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Are escaped hybrid falcons a threat to the Pannonian population of the Saker Falcon (*Falco cherrug*)?

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Abstract

To assess the impact of hybridisation in populations of the saker falcon (*Falco cherrug*) 156 individuals of seven falcon species were analysed. Two different genetic marker systems were employed: the mitochondrial control region and seven microsatellite loci. According to the mitochondrial haplotypes the three hierofalcon species (*F. cherrug*, *Falco biarmicus* and *Falco rusticolus*) do not form monophyletic groups. The microsatellite data also reveal only a low degree of differentiation between *F. cherrug* and *F. rusticolus*. Both data sets suggest that natural hybridisation has taken place in the past and is still going on in the extant populations of the eastern part of the range. However, in the Pannonian region, which harbours the westernmost population, introgression of *F. rusticolus* genes into the gene pool of *F. cherrug* has to be ascribed mainly to escaped hybrids. In the total sample from the Pannonian population (collected between 1970–2003) 21 % of the specimens were identified as potential hybrid individuals or hybrid descendants. Accordingly, the gene flow from artificially bred hybrids has a great impact on the gene pool of wild *F. cherrug* populations.

Key words: saker falcon, *Falco cherrug,* hierofalcon, Eastern Europe, hybridisation, introgression, microsatellites, mtDNA

Zusammenfassung

Gefährden künstlich erzeugte Hybriden die pannonische Population des Sakerfalken (*Falco cherrug*)?

Im Zentrum dieser Arbeit steht die genetische Analyse von Populationen des Sakerfalken (*Falco cherrug*) mit dem Ziel, den Einfluss von natürlicher und künstlicher Hybridisierung mit anderen nahe verwandten Arten des Hierofalkenkomplexes abzuschätzen. Dazu erwies es sich als notwendig, die molekulare Phylogenie der beteiligten Arten zu untersuchen. Neben *F. cherrug* wurden daher als weitere Vertreter des Hierofalkenkomplexes der Gerfalke (*Falco rusticolus*), der Lannerfalke (*Falco biarmicus*) und der Luggerfalke (*Falco jugger*) sowie als zusätzliche verwandte Arten der Präriefalke (*Falco mexicanus*) und der Wanderfalke (*Falco peregrinus*) in die Analyse mit einbezogen. Für die Untersuchung wurden verschiedene mitochondriale und nukleäre Markersysteme getestet, von denen zwei für die weiteren Untersuchungen eingesetzt wurden: eine 415 bp lange Sequenz aus der mitochondrialen Kontrollregion und sieben Mikrosatellitenloci aus dem Kerngenom. Insgesamt wurden 156 Individuen analysiert. Die Analyse der mitochondrialen Haplotypen zeigte, dass die drei Hierofalkenarten *F. biarmicus*, *F. cherrug* und *F. rusticolus* keine monophyletischen Gruppen bilden. Geklärt werden konnte die systematische Stellung von *F. mexicanus*, welcher nach den vorliegenden Ergebnissen nicht zu den Hierofalken gehört. Auch mittels Mikrosatellitenanalyse war nur eine schwache Differenzierung zwischen *F. cherrug* und *F. rusticolus* festzustellen, was auf relativ häufige natürliche Hybridisierung in den rezenten östlichen Populationen hinweist. Im Gegensatz dazu muss man bei den westlichen Populationen davon ausgehen, dass die *F. rusticolus* Genomanteile in *F. cherrug* Individuen auf künstliche Introgression durch Beizvogelhybride zurückzuführen sind. Von den zwischen 1970–2003 gesammelten Proben aus der pannonischen Population wurden 21 % als potenzielle Hybride oder Hybridnachkommen diagnostiziert. Demnach führt der Genfluss durch künstlich erzeugte Hybride zu beträchtlichen Änderungen des Genpools der Wildpopulation des Sakerfalken.

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Indroduction

The saker falcon (*Falco cherrug*) is a rare breeding species in the Pannonian region with a current estimated population size of 173–225 pairs: Austria 15-25 (Berg 2000, A. Gamauf in Gensbol 2004), Hungary 113–145 (Bagyura et al. 2003), Czech Republic ≤ 15 (Horák 2000), and Slovakia 30–40 (J. Chavko in Danko et al. 2002). Man-induced hybridisation between hybrid falcons escaped from falconry and individuals from the Pannonian population of *F. cherrug* has become a main issue of interest for conservation aspects. Possible sources of interspecific gene flow are beside the frequently practised artificial hybridisation for falconry also sporadically observed natural hybridisation events in the wild. The present paper is focussed on the genetic analysis of wild populations to assess the impact of hybridisation with closely related species of the Hierofalcon-complex. The study was performed using nuclear markers (microsatellites) as well as mitochondrial sequences (control region).

The drastic decline of some European falcon populations (especially the peregrine falcon, *Falco peregrinus*) in the second half of the 20th century was caused by habitat fragmentation and the widespread use of DDT and other insecticides (Rockenbauch 1998). New methods of artificial insemination were initially developed to produce falcons for falconry, and later for re-introduction programs. Artificial insemination opened the possibility to produce intercrosses even between different species of large falcons. As a consequence, escaped hybrid falcons bred in captivity are suspected to produce fertile offspring with individuals from the wild populations of *F. cherrug*. The mere presence of escaped hybrids generates a continuous source of interspecific gene flow. However, exact numbers of hybrids produced in captivity are not available. Nevertheless, some examples illustrate the dimensions of the problem: One third of the 127 falcons bred in 1999 by one particular breeder in Lower Austria were *F. cherrug* hybrids (Source: Provincial Government of Lower Austria). More is known about exported falcons, e.g., 175 falcon hybrids have been exported officially from Austria in the years 1999 to 2001. Among these hybrids 51 (29 %) stemmed from crosses with *F. cherrug* (Source: Federal Environment Agency, Vienna). From Germany 673 falcon hybrids have been exported in the year 2000, mainly to the Arabic Emirates (Source: Federal Nature Conservation Agency, Bonn). Most of the hybrids produced originate from crosses between *F. peregrinus* and *Falco rusticolus* or between *F. cherrug* and *F. rusticolus* (Brücher 2000, Wegner 2000, Augst 2002). The problem is that a certain part of these hybrid falcons bred in captivity are released or escape within the breeding area of feral falcon populations in Europe. The latter one happens either during hunting or training activities. The total number of escaped falcons is unknown, but was estimated at 10–20 % of all falcons used in falconry (Wegner 2000).

Because individuals from different regions and even related species are used for hybridisation, the material of the present investigation comprised a broad taxonomic spectrum as well as a large geographic range. The distribution area of *F. cherrug* extends from Eastern Europe to the steppes of Central Asia and the high plateaus of China. Currently two subspecies are recognised (del Hoyo et al. 1994, Ferguson-Lees & Christie 2001): the nominate form *F. c. cherrug* (Eastern Europe to Kazakhstan) and the Central Asian *F. c. milvipes* (Central Siberia to Tibet). Several authors list additional subspecies, e.g., *Falco c. cyanopus* for Central and Eastern Europe and *Falco c. altaicus* in the Altay and Sayan Mountains (Brown and Amadon 1968, Glutz von Blotzheim et al. 1971, CADE 1982, BAUMGART 1991). Besides *F. cherrug* further representatives of the Hierofalcon-complex were included: (1) the gyr falcon (*F. rusticolus*) as the species with the northernmost distribution. It occurs circumpolar from North America to northern Russia, Greenland, Iceland, and Fennoscandia. (2) the lanner falcon (*Falco biarmicus*), which occurs from the Mediterranean to East and South Africa, and (3) the lagger falcon (*Falco jugger*) from the Indian subcontinent. In addition, we analysed the North American prairie falcon (*Falco mexicanus*) and the peregrine falcon (*Falco peregrinus*), which has an almost worldwide distribution being absent only from Antarctica, large parts of South America, and parts of the Arctic.

Since the phylogenetic relationships among these species had not been clearly resolved so far, it was necessary for the interpretation of the results to establish a molecular systematics of the species involved. For this purpose we used the Eurasian kestrel (*Falco tinnunculus*) as an outgroup.

Material and Methods

Various mitochondrial and nuclear marker systems were tested. Two of them were employed for further investigations: 1) A 415 bp sequence of the mitochondrial control region, and 2) seven microsatellite loci of the nuclear genome. Altogether, 156 individuals were analysed. In order to detect changes of the gene pool after the beginning of artificial breeding, historical samples (up to 150 years old) from museum collections were also studied in addition to the recent populations. In some cases where it was not possible to obtain fresh tissue (blood, moulted feathers, muscle tissue) of the relevant taxa, samples of museum material were analysed. DNA extractions from fresh tissue and from museum material (skin from the foot pads of study skins) were performed in a 10 % Chelex solution containing proteinase K (0.5 mg/ml). After incubation the extractions were purified using the QIA Quick PCR Purification Kit (QIAGEN). All PCR products were cloned before sequencing (both directions).

Results and Discussion

The analysis of the mitochondrial haplotypes revealed that Hierofalcon species (*F. cherrug*, *F. biarmicus*, *F. rusticolus*) do not form monophyletic groups with the exception of *F. jugger*. However, the latter species is represented in our data set by only two individuals, a sample too small to draw conclusions about monophyly. Moreover, the molecular analysis showed that *F. mexicanus* does not belong to the Hierofalcons. Among the Hierofalcons 70 haplotypes were found. In an unrooted network the haplotypes fall into three groups, each with one main haplotype: 1) Group 1 comprises only *F. cherrug*. 2) Group 2 contains representatives of all four Hierofalcon species. 3) Group 3 connects groups 1 and 2 and includes most individuals of *F. biarmicus* except two individuals from Israel, which cluster in group 2. The central haplotype of group 2 is found in *F. cherrug* as well as in *F. rusticolus*. These results suggest that introgression of *F. rusticolus* genes into the gene pool of the eastern *F. cherrug* populations must have occurred in the course of postglacial range shifts. The more pronounced genetic differentiation and the higher haplotype diversity of *F. biarmicus* in the African populations could be taken as indication for an African origin of the Hierofalcon-complex.

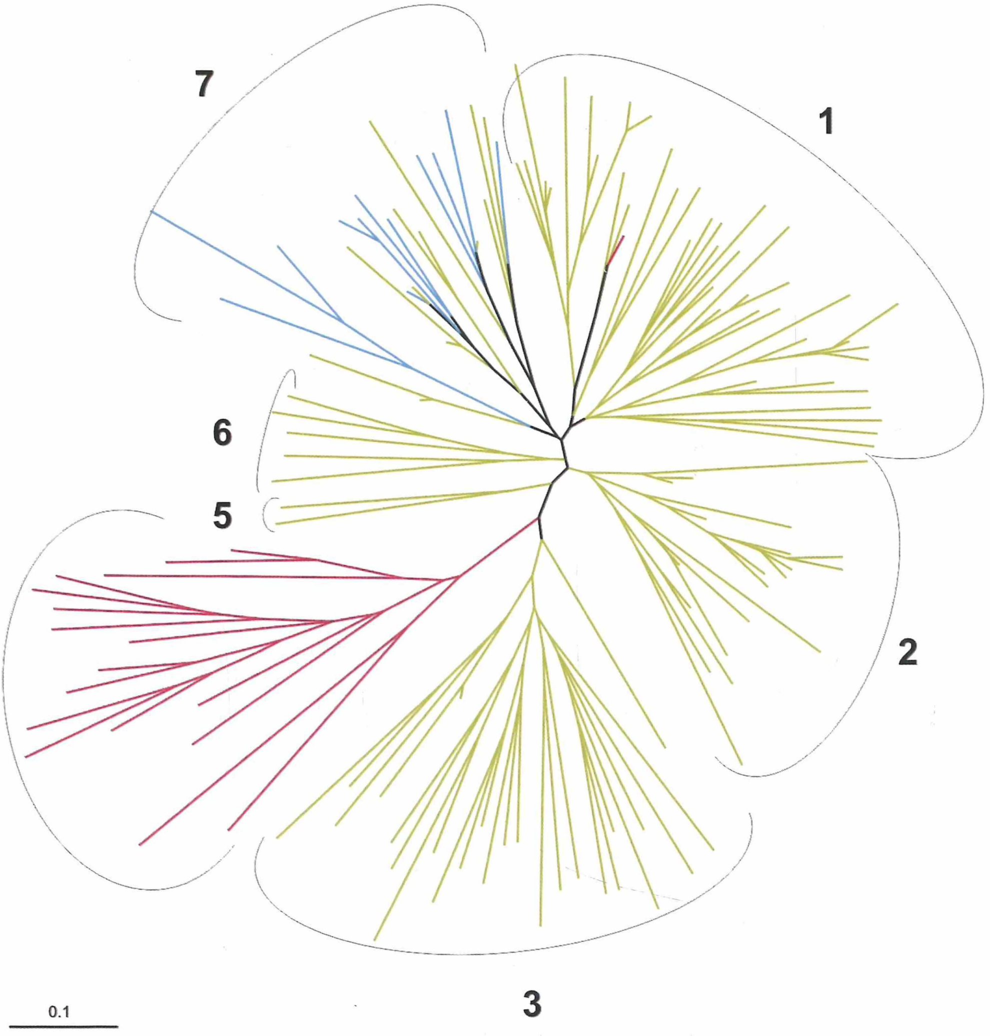

Fig. 1: NJ-tree based on seven microsatellite loci (after NITTINGER 2004). Seven clusters can be distinguished: five sakerfalcon *F. cherrug* cluster (1, 2, 3, 5, 6; green), one pure lannerfalcon *F. biarmicus* cluster (4; red), and one mixed cluster (7) containing sakerfalcon *F. cherrug* (green) and gyrfalcon *F. rusticolus* (blue). The green individuals in clade 7 as well as the red individual in clade 1 are potential hybrids or their descendants.

Abb. 1: NJ-Baum basierend auf sieben Mikrosatelliten-Loci (nach NITTINGER *2004). Sieben Cluster können unterschieden werden: fünf reine Sakerfalken* F. cherrug *Cluster (1, 2, 3, 5, 6; grün), ein reiner Lannerfalken* F. biarmicus *Cluster (4; rot), und ein gemischter Cluster (7), der Sakerfalken* F. cherrug *(grün) und Gerfalken* F. rusticolus *(blau) enthält. Die grünen Individuen in Clade 7 und das rote in Clade 1 sind potenzielle Hybriden oder deren Nachkommen.*

No recent depauperation of the mitochondrial gene pool was observed in the western populations of *F. cherrug*. In contrast to the historical populations the genetic variation was even slightly increased due to the occurrence of haplotypes from Group 2. This can be interpreted as evidence for gene flow or interspecific introgression from escaped falcons from falconry.

The microsatellite data (Fig. 1) also indicate a rather low degree of differentiation between *F. cherrug* and *F. rusticolus*, again suggesting frequent recent hybridisation: 1) In the eastern populations (Mongolia and Altay mountains) natural hybridisation seems to occur between the two species. 2) In contrast, for the western populations it has to be assumed that the contribution of *F. rusticolus* to the gene pool of *F. cherrug* can be traced back to introgression from escaped hybrids. In the total sample from the most western (= Pannonian) population (collected between 1970–2003) 21 % of the specimens were identified as potential hybrids or descendants of hybrids (1977–89: 8.3 %, 1990–2003: 26.7 %). Accordingly, the gene flow from artificially bred hybrids has a great impact on the gene pool of wild *F. cherrug* populations.

The study confirmed that only the combination of mitochondrial and nuclear analyses of recent as well as historical populations can provide a comprehensive picture of the genetic structure of recent populations.

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