,

540 m a.s.l.) and the eastern one is the Mejdenishki Gorge (N 42°35` E 26°05`, 190 m a.s.l.) of the Tundzha River. The mostly flat valley floor is interrupted by superficial cones formed by rivers flowing down from the two mountains and the Tundzha River that drains the valley. Two reservoirs and irrigation channels are presented. The climate is moderate continental with mean temperatures ranging from 0 °C up to +1 °C in January (Kopralev 2002). Open habitats with prevalence of cultivated areas and low-intensity grazing pastures dominate the Valley. Major agricultural crops are wheat, barley and sunflower. The rose fields, which confer the popular name Rose Valley to the area, and lavender fields cover larger area of the northwestern and the western parts of the region. The forests are broad-leaved deciduous and comprise a small area, remaining mostly in riparian zones. Human settlements are mostly villages, with the exception of few small towns as the regional center Kazanlak, without any strongly developed industry now.

Data on Barn Owl's presence in the valley were collected in mid-June and early September 2012. Additional information was collected for three settlements in UTM square LH51 in mid-July 2013. We followed the methods described in Miltschev *et al*. (2002): (1) to look for pellets, faeces markings, feathers and nests of Barn Owls mainly in agricultural and stock-breeding compounds and separate buildings (n = 62 places). These sites were easier to access than residential and other buildings and were situated in the periphery of or away from settlements, but close to owl hunting grounds in nearby open habitats; (2) to search for Barn Owl remains (bones, feathers) in the Eagle Owl *(Bubo bubo)* pellets; (3) rocky slopes, single rocks and rocky gorges, quarries and steep riverbanks (n = 46) were stu-
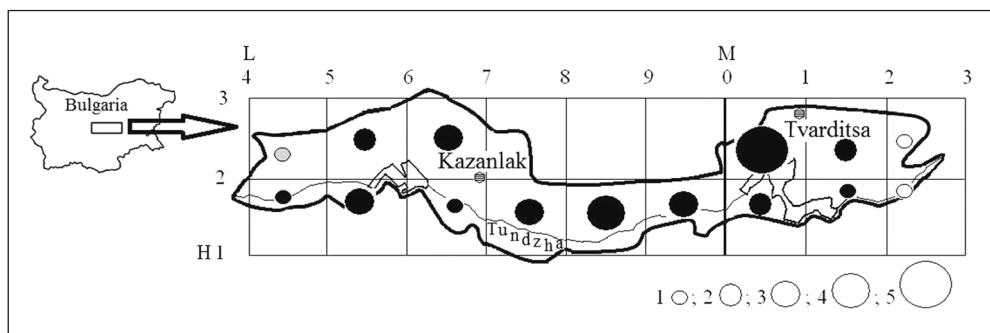
Figure 1. Breeding distribution and number of the Barn Owl *(Tyto alba)* in the Kazanlak Valley (CS Bulgaria): the five dimensions of circles (1–5) specify the number of breeding localities in the respective UTM square: 1 locality/square (6 squares, 30%, *n* = 20); 2 localities/square (3 squares, 15%); 3 localities/square (4 squares, 20%); 4 localities/square (1 square, 5%), 5 localities/square (1 square, 5%); the highest level of the breeding evidence in the respective square: black circle – confirmed breeding (12 squares, 60%, *n* = 20); grey circle – probable breeding (1 square, 5%); empty circle – possible breeding (2 squares, 10%)

1. ábra A gyöngybagoly fészkelések eloszlása és száma a Kazanlak-völgyben (Dél–Közép Bulgária) fekete kör – biztos költés, szürke kör – valószínű költés, fehér kör – bizonytalan költés

died as potential Barn Owl breeding places in conformity with a rock nest in SE Bulgaria (Milchev 2013). In this way, the variety of known breeding places in the country was covered. Species breeding was assessed as 'certain', 'probable' or 'possible' following Hagemeijer and Blair (1997) with specifications of Miltschev *et al.* (2002). All food remains and egg shells were deposited in the collections of the National Museum of Natural History (Milchev 2012). Breeding localities were mapped on a 10×10 km Universal Transverse Mercator (UTM) grid. Statistical differences in the frequency of the nest site types were calculated by chi-square tests.

Results

The study area falls within 20 UTM squares and Barn Owl bred in 15 of them (75%, *n* = 20), *(Figure 1)*. We discovered 33 breeding localities (55% confirmed, 12% probable and 33% possible breeding), and 31 of these loca-

lities (93.9%) were found in buildings. Two localities (6.1%, *n* = 33) were identified by finding the remains of five (one fledgling) and two specimens of Barn Owls respectively in the Eagle Owl pellets, which were assigned to the nearest settlement. One breeding pair per settlement was the average, and only two settlements (8.3%, *n* = 24 settlements) hosted two breeding sites. These nests were situated in the opposite ends of the settlements at distance 1.2 and 1.8 km respectively. One to five breeding localities (mean 2.2±1.3) were detected in the UTM square which having evidence of breeding. The breeding density in the Valley was 4.1 bp/100 km².

Barn Owls bred more often in habitable buildings (52.9%, *n* = 17), *(Table 1)*. The difference in the frequency of their use in the valley and neighbouring SE Bulgaria was insignificant. The most common nest sites in the Valley was inside rigid metal frames (41.2%, *n* = 17). Their use and breeding inside or on ventilation ducts were significantly more frequent in the Valley while

Nest site	Nest number		Number of buildings/bridges	
	CS Bulgaria (%, *n*=17)	SE Bulgaria (%, *n*=33)	abandoned CS Bulgaria (SE Bulgaria)	habitable CS Bulgaria (SE Bulgaria)
inside a rigid metal frame*	7 (41.2%)			7 (0)
on a cross-beam*	4 (23.5%)	9 (27.3%)	4 (5)	0 (4)
in an attic*	2 (11.8%)	12 (36.4%)	0 (7)	2 (5)
inside a ventilation duct*	3 (17.6%)	1 (3.0%)	3 (1)	
on a flat-topped ventilation duct	1 (5.9%)	1 (3.0%)	1 (1)	
between roofing plates		5 (15.2%)	0 (3)	0 (2)
niche with a ventilator		1 (3.0%)		0 (1)
on an interior wall		1 (3.0%)		0 (1)
under a bridge		2 (6.1%)		0 (2)
historical ruin		1 (3.0%)		0 (1)

Table 1. Barn Owl *(Tyto alba)* nest sites in Kazanlak Valley (CS Bulgaria) and neighboring SE Bulgaria (Miltschev *et al.* 2002, B. Milchev unpubl. data). * – a destroyed brood in a respective nest site in the Valley

1. táblázat A gyöngybagoly *(Tyto alba)* fészkelőhelyei a Kazanlak-völgyben Dél–Közép-Bulgáriában és a szomszédos Délkelet-Bulgáriában (Miltschev *et al.* 2002, B. Milchev unpubl. data)

the attics were preferred in SE Bulgaria (χ^2 = 25.20, *df* = 10, *P* < 0.01).

Inside buildings darker places were selected as nest sites and their height was between 2.5 m and 6 m (mean 3.9±1.0). Barn Owls accessed them through missing windows, doorways and holes in walls (58.8%, *n* = 17) or through existing openings in the design of buildings (41.2%). Nest sites ranged from almost inaccessible to highly accessible for people. Four broods appeared to have been destroyed by mammalian predators (23.5%, *n* = 17), *(Table 1)*. The discrepancy between the observed and expected frequency of destroyed broods in different nest sites was statistically insignificant (χ^2 = 0.64, *df* = 4, *P* > 0.05). Workers found between one and four fledglings under three nests located inside rigid metal frames, but only once two fledglings died because of inadequate human care. The owners and the workers in all inhabitable buildings with nests have a posi-

tive attitude towards the Barn Owls despite the necessity of regular cleaning of their pellets and excrement.

The subspecies *Tyto alba guttata* breeds in the Kazanlak Valley according to feathers of molting owls and prey remains from Eagle Owls and from four well observed birds in a total 21 localities.

Discussion

The secretive lifestyle of the Barn Owl has hampered locating them considerably as subjects for ornithological research (de Bruijn 1994, Taylor 1994), and Iankov (2007) noted the insufficient knowledge about the distribution of owls and other nocturnal birds in Bulgaria. Therefore, the fivefold broader breeding distribution and tenfold higher population size in the present study than previously thought (Iankov

2007) is not a surprise. This study corroborates the results of Miltschev *et al*. (2002), Milchev *et al*. (2006) and Boev *et al*. (2007) that the flat and hilly agricultural landscapes in south Bulgaria is the most suitable area for Barn Owls breeding in the country.

The breeding density in optimal regions of Europe can reach as high as 10-30 bp/100 km², but usually their density is only 5 bp/100 km² of Central Europe (Mebs & Scherzinger 2000, Golawski & Kasprzykowski 2006). In the Kazanlak Valley, Barn Owl density was close to the norm for Central Europe, but a comparison with data within Bulgaria is difficult. The entire Bulgarian population with 500-1000 pairs bred in 152 squares (10 km UTM grid, Iankov 2007). Therefore, the average density should be 3.3-6.6 bp/square, but it is several times greater than 'single or up to 2-3 bp/square' as a norm according to Iankov (2007).

The Barn Owl adapts to human presence and highly depends on man-modified habitats especially in Europe (Glutz von Blotzheim & Bauer 1994, Hagemeijer & Blair 1997, Mebs & Scherzinger 2000). Accordingly, our study identified some diverse characteristics of nest site in the region. Barn Owls have continued to breed mainly in poorly maintained and abandoned buildings similar to the situation in SE Bulgaria ten years ago (Miltschev *et al*. 2002). Their presence has not decreased significantly since Bulgaria has joined the EU and farm subsidies have been introduced. The number of buildings with potential breeding and roosting sites in villages earlier had increased as a result of the national and world economic crises and the demographic exodus from the countryside. The widespread availability of suitable nest sites inside villages corresponds to the large number of localities with probable and possible breeding in this study (45%, *n* = 33), where

agricultural and stock-breeding compounds were used for roosting only. These results combined with the predominant positive attitude of local people towards the Barn Owl do not portend a negative population trend on account of the loss of suitable roosting and nesting sites in the Valley.

The nest site characteristics for dimensions and height coincided with published information (Simeonov *et al*. 1990, Glutz von Blotzheim & Bauer 1994, Taylor 1994, Miltschev *et al*. 2002). The nests inside or on metal installation were typical for the Barn Owl in Kazanlak Valley and may indicate the potential to breed successfully in more of the habitable buildings. But, nest types that afforded more protection from mammalian predation were not in evidence. But, there were not any definite kind of nest site that protects significantly better the broods from mammalian predation.

The finding that *Tyto alba guttata* is the only breeding subspecies in the Kazanlak Valley confirms that the hybrid zone with *Tyto a. alba* occurs just in SE Bulgaria (Georgiew 1998, Miltschev *et al*. 2002).

Barn Owls breed mainly in settlements in the valley, but their population depends greatly on the food supply of their main prey, small mammals, in open non-forest habitats (Glutz von Blotzheim & Bauer 1994, Taylor 1994, Miltschev *et al*. 2004). Nevertheless their nest and roost sites are usually in buildings outside Natura 2000 protected sites in the Kazanlak Valley, the hunting ranges of 22 pairs fall partially or wholly into sites BG0000203, BG0000261, BG0000612, and BG0002052 (MOSW 2013). The Barn Owl is categorized as a 'vulnerable' bird in the National Red Data Book (Golemanski 2011) and needs to be included among the 'other important species' in the Natura 2000 protected sites. The preparation of management

plans for these sites has already started but they do not consider measures for Barn Owl protection. This forecast an uncertain future of its population in the Kazanlak Valley as industrialized agriculture is intensified. Agricultural intensification has been associated with decrease of Barn Owl populations elsewhere in Europe (Glutz von Blotzheim & Bauer 1994, Mebs & Scherzinger 2000, Martin *et al*. 2010).

Acknowledgements

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DE GRUYTER OPEN

An unexpected case of heterospecific altruistic behaviour in a non-breeding migrant tern (Charadriformes, Sternidae)

Giacomo Bruni[1], Mattia Menchetti[1*], Giulia Ricciardi[1], Andrea Vannini[2] & Emiliano Mori[3]

Giacomo Bruni, Mattia Menchetti, Giulia Ricciardi, Andrea Vannini & Emiliano Mori 2014. An unexpected case of heterospecific altruistic behaviour in a non-breeding migrant tern (Charadriformes, Sternidae). – Ornis Hungarica 22(1): 76–80.

Abstract Observations of birds feeding chicks or fledglings of a different species have already been reported in many publications. However, the benefits of the altruistic behaviour are not easy to understand, as benefits and costs of this behaviour have been poorly identified. In May 2013, in a wetland in Central Italy (Piana Fiorentina, Tuscany), some cases of interspecific feeding of an Eurasian Coot *Fulica atra* chick by an adult non breeding Whiskered Tern *Chlidonias hybrida* were witnessed. We suggest that the behaviour of the Tern was triggered by the begging of the chick or by its own hormonal status.

Keywords: interspecific feeding, *Fulica atra*, *Chlidonias hybrida*, chicks

Összefoglalás A más fajok fiókáit etető madarakról számos beszámolót publikáltak az ornitológiai szakirodalomban. Azonban evolúciós szempontból az ilyen altruisztikus viselkedés értelmezése nehéz feladat, ugyanis az önzetlen egyed számára a viselkedés előnye még kevéssé ismert. Egy közép-olaszországi (Piana Fiorentina, Toszkána) vizes élőhelyen 2013 májusában több alkalommal megfigyeltük, hogy szárcsa *(Fulica atra)* fiókát etetett egy kifejlett, de nem költő fattyúszerkő *(Chlidonias hybrida)*. Véleményünk szerint a szerkő viselkedését a szárcsa fióka kéregetése, vagy a saját hormonális állapota válthatta ki.

Kulcsszavak: interspecifikus etetés, *Fulica atra*, *Chlidonias hybrida*, fiókák

[1] *Department of Biology, University of Florence, Via Madonna del Piano, 6 – 50019 Sesto Fiorentino (Florence), Italy, e-mail: mattiamen@gmail.com*
[2] *Environmental Biologist, Landscape Ecologist, via Pompeo Ciotti 60/2 – 59100 Prato, Italy*
[3] *Di.S.A.F.A., Entomology and Zoology, University of Turin, Via Leonardo da Vinci, 44 – 10095 Grugliasco (Turin)*
corresponding author

Introduction

Feeding of the chicks or fledglings of other species has frequently been observed in birds (Shy 1982, Koenig 1988), and is not easily explained by evolutionary theory. In her review, Shy (1982) tried to define the possible ethological mechanisms underlying these behaviours. In most cases, both species involved in these displays are breeding in the same

area (McNair & Duyck 1991, Dróżdż *et al.* 2004) and interspecific altruistic behaviour might decrease competition for nesting sites ('mixed clutches' if idoneous/suitable net sites represent limiting resources) or be due to loss of the clutch by one of the two species and/or proximity between nests of the two species (Shy 1982).

Whiskered Tern *Chlidonias hybrida* is a polytypic sub-cosmopolitan species (Cramp

& Simmons 1980, IUCN 2012) with migratory habits (Cramp & Simmons 1980, Svensson 2009). Distribution range is highly fragmented (Spina & Volponi 2008). European populations winter mainly in tropical West Africa (Cramp & Simmons 1980, Spina & Volponi 2008), although there are known cases of wintering in Mediterranean areas (Spain, Algeria, Tunisia) (Cramp & Simmons 1980). Nesting takes place in colonies of various size (Cramp & Simmons 1980), and exclusively in flooded areas (e.g. marshes), characterised by the presence of aquatic plants appearing on the surface (Spina & Volponi 2008, IUCN 2012). The diet is carnivorous (e.g. fishes, frogs and macroinvertebrates) (Cramp & Simmons 1980, IUCN 2012). As for Italy, the species is classified as regular migratory, wintering and irregular breeding (Tinarelli 2006, Spina & Volponi 2008). *C. hybrida* is declining all over the Europe (SPEC3: Tucker & Heath 1994); as for Italy, it is classified as 'vulnerable' by the Red List of breeding birds (Peronace *et al.* 2012), as nesting sites are located only within Emilia-Romagna Region (Frugis *et al.* 1978, Tinarelli 2006). Whiskered Terns are known to nest near other species' nests (Cramp & Simmons 1980), and cases of conspecific nest parasitism were also reported (Yom Tov 2001, Paillison *et al.* 2008). However, heterospecific altruistic behaviour had never been recorded for this species. In this note, we describe observations of an adult non-breeding Whiskered Tern feeding a Eurasian Coot chick and speculate on possible causes of this enigmatic behaviour.

Materials and Methods

Observations, done by photographers and birdwatchers, who regularly frequent the area, took place from a bird-watching hut, in the Natural Area of Local Interest (ANPIL) 'Podere La Querciola', located in Piana Fiorentina (Tuscany, Central Italy). The study-wetland (43.824558° N, 11.172574° E; *c.* 50 ha large) has been described in details by Bruni *et al.* (2013). Fish species present in these ponds include *Gambusia holbrooki* and *Pseudorasbora parva*. *F. atra* is a known breeding species in this site (Bruni *et al.* 2013), whereas this work report for the first time the presence of the Whiskered Tern (a single individual) in Piana Fiorentina. This tern species is listed as regular migrant in Tuscany (Tellini Florenzano *et al.* 1997): observations of *C. hybrida* in this region belong to migrant individuals during the route from the African wintering site to the breeding sites (e.g. Northern Italy: Frugis *et al.* 1978, Tinarelli 2006, Spina & Volponi 2008). The individual of *C. hybrida* stayed in the study site from 18th to 23rd May 2013, doing its feeding activity in one of the four lakes (named Lago della Querciola). Two nests (with two and four nestlings respectively) of Eurasian Coot are present in the part visited by the Tern.

Results

On 20th May (h. 17:45), the Whiskered Tern caught a fish, and then stopped on a perch without swallowing the prey. After a few seconds, it flew towards a little islet where two Coot chicks were present, hidden by bulrushes (*Juncus* sp., Cyperaceae). The Tern approached the bulrushes twice, then dropped the fish. Adult Coots were not observed in the surroundings. The day after (21st May, h. 8:00–11:00), the Whiskered Tern tried to approach two Coot chicks many times, hovering above them while

holding fishes in its beak. Some preys were dropped towards the chicks, others eaten by the Tern itself on a perch. In the meanwhile, parents stood near the chicks, showing no concern about the behaviour of the Whiskered Tern. Then, on 22th May (14:00), two Coot chicks were swimming around the smallest islet of the lake and one adult individual was about two meters from them. The Whiskered Tern was fishing, resting sometimes on two perches. Once it caught a *P. parva*, the Whiskered Tern approached one of the chicks, extending the beak with the prey towards it *(Figure 1a, 1b)*. The chick responded with a defence posture, raising its legs towards the Whiskered Tern *(Figure 1c)*, which dropped the prey. Then, the chick ate the fish *(Figure 1d)*.

Discussion

Altruistic behaviours displayed by another tern species (i.e. *Sterna hirundo*) are recorded in literature only for a breeding population, whose nests were localised in the proximity of a breeding colony of European Herring Gull *Larus argentatus* (Kuhlemann 1939). Although Whiskered Terns do not reproduce in Tuscany, this observation fall into the breeding period of the species in Europe (Paillison *et al.* 2006, Paillison *et al.* 2007), and the individual observed in Piana Fiorentina was considered to be an adult, according to the colours of the plumage (Cramp & Simmons 1980). Moreover, it is likely that this individual observed in Piana Fiorentina was on route to reach the only Italian bree-
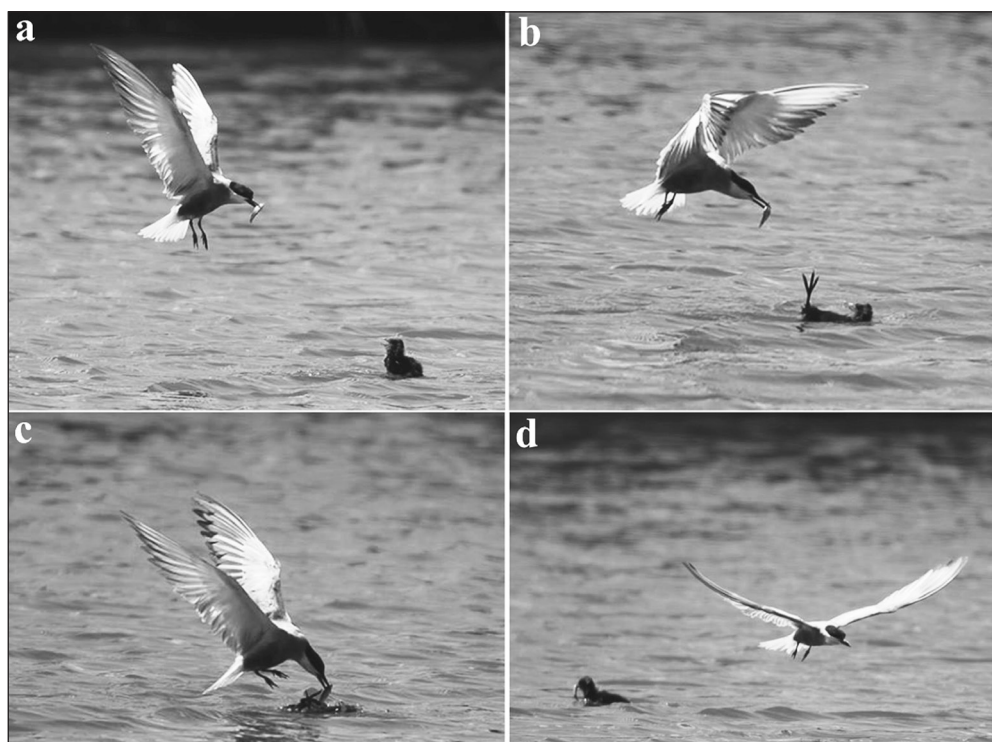

Figure 1. Whiskered Tern feeding the chick of Eurasian Coot with a *Pseudorasbora parva*
(photo Alessandro Piazzini). Chronology reflect the alphabetical sequence of letters
1. ábra Fattyúszerkő szárcsa fiókát etet kínai razbórával *(Pseudorasbora parva)*

ding area; this means that its hormonal status was close to that experiences during breeding, and may have elicited the altruistic behaviour described here (e.g. Buntin 1996). Moreover, the colonial status of the tern species would favour social intra – but also inter – specific interactions. It is noteworthy that the behaviour of the Coot chick mimics that of Whiskered Tern chicks that often go away from the nest (Cramp & Simmons 1980). Coots are omnivorous, eating mainly plant material, but also consume small fishes (Cramp & Simmons 1980), thus, the behaviour of Coot chicks could mimic that of Whiskered Tern chicks. Hence these observations would be considered as a kind of interspecific begging trials. Although chicks of *C. hybrida* and *F. atra* are markedly different both in physical aspects and in voices (Cramp & Simmons 1980), this interspecific feeding could also be explained as a response to the begging of the chick of *F. atra*, which represents a known feeding stimulus in birds (Shy 1982, Dróżdż *et al*. 2004).

Shy (1982) and Trombino (1999) claimed also that mateless/non-breeding heterospecific adults may gain experience by feeding chicks of other species, increasing the probability of pairing in the next breeding season.

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