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MORPHOMETRIC ANALYSIS OF LARGE *FALCO* SPECIES AND THEIR HYBRIDS WITH IMPLICATIONS FOR CONSERVATION

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ABSTRACT.—Morphometric examination of several large falcon species and their hybrids was conducted to ascertain whether phenotype was an accurate indicator of hybrid parentage. Six external body measurements were recorded from 167 Gyrfalcons (*Falco rusticolus*), Saker (*F. cherrug*), Peregrine (*F. peregrinus*), and New Zealand Falcons (*F. novaezeelandiae*) and from 100 F1, F2, and backcross hybrids of these species. Principal Component Analysis separated pure species and also indicated clusters for F1 peregrine × saker, gyr × peregrine, and gyr × saker hybrids. Gyr × peregrine hybrids were distinguishable from their parent species, but it was impossible to discriminate accurately between a complex (F1, F2, and backcross) of gyr × saker hybrids and between these and the parent species. Escaped or released falconry hybrids are perceived as a significant threat to the conservation of wild falcon populations. Under current legislation, gyrs and their hybrids are CITES Appendix I species, and sakers are Appendix II species. We suggest that phenotypic characteristics are not reliable for identification of such hybrids for legal purposes. Furthermore, analysis of measurements also identified a "paternal effect," whereby F_1 hybrids, irrespective of gender, were phenotypically more similar to their paternal than their maternal progenitors.

KEY WORDS: *Peregrine Falcon;* Falco peregrinus; *Gyrfalcon;* Falco rusticolus; *Saker Falcon;* Falco cherrug; *New Zealand Falcon;* Falco novaezeelandiae; *Falcon hybrids; morphometric; principal component analysis; PCA; CITES.*

ANÁLISIS MORFOMÉTRICO DE LAS ESPECIES DE *FALCO* DE TAMAÑO GRANDE Y DE SUS HIBRIDOS, E IMPLICACIONES PARA LA CONSERVACIÓN

RESUMEN.—Se analizó la morfología de varias especies de halcones y de sus híbridos para averiguar si el fenotipo es un indicador preciso de la paternidad de los híbridos. Se registraron seis medidas corporales para un total de 167 individuos pertenecientes a las especies *Falco rusticolus, F. cherrug, F. peregrinus* y *F. novaezeelandiae,* y para un total de 100 híbridos F1, F2 y retrocruces de estas especies. Un análisis de componentes principales separó a las especies puras e identificó grupos formados por híbridos F1 *F. peregrinus* × *F. cherrug, F. rusticolus* × *F. peregrinus* y *F. rusticolus* × *F. cherrug.* Los híbridos *F. rusticolus* × *F. peregrinus* se diferenciaron de las especies parentales, pero fue imposible distinguir claramente entre un complejo (F1, F2, retrocruces) de híbridos *F. rusticolus* × *F. cherrug,* y entre este complejo y las especies parentales. Los halcones híbridos de cetrería que escapan o son liberados se consideran una amenaza para la conservación de las poblaciones silvestres. Bajo la actual legislación, *F. rusticolus* y sus híbridos están registradas en el Apéndice I de CITES y *F. cherrug* en el Apéndice II. Consideramos que las características fenotípicas no son confiables para la identificación de estos híbridos con propósitos legales. Además, el análisis morfométrico identificó "efectos paternos," en donde los híbridos F1, independientemente de su sexo, fueron fenotípicamente más similares a sus progenitores paternos que a los maternos.

[Traducción del equipo editorial]

One of the first domestic hybrid falcons was produced in 1971 from a female Saker Falcon (*Falco cherrug*) and male Peregrine Falcon (*F. peregrinus;* Morris and Stevens 1971, Morris 1972). Since then, falconers and raptor breeders have produced many different hybrids from members of the Falconifor-

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Table 1. Identity of hybrid falcons used in the analysis.

HYBRID IDENTITY[a]	SAMPLES SIZES	MALE PARENT	FEMALE PARENT
F1s			
Gyr × Peregrine	6 ♂, 7 ♀	Gyr	Peregrine
Gyr × Saker	7 ♂, 5 ♀	Gyr	Saker
Peregrine × Saker	3 ♂, 13 ♀	Peregrine	Saker
Peregrine × Gyr	1 ♂	Peregrine	Gyr
Peregrine × New Zealand	1 ♂	Peregrine	New Zealand
Gyr/Saker × Peregrine	1 ♂, 1 ♀	Gyr × Saker F2 hybrid	Peregrine
F2s			
Gyr × Saker	4 ♂, 5 ♀	Gyr × Saker F1 hybrid	Gyr × Saker F1 hybrid
Backcrosses—1st generation			
Gyr × Gyr/Saker	3 ♂, 1 ♀	Gyr	Gyr × Saker F1 hybrid
Saker × Gyr/Saker	3 ♂, 3 ♀	Saker	Gyr × Saker F1 hybrid
Gyr/Saker × Saker	14 ♂, 17 ♀	Gyr × Saker F1 hybrid	Saker
Gyr/Peregrine × Peregrine	2 ♂	Gyr × Peregrine F1 hybrid	Peregrine
Backcrosses—2nd generation			
Gyr (3/8)[b]/Saker	1 ♂	Gyr × Saker F1 hybrid	Gyr/Saker × Saker (backcross hybrid)
Gyr (5/8)[b]/Saker	1 ♂, 1 ♀	Gyr	Gyr/Saker × Saker (backcross hybrid)

[a] When naming hybrids, the paternal species is cited first. For example, a cross between a male gyr and female saker is a gyr × saker (or gyr/saker) hybrid, whereas a male saker crossed with a female gyr is a saker × gyr (saker/gyr) hybrid.

[b] These numbers represent a simple way to show the proportion of genes from the parent species, assuming that a F1 hybrid inherits $\frac{1}{2}$ of the genes from both the male and female parent species. For example, a gyr ($\frac{3}{8}$)/saker, produced by backcrossing a gyr × saker F1 hybrid with a gyr/saker backcross hybrid, has $\frac{3}{8}$ gyrfalcon and $\frac{5}{8}$ saker genes.

mes (Boyd and Boyd 1975, Cade and Weaver 1976, Bunnell 1986, Weaver and Cade 1991), including intergeneric hybrids (e.g., Harris's Hawks [*Parabuteo unicinctus*] × Cooper's Hawk [*Accipiter cooperii*] and Harris's Hawk × Ferruginous Hawk [*Buteo regalis*]; Fox and Sherrod 1999a) for falconry purposes.

Many F_1 hybrids are fully viable (Heidenreich 1997), in their turn producing F_2 hybrids or backcrosses (B_1 and B_2 representing 1st and 2nd generation backcrosses) to one or other parent species. Indeed, hybrids from within the subgenus *Hierofalco,* the "desert falcon" group (Heidenreich 1997), exhibit full fertility, presumably over indefinite generations. Less closely-related pairs of species, such as gyr (*F. rusticolus*) and peregrine, produce hybrids with reduced fertility, manifest as deformed spermatozoa, completely sterile females (Heidenreich and Kuspert 1992), or unviable embryos (Rosenkranz 1995).

This extended viability of some falcon hybrids coupled with increasing demand over the last 10 yr for domestic falcons from North American, European, and Arabian falconry markets (Fox and Sherrod 1999b) has prompted conservation concerns. Escaped domestic hybrids may be merely a curiosity (Forseman 1999), a nuisance for bird watchers (Gantlett and Millington 1992), or a threat to the integrity of wild populations. Indeed, falcon pairs made up of an escaped hybrid and a wild, pure individual have been documented several times (e.g., Kleinstäuber and Seeber 2000, Lindberg 2000). A further conservation issue presumably concerns illegal-trade in falcons, whereby protected falcon species may be "laundered" as domestic hybrids. In this study, we examine the relationship between falcon species and their hybrids, particularly the accuracy of using morphometric characters for identification, and discuss the conservation issues concerning falcon hybrids.

METHODS

We investigated four large falcon species, namely Peregrine, Gyr, Saker, and New Zealand falcons (*F. novaezeelandiae*) and several of their hybrid types used for falconry. Hybrid falcons were all bred in captivity and, therefore, their parentage was known. Six external body

Table 2. Principal Component Analysis (PCA) of six anatomical measurements from juvenile male Gyrfalcon, Saker, Peregrine, and New Zealand falcon species and hybrids of those species. Eigenvalues and eigenvectors (based on the correlation matrix).

	PRINCIPAL COMPONENT			
	1	2	3	4
Eigenvalue	3.0328	1.3691	0.7459	0.6833
Percent of variability	0.5055	0.2282	0.1243	0.1139
Cumulated Percent	0.5055	0.7336	0.8580	0.9718
CHARACTERS	EIGENVECTORS			
Wing chord	0.4990	−0.2324	0.1490	−0.3852
Wing width	0.5552	−0.0321	−0.0688	−0.1697
Tail length	0.5195	0.2308	−0.2347	−0.1471
Tail step	0.0247	0.6402	0.7536	−0.1395
Tarsus length	0.3536	0.3591	−0.1598	0.7769
Digit three length	0.2170	−0.5940	0.5697	0.4221

measurements were collected from live juvenile Gyrfalcons ($N = 7$ males and 6 females), Saker ($N = 34$ males and 40 females), Peregrine ($N = 17$ males and 24 females), and New Zealand falcons ($N = 25$ males and 14 females), and their various hybrids (Table 1). Apart from European Peregrine Falcon subspecies, the majority of which were *F. peregrinus peregrinus,* no other differentiation was made between subspecies or geographic morphs. All birds were kept at the National Avian Research Center's Falcon Facility in Carmarthen, Wales, U.K. The majority of F_2 and backcross 1 and 2 hybrids were between gyrs and sakers. This is because hybrids between members of the subgenus *Hierofalco* remain fertile for an indefinite number of generations, whereas hybrids between more out-crossed falcon species, such as peregrines and sakers, have a reduced fertility. Some of the hybrids included are produced in very low numbers (e.g., Peregrine Falcon × New Zealand Falcon), and published data on these are rare. Therefore, we included them in the analysis.

One of us (C. Eastham) took six measurements, namely wing chord length and width, tail length, tail step (the difference between the outermost tail feather [rectrix 6] and the tip of the center tail feather [rectrix 1] on the same side), tarsus length, and third digit length from each bird. Measurement protocols followed standard methods described by Baldwin et al. (1931), Fox (1977), Biggs et al. (1978), Kemp (1987), and Fox et al. (1997). Feather characters were measured to the nearest 1 mm and non-feather characters to the nearest 0.1 mm using a pair of digital calipers, a steel ruler, and tape measure. Inclusion of single individuals, for example, a male Peregrine Falcon × New Zealand Falcon, allowed us to employ Principal Component Analysis (PCA) on XLSTAT-Pro (Fahmy 1998) statistical software as a suitable method for data analysis. Male and female data were analyzed separately to eliminate background variation due to reversed sexual size dimorphism (Brown and Amadon 1968, Cade 1982), or other sex-linked or sex-limited characters. We used wing chord length to distinguish males and females, as this measurement was reported by Wyllie and Newton (1994) and Eastham (2000) to be the most reliable indicator of overall body size.

RESULTS

Males. Principal Component (PC) 1 (Table 2, Fig. 1) accounted for the majority (50.5%) of variation. Because all eigenvectors for PC1 showed positive and nearly equal values, we concluded this component represents overall body size (Wiley 1981). Male gyrs and F1 and F2 gyr/saker hybrids had the largest body size, whilst male peregrines and New Zealand Falcons were the smallest.

PC 2 (Table 2, Fig. 1) accounted for 22.8% of the variation, as indicated by a contrast in eigenvectors between the positively weighted tail step, tail and tarsus length, the negatively weighted digit three length, and wing chord length and width (Table 2). This component summarizes variation related to body shape. Tail step and digit three length showed the strongest positive and negative weightings, respectively. With a low negative weighting, wing width was of limited use in further analysis of PC 2. New Zealand Falcons had the relatively longest tail step (indicating a more rounded tail), tail and tarsus length, and shortest digit three and wing chord, whilst peregrines, the single peregrine × New Zealand hybrid and gyr/saker × peregrine hybrid had the relatively longest digit three and wing chord length and shortest tail step and tail and tarsus length. F1 gyr × peregrines and sakers showed a wide variation in PC 2 values, with an individual saker having the highest PC 2 value.

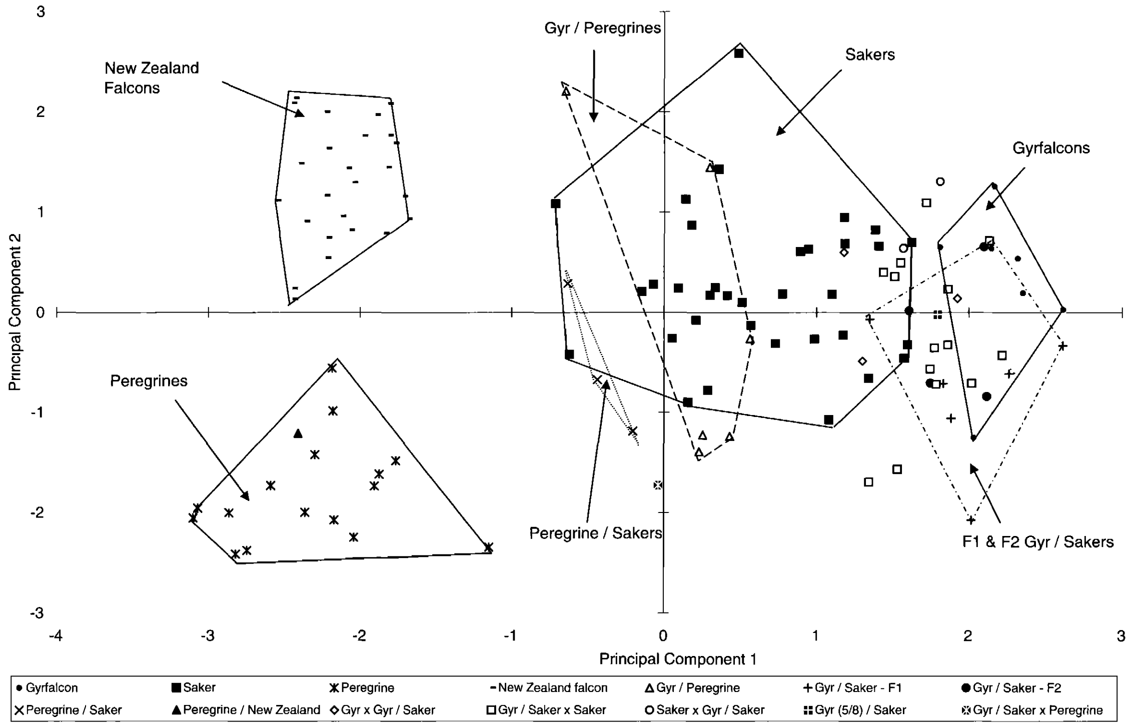

Figure 1. Principal component scores from morphometric comparison of various male falcon species and their hybrids.

PC 3 and 4 (Table 2) accounted for only 12.4% and 11.3% of the residual variation, respectively. Tail step and digit three length had a high positive weighting in PC 3, and in PC 4, there was a contrast between positively weighted tarsus and digit three length and negatively weighted wing chord length. As PC 1 and 2 together accounted for the majority (73%) of variation, we did not consider PC 3 and 4 further.

Females. The PCA for juvenile female falcons showed a similar pattern of variation as that seen in juvenile males. Again PC 1 (Table 3, Fig. 2) accounted for the largest proportion (44.7%) of variation and as indicated by mostly positive and nearly equal values represents, as with males, overall size (Wiley 1981). Gyrs and the various gyr/saker F1, F2 and backcrosses had the largest size, whilst Peregrine and New Zealand falcons were the smallest.

PC 2 (Table 3, Fig. 2) accounted for a further 21.8% of the variation, and we concluded that this, again like males, was related to shape. This was indicated by a contrast in eigenvectors between the positively weighted tail step, tail and tarsus length, the negatively weighted digit three length, and wing chord length and width (Table 3). Positively weighted tail step and negatively weighted digit three and wing chord length had the highest eigenvectors for this PC. New Zealand Falcons had the longest tail step and the shortest digit three and wing chord length, whilst F1 gyr × peregrines and peregrines had the shortest tail length and the longest digit three and wing chord length. PC 3 and PC 4 (Table 3) accounted for 18.4% and 11.4% of the variation, respectively. As for males, we did not consider these principal components further.

DISCUSSION

Using PCA we found that the four falcon species, irrespective of sex, were clearly separated into groups: New Zealand Falcons with a small size, long rounded tails and tarsi, and short wings; peregrines, also with a small size, long digit three lengths, and long narrow wings; sakers with a large

Table 3. Principal Component Analysis (PCA) of six anatomical measurements from juvenile female Gyrfalcon, Saker, Peregrine, and New Zealand falcon species and hybrids of those species. Eigenvalues and eigenvectors (based on the correlation matrix).

	PRINCIPAL COMPONENT			
	1	2	3	4
Eigenvalue	2.6826	1.3071	1.1023	0.6864
Percent of variability	0.4471	0.2179	0.1837	0.1144
Cumulated percent	0.4471	0.6649	0.8487	0.9631
CHARACTERS	EIGENVECTORS			
Wing chord	0.4717	−0.3853	−0.1963	0.4118
Wing width	0.5765	−0.1767	−0.0356	−0.0129
Tail length	0.5737	0.1670	−0.0642	−0.1107
Tail step	0.0866	0.6865	0.1871	0.6869
Tarsus length	0.3077	0.2169	0.6899	−0.4484
Digit three length	−0.1177	−0.5236	0.6672	0.3809

size, long rounded tails, and short digits; and gyrs with the largest size.

Using these external body measurements, we also found it possible to identify three main hybrid groups: a complex of F1, F2 and backcross gyr/sakers; F1 gyr × peregrines and F1 peregrine × sakers. Further, it was possible to separate gyr × peregrines from their parent species, but impossible to separate completely the F1, F2, and backcross gyr/sakers hybrid-complex from pure sakers or particularly, from pure gyrs.

Overall, we found that the hybrids were generally of intermediate phenotype between their parents. However, beyond this it appears that the paternal progenitor influences the phenotype to a greater extent than maternal. For example, for both males and females, the clusters representing F1 gyr × peregrine hybrids, hybrids whose male parents were gyrs, were spatially closer to the gyr clusters than to the peregrine clusters (Fig. 1, 2). Thus, both male and female gyr × peregrine hybrids have a morphology closer to that of gyrs than to peregrines. Further, that the single female peregrine × gyr, whose sire was a peregrine, was spatially closer to the peregrine cluster than the gyr cluster, adds further weight to this proposed generality. Similarly, the male and female F1 gyr × sakers, both with gyrs as male parent, appear more gyr-like than saker-like in morphology. Except for male F1 peregrine × sakers this "paternal effect" seems true for all species combinations. We explain this by considering that two thirds of the sex linked genes in a population are carried by the homogametic sex (male in birds; Mittwoch 1977) and only one third by the heterogametic sex (Falconer 1967). Therefore, falcon sires (the homogametic sex) will contribute more sex-linked alleles to their hybrid offspring than will (heterogametic) dams.

International trade in endangered species, such as some falcons, can be a profitable enterprise and, if unregulated, can threaten their conservation. Regulation of the trade in such endangered species is by international agreements, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). According to their degree of endangerment in the wild, all species are classed in one of three CITES appendices. Special conditions apply to the most endangered, known as Appendix I species (i.e., those threatened with extinction and whose survival could be impaired by trade), which allows restricted trade in captive and domestic bred individuals. Appendix II includes species considered less threatened. The saker is an Appendix II species, and although trade is regulated, this is less exacting than for Appendix I species. Despite relatively healthy world populations and for reasons which are largely political (White and Kiff 1998), gyrs and peregrines and their hybrids are included in Appendix I.

The results we present here show that it can be difficult to discriminate falcon species accurately from their hybrids, especially hybrids of Appendix I gyrs and Appendix II sakers. Similarly, plumage variation, especially in juvenile falcons, is difficult

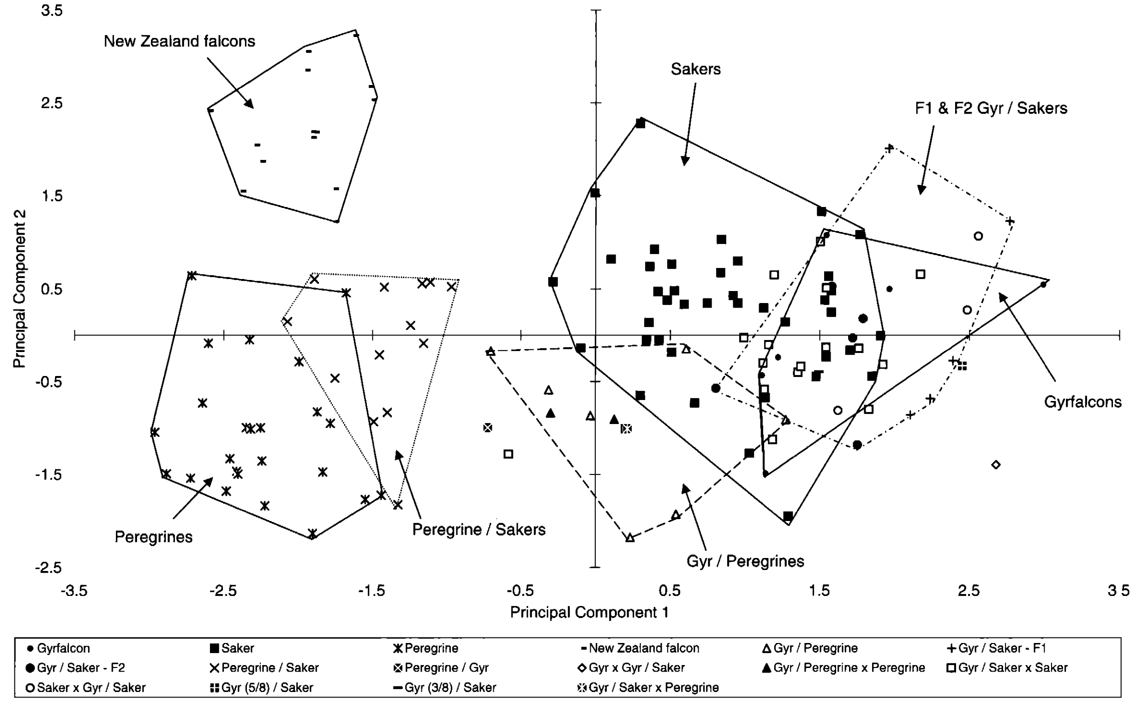

Figure 2. Principal component scores from morphometric comparison of various female falcon species and their hybrids.

to assess objectively and make comparisons between species and their hybrids. These observations may provide fuel for two separate arguments.

Ornithologists are increasingly aware of the widespread genomic compatibility and potential for hybridization amongst what appear to be very dissimilar species (Grant and Grant 1992), such that hybridization between avian species is considered more common than originally thought (Gill 1998). Mayr and Short (1970) estimated that up to 10% of North American bird species regularly hybridize; it's so common that hybrids are even included in birdwatchers' field guides (Sibley 2000). The presence of natural hybrids is not believed to be a threat to the integrity of a species, even though they may challenge the biological species concept of taxonomists (Brookes 1999). Amongst free-living, wild birds of prey such hybridization is increasingly documented at the subspecific (Fefelov 2001), specific (Hamer et al. 1994), and even to the intergeneric levels (Corso and Gildi 1998, Yosef et al. 2001).

Introgressive hybridization may therefore be a process by which species evolve, rather than something that will corrupt them. Thus, if the species concept for birds is much looser than conservation law dictates, then perhaps it is the legislation and not the species concept that must be challenged. For example, the so-called "Altai falcon" (*Falco altaicus* Menzbier), whose phenotype seems to share characters with both gyrs and sakers, is believed by some to be the result of introgressive hybridization between gyrs and sakers, rendering all these as allospecies within a single superspecies (Pfander 1987, Ellis 1995a, 1995b). This being so, then to discriminate between Appendix I gyrs and Appendix II sakers may be irrelevant, and artificially produced crosses between these two may be of no evolutionary threat should they escape to the wild. If, however, the Altai Falcon is merely a large, dark race of the saker (Eastham and Nicholls 2002), and any resemblance to gyrs is merely superficial, then escaped hybrids between these species could potentially compromise wild populations, and the integrity of gyrs and sakers must be recognized and CITES regulations enforced.

A different view of the role of natural hybridization accepts that avian species are dynamic entities, which in certain circumstances, freely exchange genes with other such entities. Despite these interactions, the integrity of the whole is a fragile one, and to short circuit gene flow *via* artificial hybrids is a danger to this integrity. CITES protocols are the response to perceived conservation status, and therefore, it should be mandatory to discriminate between species as we know them. Accurate identification to assist in controlling the trade in falcons is paramount, and we have shown that criteria other than phenotypic characteristics (e.g., DNA markers) must be employed to identify individuals and species. This is imperative if CITES is to remain an effective means of regulating legitimate trade and protecting species in the wild.

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LITERATURE CITED

BALDWIN, S.P., H.C. OBERHOLSER, AND L.G. WORLEY. 1931. Measurements of birds. *Sci. Publ. Clevel. Mus. Nat. Hist.* 2:1–65.

BIGGS, H.C., R. BIGGS, AND A.C. KEMP. 1978. Measurements of raptors. Pages 77–82 *in* A.C. Kemp [ED.], Proceedings of a Symposium on African Predatory Birds. Northern Transvaal Ornithological Society, Pretoria, South Africa.

BOYD, L.L. AND N. BOYD. 1975. Hybrid falcons. *Hawk Chalk* 14:53–54.

BROOKES, M. 1999. Live and let live. *New Scientist* 2193: 32–36.

BROWN, L. AND D. AMADON. 1968. Eagles, hawks and falcons of the world. Vol. 2. The Wellfleet Press, Secaucus, NJ U.S.A.

BUNNELL, S. 1986. Hybrid falcon overview—1985. *Hawk Chalk* 25:43–47.

BURTON, J.F. 1995. Birds and climate change. Christopher Helm Publishers, London, England.

CADE, T.J. 1982. Falcons of the world. William Collins Sons and Co. Ltd., London, England.

——— AND J.D. WEAVER. 1976. Gyrfalcon × peregrine hybrids produced by artificial insemination. *J. North Am. Falconers Assoc.* 15:42–47.

CORSO, A. AND R. GILDI. 1998. Hybrids of Black Kite and Common Buzzard in Italy in 1996. *Dutch Birding* 20: 226–233.

EASTHAM, C.P. 2000. Morphological studies of taxonomy of the Saker (Falco cherrug: Gray 1833) and closely allied species. Ph.D. thesis, University of Kent at Canterbury, Canterbury, Kent, England.

——— AND M.K. NICHOLLS. 2002. Morphological classification of the so-called "Altai Falcon." Pages 211–219 *in* R. Yosef, M.L. Miller, D. Pepler [EDS.], Raptors in the new millennium. Int. Birding and Res. Centre, Eilat, Israel.

ELLIS, D.H. 1995a. The Altai falcon: origin, morphology, and distribution. Pages 143–168 *in* Middle East Falcon Research Group [EDS.], Proceedings of the Specialist Workshop. Abu Dhabi, United Arab Emirates.

———. 1995b. What is *Falco altaicus* Menzbier? *J. Raptor Res.* 29:15–25.

FAHMY, T. 1998. XLSTAT-PRO statistical software. Paris, France.

FALCONER, D.S. 1967. Introduction to quantitative genetics. Oliver and Boyd, London, England.

FEFELOV, I.V. 2001. Comparative breeding ecology and hybridization of eastern and western Marsh Harriers *Circus spilonotus* and *C. aeruginosus* in the Baikal region of eastern Siberia. *Ibis* 143:587–592.

FORSEMAN, R. 1999. The raptors of Europe and the Middle East: a handbook for field identification. T. and A.D. Poyser, Ltd., London, England.

FOX, N.C. 1977. The biology of the New Zealand Falcon *(Falco novaezeelandiae;* Gmelin 1788*)*. Ph.D. dissertation, University of Canterbury, New Zealand.

———, C.P. EASTHAM, AND H.J. MACDONALD. 1997. The ERWDA handbook of falcon protocols. Environmental Research and Wildlife Agency, Abu Dhabi, United Arab Emirates.

——— AND S. SHERROD. 1999a. The use of exotic and hybrid raptors in falconry. Information arising from the International Committee on Hybrids. International Wildlife Consultants Ltd., Carmarthen, Wales, England.

——— AND S. SHERROD. 1999b. Cited in "Scale production and use of hybrids in falconry." *Falco 13,* Middle East Falcon Research Group, International Wildlife Consultants Ltd., Carmarthen, Wales, England.

GANTLETT, S. AND R. MILLINGTON. 1992. Identification of large falcons. *Birding World* 5:101–106.

GILL, F.B. 1998. Hybridization in birds. *Auk* 115:281–283.

GRANT, P.R. AND B.R. GRANT. 1992. Hybridization of bird species. *Science* 256:193–197.

HAMER, T.E., E.D. FORSMAN, A.D. FUCHS, AND M.L. WALTERS. 1994. Hybridization between Barred and Spotted owls. *Auk* 111:487–492.

HEIDENREICH, M. 1997. Birds of prey: medicine and management. Blackwell Scientific Ltd., Oxford, England.

——— AND H. KUSPERT. 1992. Metodos de la reproduccion en cautividad de las diferentes especies de halcones. El problema de los hibridos y la cooperacion entre criadores y autoridades. *Proc. Congr. Nac. Cria. Aves Cetreria* 1:15–17.

HOELLER, T. AND P. WEGNER. 2001. Der Wanderfalke ist in Gefahr! Die zweite Hybridfalken-Wildbrut in

Deutschland zeigt die Brisanz der Hybridfalkenzucht. *Greifvögel u. Falknerei* 2000:64–66.

KEMP, A.C. 1987. Taxonomy and systematics. Pages 251–259 *in* B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [EDS.], Raptor management techniques manual. National Wildlife Federation Scientific and Technical Series No. 10.

KLEINSTÄUBER, G. AND H.J. SEEBER. 2000. Die erfolgreiche Brut eines Gerfalke-×-Wanderfalke-Hybriden (*Falco rusticolus* × *Falco peregrinus*) *in* freier Wildbahn-Report, Maßnahmen, Schlußfolgerungen. Poplationsökol. *Greifvogel- u. Eulenarten* 4:323–332

LINDBERG, P. 2000. Hybridfalk häckar igen. *Vår Fågelvärld* 8:28–29.

MAYR, E. 1963. Animal species and evolution. Belknap Press of Harvard University Press, Cambridge, MA U.S.A.

——— AND L.L. SHORT. 1970. Species taxa of North American birds. No. 9 *Publ. Nuttal Ornithol. Club.*

MITTWOCH, U. 1977. Genetics of sex differentiation. Academic Press, Burlington, MA U.S.A.

MORRIS, J. 1972. Peregrine/Saker breeding. *Cap. Breed. Diurn. Birds of Prey* 1:14–15.

——— AND R. STEVENS. 1971. Successful cross-breeding of Peregrine tiercel and a Saker falcon. *Cap. Breed. Diurn. Birds of Prey,* 1:5–7.

PENNYCUICK, C.J. 1989. Bird flight performance: a practical calculation manual. Oxford University Press, Oxford, England.

PFANDER, P.V. 1987. Once again concerning the Altay Gyrfalcon. *Selevinia* 2:38–42.

ROSENKRANZ, D. 1995. Cited *in* M. Heidenreich. 1997. Birds of prey: medicine and management. Blackwell Scientific Ltd., Oxford, England.

SIBLEY, C. 2000. The North American bird guide. Christopher Helm, London, England.

WEAVER, J.D. AND T.J. CADE. 1991. Falcon propagation. The Peregrine Fund, Inc., Boise, ID U.S.A.

WHITE, C.M. AND L.F. KIFF. 1998. Language use and misapplied, selective "science;" their roles in swaying public opinion and policy as shown with two North American raptors. Pages 547–560 *in* R.D. Chancellor, B.-U. Meyburg, and J.J. Ferrero [EDS.], Holarctic birds of prey. ADENEX-WWGBP, Badajoz, Spain.

WILEY, E.O. 1981. Phylogenetics: the theory and practice of phylogenetic systems. Wiley/Interscience, Hoboken, NJ U.S.A.

WYLLIE, I. AND I. NEWTON. 1994. Latitudinal variation in the body-size of Sparrowhawks (*Accipiter nisus*) within Britain. *Ibis* 136:434–440.

YOSEF, R., A.J. HELBIG, AND W.S. CLARK. 2001. An intrageneric *Accipiter* hybrid from Eilat, Israel. *Sandgrouse* 23:141–144.

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