A case study on the phylogeny and conservation of Saker Falcon

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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.

Keywords: Falco cherrug, phylogenetics, taxonomy, hybridization, conservation

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 veszélyezteti 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.

Kulcsszavak: Falco cherrug, filogenetika, taxonómia, hibridizáció, természetvédelem

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

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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. cvanopus (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 Altai 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 Paleartic. 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 mitochondrial 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 (Karvakin 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. rusti-colus/F. jugger* and *F. biarmicus/F. rusti-colus*, 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). Accurate 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.

References

Angelov, I., Lei, L., You, M., Balázs, I., Ming, M. & Dixon, A. 2006. Possible mixed pairing between Saker Falcon (Falco cherrug) and Barbary Falcon (Falco pelegrinoides) in China. – Falco 28: 14–15.

Avise, J. C., Nelson, W. S. & Sibley, C. G. 1994. DNA sequence support for a close phylogenetic relationship between some storks and New World vultures. – Proceedings of the National Academy of Sciences 91(11): 5173–5177.

Bagyura, J., Szitta, T., Haraszthy, L., Demeter, I., Sándor, I., Dudás, M., Kállay, Gy. & Viszló, L. 2004. Population trend of the Saker Falcon (Falco cherrug) in Hungary between 1980 and 2002. – In: Chancellor, R. D. & Meyburg, B. U. (eds.) 2004.

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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Raptors worldwide. – Downloaded from: www. raptors-international.org on 24/03/2012.

Bagyura, J., Szitta, T., Haraszthy, L., Demeter, I., Sándor, I., Dudás, M., Viszló, L., Klébert, A., Váczi, M., Fatér, I. & Zalai, T. 2007. Kerecsensólyom-védelmi Munkacsoport 2005. évi beszámolója [Annual Report of the Hungarian Saker Falcon Working Group]. – Heliaca 3: 17–21. (in Hungarian with English Summary)

Bagyura, J., Fidlóczky, J., Szitta, T., Prommer, M., Ti-hanyi, G., Zalai, T., Balázs, I., Váczi, M., Viszló, L., Klébert, A., Haraszthy, L., Tóth, I., Török, H. A., Demeter, I., Serfőző, J., Pigniczki, Cs., Kazi, R. & Erdélyi, K. 2012. A kerecsensólyom-védelmi Munkacsoport 2010. évi beszámolója [Annu-

- al Report of the Hungarian Saker Falcon Working Group]. – Heliaca 8: 12–16. (in Hungarian with English Summary)
- Ballard, J. W. O. & Rand, D. M. 2005. The population biology of mitochondrial DNA and its phylogenetic implications. – Annual Review of Ecology, Evolution, and Systematics 36: 621–642. DOI: 10.1146/annurev.ecolsys.36.091704.175513
- Bazin, E., Glémin, S. & Galtier, N. 2006. Population size does not influence mitochondrial genetic diversity in animals. – Science 312(5773): 570–572. DOI: 10.1126/science.1122033
- Bensch, S., Irwin, D. E., Irwin, J. H., Kvist, L. & Aakesson, S. 2005. Conflicting patterns of mitochondrial and nuclear DNA diversity in *Phylloscopus* warblers. – Molecular Ecology 15(1): 161– 171. DOI: 10.1111/j.1365-294X.2005.02766.x
- BirdLife International 2008. Minimising threats from hybrid falcons (originating from captive-bred birds) on wild European falcon populations. Downloaded from: http://www.birdlife.org on 13/12/2013.
- BirdLife International 2012. Species Factsheet: *Falco cherrug.* Downloaded from: http://www.birdlife.org on 12/04/2012.
- Boev, Z. N. & Dimitrov, D. S. 1995. On the Lanner Falcon (*Falco biarmicus*, Temminck, 1825) in Bulgaria. Acta Zoologica Bulgarica 48: 105–112.
- Bonifay, E., Bassiakos, Y., Bonifay, M. F., Louchart,
 A., Mourer-Chauvire, C., Rereira, E., Quinif, Y. & Salotti, M. 1998. La grotte de la Coscia (Rogliano, Macinaggio): étude préliminaire d'une nouveau site du Pléistocéne supérieur de Corse. Paleo 10: 17–41. (in French with English Summary) In: Nittinger, F., Haring, E., Pinsker, W., Wink, M. & Gamauf, A. 2005. Out of Africa? Phylogenetic relationships between *Falco biarmicus* and the other hierofalcons (Aves: Falconidae). Journal of Zoological Systematics and Evolutionary Research 43(4): 321–331.
- Brito, P. H. 2007. Contrasting patterns of mitochondrial and microsatellite genetic structure among Western European populations of Tawny Owls (Strix aluco). Molecular Ecology 16(16): 3423–3437. DOI: 10.1111/j.1365-294X.2007.03401.x
- Clements, J. F., Schulenberg, T. S., Illiff, M. J., Sullivan, B. L., Wood, C. L. & Roberson, D. 2011. The Clements checklist of birds of the world: Version 6.6. – Downloaded from: http://www.birds.cornell.edu/clementschecklist
- Dawnay, N., McEwing, R., Thorpe, R. S. & Ogden, R. 2008. Preliminary data suggests genetic distinctiveness of Gyr and Saker Falcons. – Conservation Genetics 9(3): 703–707. DOI: 10.1007/ s10592-007-9392-1

- Drovetski, S. V., Raković, M., Semenov, G., Fadeev, I. V. & Red'kin, Y. A. 2014. Limited phylogeographic signal in sex-linked and autosomal loci despite geographically, ecologically, and phenotypically concordant structure of mtDNA variation in the Holarctic avian genus *Eremophila*. PLoS ONE 9(1): e87570 DOI: 10.1371/journal. pone.0087570
- Eastham, C. P. & Nicholls, M. K. 2005. Morphometric analysis of large *Falco* species and their hybrids with implication for conservation. Journal of Raptor Research 39(4): 386–393.
- Everitt, P., J. & Franklin, J. 2009. First UK record of free-living Peregrine Falcon female breeding and producing young with a hybrid male falcon of domestic origin. – In: Sielicki, J. & Mizera, T. (eds.) – Peregrine Falcon populations – status and perspectives in the 21th century. – Turul / Poznań University of Life Sciences Press, Warsaw – Poznań, pp. 585–592.
- Ferguson-Lees, J. & Christie, D. A. 2001. Raptors of the World. – Christopher Helm, London, pp. 992
- Fleming, L., Douse, A. F. & Williams, N. P. 2011. Captive breeding of Peregrine and other falcons in Great Britain and implications for conservation of wild populations. – Endangered Species Research 14(3): 243–257. DOI: 10.3354/esr00352
- Fox, N. 1999. The use of exotic and hybrid raptors in falconry. – Downloaded from: http://www.falcons.co.uk on 29.04.2012.
- Friesen, V. L. 2007. New roles for molecular genetics in understanding seabird evolution, ecology and conservation. – Marine Ornithology 35: 89–96.
- Funk, D. J. & Omland, K. E. 2003. Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology, Evolution, and Systematics 34: 397–423. DOI: 10.1016/j.ympey.2009.08.024
- Hebert, P. D., Stoeckle, M. Y., Zemlak, T. S. & Francis, C. M. 2004. Identification of birds through DNA barcodes. PLoS Biology 2(10): 312. DOI: 10.1371/journal.pbio.0020312
- Karyakin, I. V. & Pfeffer, R. 2009. About subspecies and scientific name of the Saker Falcon in North-Western Middle Asia. – Raptors Conservation 17: 89–92.
- Karyakin, I. V. 2011. Subspecies population structure of the Saker Falcon range. – Raptors Conservation 21: 116–171.
- Kenward, R. E. 2009. Conservation values from falconry. – In: Dickson, B., Hutton, J. & Adams, B. (eds.) 2009. Recreational hunting, conservation and rural livelihoods: science and practice. – Blackwell Publishing 1st Edition, pp. 384

- Kleinstauber, G. & Seeber, H. J. 2000. Die erfolgreiche Brut eines Gerfalke-X-Wanderfalke-Hybriden (Falco rusticolus × Falco peregrinus) [A succesfull breeding of a Gyrfalco × Peregrine hybrid].
 In: Freier Wildbahn-Report, Massnahmen, Schlussfolgerungen Populationsökologie. Greifvogel- und Eulenarten 4: 323–332.
- Lerner, H. R. & Mindell, D. P. 2005. Phylogeny of eagles, Old World vultures, and other Accipitridae based on nuclear and mitochondrial DNA. – Molecular Phylogenetics and Evolution 37(2): 327– 346. DOI: 10.1016/j.ympev.2005.04.010
- Lindberg, P. 2006. Do hybrid falcons cause, genetic pollution' among wild falcon populations? Wings without borders. – Conference paper, Poster Presentation, North American Ornithology Congress
- Lovette, I. J., Clegg, S. M. & Smith, T. B. 2004. Limited utility of mtDNA markers for determining connectivity among breeding and overwintering locations in three neotropical migrant birds. Conservation Biology 18: 155–156. DOI: 10.1111/j.1523-1739.2004.00239.x
- McKay, B. D. & Zink, R. M. 2010. The causes of mitochondrial DNA gene tree paraphyly in birds. Molecular Phylogenetics and Evolution 54(2): 647–650. DOI: 10.1016/j.ympev.2009.08.024
- Moritz, C. 1994a Defining 'evolutionarily significant units' for conservation. Trends in Ecology & Evolution 9(10): 373–375. DOI: 10.1016/0169-5347(94)90057-4
- Moritz, C. 1994b Applications of mitochondrial DNA analysis in conservation: a critical review. – Molecular Ecology 3(4): 401–411. – In: Friesen, V. L. 2007. New roles for molecular genetics in understanding seabird evolution, ecology and conservation. – Marine Ornithology 35: 89–96.
- Moseikin, V. & Ellis, D. 2004. Ecological aspects of distribution for Saker Falcons *Falco cherrug* and Altai Gyrfalcon *F. altaicus* in the Russian Altai.
 In: Chancellor, R. D. & Meyburg, B. U. (eds.) 2004. Raptors Worldwide. Downloaded from: www.raptors-international.org on 24/03/2012.
- Nittinger, F., Haring, E., Pinsker, W., Wink, M. & Gamauf, A. 2005. Out of Africa? Phylogenetic relationships between *Falco biarmicus* and the other hierofalcons (Aves: Falconidae). Journal of Zoological Systematics and Evolutionary Research 43(4): 321–331. DOI: 10.1111/j.1439-0469.2005.00326.x
- Nittinger, F., Haring, E., Pinsker, W. & Gamauf, A. 2006. Are escaped hybrid falcons a threat to the Pannonian population of the Saker Falcon *Falco cherrug?* – Greifvögel & Eulen in Österreich, pp. 20–26.
- Nittinger, F., Gamauf, A., Pinsker, W., Wink, M. & Haring, E. 2007. Phylogeography and popula-

- tion structure of the Saker Falcon (Falco cherrug) and the influence of hybridization: mitochondrial and microsatellite data. Molecular Ecology 16: 1497–1517. DOI: 10.1111/j.1365-294X.2007.03245.x
- Oliphant, L. W. 1991. Hybridization between a Peregrine Falcon and a Prairie Falcon in the wild. Journal of Raptor Research 25: 36–39.
- Pfander, P. V. 2011. Semispecies and unindefinied hidden hybrids (for example of birds of prey). – Raptors Conservation 23: 74–105.
- Pfeffer, R. 2009. About geographical variances of the Saker Falcon. Raptors Conservation 16: 68–95.
- Pfeffer, R. 2012. The role of hybridization in the origin of forms in the *Hierofalco* complex. Raptors Conservation 24: 148–164.
- Pierotti, R. & Annett, C. A. 1993. Hybridization and male parental investment in birds. – The Condor 95: 670–679.
- Potapov, E. & Sale, R. 2005. The Gyrfalcon. Yale University Press, New Haven, Connecticut, USA, pp. 288
- Ragyov, D., Kmetova, E., Dixon, A., Franz, K., Koshev, Y. & Nedialkov, N. 2009. Saker Falcon (Falco cherrug) reintroduction in Bulgaria; Feastability study. Downloaded from: https://doveraccomodation.co.uk on 06/05/2012.
- Ragyov, D., Dixon, A. & Kowalczyk, K. 2010. Re-introduction of the Saker Falcon to Bulgaria, South-East Europe. In: Soorae, P. S. (ed.) 2010. Global re-introduction perspectives: 2010. IUCN/SSC Re-introduction Specialis Group & Environment Agency Abu Dhabi, pp. 143–146.
- Väli, Ü., Dombrovski, V., Treinys, R., Bergmanis, U., Daroczi, S. J., Dravecky, M., Ivanovski, V., Lontkowski, J., Maciorowski, G., Meyburg, B-U., Mizera, T., Zeitz, R. & Ellegren, H. 2010. Widespread hybridization between the Greater Spotted Eagle *Aquila clanga* and the Lesser Spotted Eagle *Aquila pomarina* (Aves: Accipitriformes) in Europe. Biological Journal of the Linnean Society 100(3): 725–736. DOI: 10.1111/j.1095-8312.2010.01455.x
- Waits, J. L., Avery, M. L., Tobin, M. E. & Leberg, P. L. 2003. Low mitocondrial DNA variation in Double-crested Cormorants in Eastern North America. – Water Birds 26: 196–200. DOI: 10.1675/1524-4695(2003)026[0196:LMDVID]2 .0.CO;2
- Wink, M. 1995. Phylogeny of Old and New World vultures (Aves: Accipitridae and Cathartidae) inferred from nucleotide sequences of the mitochondrial cytochrome b gene. – Zeitschrift fur Naturforschung C-Journal of Biosciences 50(11): 868–882.

- Wink, M. & Seibold, I. 1996. Molecular phylogeny of mediterranean raptors (families Accipitridae and Falconidae). – In: Muntaner, J. & y Mayol, J. (eds.) 1996. Biología y Conservación de las Rapaces Mediterráneas. – Downloaded from: http:// www.uni-heidelberg.de on 06/05/2012.
- Wink, M., Sauer-Gürth, H., Ellis, D. & Kenward, R.
 2004. Phylogenetic relationships in the *Hierofalco* complex (Saker-, Gyr-, Lanner-, Laggarn Falcon).
 In: Chancellor, R. D. & Meyburg, B. U. (eds.)
 2004. Raptors worldwide. Downloaded from: www.raptors-international.org on 24/03/2012.
- Wink, M. 2006. Use of DNA markers to study bird migration. – Journal of Ornithology 147: 234– 244. DOI: 10.1007/s10336-006-0065-5
- Zhan, X., Pan, S., Wang, J., Dixon, A., He, J., Muller, M. G., Ni, P., Hu, L., Liu, Y., Hou, H., Chen, Y., Xia, J., Luo, Q., Xu, P., Chen, Y., Liao, S., Cao, C., Gao, S., Wang, Z., Yue, Z., Li, G., Yin, Y., Fox, N. C., Wang, J. & Bruford, M. W. 2013. Peregrine and Saker Falcon genome sequences provide insights into evolution of a predatory lifestyle. Nature Genetics 45(5): 563–566. DOI: 10.1038/ng.2588
- Zink, R. M. & Barrowclough, G. F. 2008. Mitochondrial DNA under siege in avian phylogeography.
 Molecular Ecology 17(9): 2107–2121. DOI: 0.1111/j.1365-294X.2008.03737.x

