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GENETIC EVIDENCE FOR GLOBAL DISPERSAL IN THE PEREGRINE FALCON (*FALCO PEREGRINUS*) AND AFFINITY WITH THE TAITA FALCON (*FALCO FASCIINUCHA*)

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ABSTRACT.—We analyzed variation in cytochrome *b* mitochondrial DNA sequences in 11 subspecies of the Peregrine Falcon (*Falco peregrinus*), three samples of the Taita Falcon (*F. fasciinucha*) from Africa, and several other *Falco* and outgroup species, to assess haplotype diversity in the Peregrine Falcon on a worldwide basis. We identified 16 haplotypes from 31 Peregrine Falcon samples, of which 11 were unique and 5 were shared among two or more subspecies. There was neither concordance between cytochrome *b* variation and taxonomic designation at the subspecies level, nor any phylogeographic pattern in the genetic data. The Taita Falcon was nested within the Peregrine Falcon clade. Percent sequence divergence between the Taita Falcon and the Peregrine Falcon (0.4–1.2%) overlapped that among subspecies of the Peregrine Falcon (0.0–1.0%), suggesting very close genetic affinity between the two species. We hypothesize that historical and recent dispersal, combined with rapid morphological evolution, contributed to the lack of concordance between variation in cytochrome *b* mitochondrial DNA sequences and phylogeography in the Peregrine Falcon.

KEY WORDS: *Peregrine Falcon*; Falco peregrinus; *Taita Falcon*; Falco fasciinucha; *cytochrome* b; *genetic variation*; *dispersal*.

EVIDENCIA GENÉTICA DE DISPERSIÓN GLOBAL DE *FALCO PEREGRINUS* Y SU AFINIDAD CON *FALCO FASCIINUCHA*

RESUMEN.—Analizamos la variación en el citocromo *b* de secuencias de ADN mitocondrial en 11 subespecies de *Falco peregrinus*, en tres muestras de *F. fasciinucha* de África y en otros *Falco* y especies fuera del grupo

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para determinar la diversidad de haplotipos en *F. peregrinus* a escala mundial. Identificamos 16 haplotipos en 31 muestras de *F. peregrinus*, de las cuales 11 fueron únicas y 5 estuvieron compartidas entre dos o más subespecies. No hubo concordancia entre la variación del citocromo *b* y la designación taxonómica a nivel de subespecie, ni en el patrón filogeográfico en los datos genéticos. *F. fasciinucha* estuvo anidado dentro del clado de *F. peregrinus*. La divergencia porcentual de secuencia entre *F. peregrinus* y *F. fasciinucha* (0.4–1.2%) se superpuso con la de subespecies de *F. peregrinus* (0.0–1.0%), sugiriendo una afinidad genética muy cercana entre las dos especies. Hipotetizamos que la dispersión histórica y reciente, combinada con una evolución morfológica rápida, contribuyó a la falta de concordancia entre la variación en el citocromo *b* de secuencias de ADN mitocondrial y la filogeografía en *F. peregrinus*.

[Traducción del equipo editorial]

The Peregrine Falcon (*Falco peregrinus*) is a cosmopolitan species that inhabits every continent except Antarctica and is well known for its extensive wandering (Cade 1982). Migrants move annually great distances between the northern and southern hemispheres (Fuller et al. 1998), and records of spectacular peregrinations exist; e.g., between the United States and Japan (although possibly facilitated by maritime traffic; White et al. 2002) and between the United States and Switzerland (Doolittle and Berger 2013). Although the species is relatively philopatric, at the scale of hundreds of kilometers or less (Mearns and Newton 1984, Tordoff and Redig 1997), the potential exists for Peregrine Falcons to disperse to nearly any region of the globe.

Depending on the authority, the Peregrine Falcon is currently subdivided into 16–19 subspecies based on geographic variation (White and Boyce 1988, Ferguson-Lees and Christie 2001). Although plumage and morphological variation between some geographic races follows a clinal pattern, differences between adjacent subspecies may be striking. For example, the red-naped shaheen (*F. peregrinus babylonicus*) and the black shaheen (*F. peregrinus peregrinator*) exhibit remarkable plumage differences (Ferguson-Lees and Christie 2001). Thus, understanding the effect of the Peregrine Falcon's innate dispersal ability on its evolutionary history and current geographic diversity is a challenge.

In contrast to the Peregrine Falcon, the Taita Falcon (*Falco fasciinucha*) is a rare and local species endemic to East Africa (Ferguson-Lees and Christie 2001). Although this monotypic species has been described as a ''miniature peregrine'' based on its anatomical characters and mode of life (Brown 1971), its evolutionary relationship to the Peregrine Falcon remains obscure.

We present results from a global survey of variation in cytochrome *b* mitochondrial DNA (hereafter cyt *b* mtDNA) in 11 subspecies of Peregrine Falcon. We included in our survey the Taita Falcon, several other falcon species, and outgroup taxa. We compare genetic variation with the phylogeographic distribution of the Peregrine Falcon. We discuss possible consequences of dispersal in the Peregrine Falcon, and its close genetic affinity with the Taita Falcon.

MATERIALS AND METHODS

Taxon Sampling. We included 45 individuals in the analysis (Table 1): 31 Peregrine Falcons (from 11 subspecies), 3 Taita Falcons, and 11 outgroup samples from nine species. We downloaded six of the sequences from GenBank: one Peregrine Falcon, one Red-footed Falcon (*Falco vespertinus*), one Laughing Falcon (*Herpetotheres cachinnans*), one Collared Forest-Falcon (*Micrastur semitorquatus*), one Sharp-shinned Hawk (*Accipiter striatus*), and one American Kestrel (*Falco sparverius*). Excluding the GenBank sequences, 95% of our samples were of known geographic origin, taken from wild-caught birds or captive-bred birds from lineages of known origin.

Molecular Analysis. We preserved blood samples and, in one case a feather with bloody pulp, in Longmire's Lysis Buffer (Longmire et al. 1988) and stored them at −70°C. We extracted DNA using either standard phenol-chloroform protocols or DNeasy tissue-extraction kits (QIAGEN, Alameda, California, U.S.A.). We amplified and sequenced the cyt *b* mtDNA gene via the polymerase chain reaction (PCR) using the following combinations of primer pairs and according to standard protocols (Griffiths 1997):

(1) L 14841 (5′-CCATCCACCATCTCAGCATGATGAAA) and H 15149 (5′-CCCTCAGAATGATATTTGTCCTCA)
(2) L 15132 (5′-CTAATAGCAACAGCCTTCGTC) and H 15516 (5′-GACTAGGGGATTTGCTGGTGTAAAG)
(3) L 15489 (5′-CTAGCCCTATTTACCCCAAACCTG) and H 15915 (5′-GGAGTCTTCAGTCTCTGGTTTACAAGAC)

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Table 1. Specimen information for falcons subject to genetic analyses. Haplotype letter designations for *F. peregrinus* and *F. fasciinucha* correspond to those listed in Table 2.

SPECIES	STATUS[1]	COLLECTION LOCATION	YEAR COLLECTED	SPECIMEN ID OR GENBANK #	HAPLOTYPE
Accipiter striatus	–	–	–	U83305	–
Falco biarmicus	W	Zimbabwe, Africa	1994	RH16	–
F. biarmicus	W	Zimbabwe, Africa	1995	RH32	–
F. fasciinucha	CB	Zambia, Africa	1994	RH9	R
F. fasciinucha	W	Zimbabwe, Africa	1994	RH10	R
F. fasciinucha	CB	Zimbabwe, Africa	1994	RH11	R
F. femoralis	–	–	–	U83310	–
F. peregrinus	–	–	–	AF90388	A
F. peregrinus anatum	W	California, U.S.A.	1993	2H	B
F. peregrinus anatum	CB	Rocky Mountains, U.S.A.	1993	LB3	D
F. peregrinus anatum	CB	Rocky Mountains, U.S.A.	1993	CL2	C
F. peregrinus anatum	CB	Rocky Mountains, U.S.A.	1993	DS5	D
F. peregrinus anatum	CB	California, U.S.A.	1993	DS7	D
F. peregrinus anatum	W	California, U.S.A.	1994	JP13	G
F. peregrinus anatum	W	Oregon, U.S.A.	1994	JP14	B
F. peregrinus anatum	CB	Alberta, Canada	1993	MG6	E
F. peregrinus babylonicus	W	Unknown	1996	LO1	Q
F. peregrinus brookei	W	Spain	1994	A1	F
F. peregrinus brookei	W	Spain	1994	A8	I
F. peregrinus cassini	CB	Argentina	1994	ALB1	E
F. peregrinus macropus	W	Australia	1994	DS1	B
F. peregrinus minor	W	South Africa	1995	ZFC1	E
F. peregrinus minor	W	South Africa	1995	ZFC2	B
F. peregrinus minor	W	South Africa	1995	ZFC4	B
F. peregrinus minor	CB	Zimbabwe, Africa	1994	RH3	J
F. peregrinus minor	W	Zimbabwe, Africa	1994	RH6	K
F. peregrinus minor	CB	Zimbabwe, Africa	1994	RH12	L
F. peregrinus nesiotes	W	Fiji, South Pacific	1993	DS3	M
F. peregrinus nesiotes	CB	Fiji, South Pacific	1993	DS9	N
F. peregrinus pealei	W	British Columbia, Canada	1993	WN29	D
F. peregrinus pelegrinoides	W	Unknown	1996	LO2	E
F. peregrinus peregrinus	W	Great Britain	1993	FE2	O
F. peregrinus tundrius	W	NWT, Canada	1993	SAS229	B
F. peregrinus tundrius	W	NWT, Canada	1993	SAS330	H
F. peregrinus tundrius	W	Quebec, Canada	1993	MG2	I
F. peregrinus tundrius	W	Quebec, Canada	1993	MG5	I
F. peregrinus tundrius	W	Labrador, Canada	1993	LAB1	K
F. peregrinus tundrius	W	Labrador, Canada	1993	LAB4	E
F. peregrinus tundrius	W	Labrador, Canada	1993	LAB8	P
F. rupricoloides	W	Zimbabwe, Africa	1995	RH35	–
F. sparverius	W	California, U.S.A.	1994	EV1	–
F. sparverius	–	–	–	U83306	–
F. subbuteo	W	Botswana, Africa	1996	GM3	–
F. vespertinus	–	–	–	U83311	–
Herpetotheres cachinnans	–	–	–	U83319	–
Micrastur semitorquatus	–	–	–	U83315	–

[1] W = wild caught; CB = captive-bred with known parental origin.

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(4) 6F (ND5) (5′-GGGTCTTTCGCCCTATCAATC) and 6R (tRNA thr) (5′-CTAAGAAGGTTATAGGCCTTCAC).

The first three primer pairs amplified internal segments of 307 base pairs (bp), 337 bp, and 376 bp in length, respectively, while the latter pair amplified the entire cyt *b* mtDNA gene. For quality control purposes, we extracted all but two samples (LO1 and LO2) at least twice (Table 1). To control for the presence of nuclear pseudogenes (Sorensen and Fleischer 1996), we cross-checked sequences resulting from internally amplified segments of the cyt *b* gene with sequences resulting from entire-gene amplifications. We cycle sequenced the PCR products using an ABI PRISM Model 310 sequencer (Applied Biosystems, Foster City, California, U.S.A.) or other automated sequencers.

Data Analysis. We trimmed primer sequences and assembled them as contiguous fragments using Sequencher software (Gene Codes Corp., Ann Arbor, Michigan, U.S.A.). There were no indels and we aligned final sequences by eye.

To examine homogeneity of base composition among study taxa, we used a chi-square test implemented in PAUP* (Swofford 2001) to ensure that rooting of outgroups was not influenced by base composition heterogeneity. We performed phylogenetic analyses with maximum parsimony using the branch-and-bound algorithm in PAUP*. To calculate support for nodes, we ran 100 replicate bootstrap searches with maximum parsimony, using the heuristic algorithm with TBR (tree bisection and reconnection) branch swapping. We used the Sharp-shinned Hawk, representing the family Accipitridae, as an outgroup to the Falconidae (Griffiths 1994). *Herpetotheres cachinnans* and *Micrastur semitorquatus*, representing the subfamily Herpetotherinae, served as a nested clade that was basal to *Falco* (Griffiths et al. 2004).

Population-level analyses may lack phylogenetic structure, because ancestral and descendant haplotypes may coexist or reticulate relationships may exist among haplotypes. Thus, the hierarchical tree format may be inappropriate for representing relationships among haplotypes (Posada and Crandall 2001). In such cases, haplotype networks more consistently depict relationships among the sampled haplotypes. We used TCS software (phylogenetic network estimation using statistical parsimony; Clement et al. 2000) to construct a haplotype network for the Peregrine Falcon and Taita Falcon sequences, using a representative of the ''hierofalco'' complex, the Lanner Falcon (*Falco biarmicus*), as an outgroup (Nittinger et al. 2005).

RESULTS

Sequence Divergence. Amplification and sequencing of the 41 individuals yielded 1044 bp of cyt *b*. We included four additional outgroup sequences (trimmed to the same 1044 bp region) downloaded from GenBank. Among these 45 sequences, 352 (34%) of the 1044 characters were variable and 234 (22%) were phylogenetically informative.

Sequence divergence between pairs of Peregrine Falcon sequences was low (0.0–1.0%). Divergence between Peregrine Falcons and Taita Falcons ranged from 0.5–1.1%. Divergence between Peregrine Falcons and outgroups was greater, ranging from 3.8–11.0% for other *Falco* species, 14.8–17.1% for *Herpetotheres* and *Micrastur*, and 17.6–18.0% for *Accipiter*.

Our analyses revealed 16 Peregrine Falcon haplotypes among the 31 sequences (Tables 1 and 2). Haplotype A, not found in any of our samples, corresponded to the published mtDNA genome of the Peregrine Falcon (Mindell et al. 1999). Eleven haplotypes (C, F, G, H, J, L, M, N, O, P, and Q) were unique (found in only one subspecies or geographic area) and the remaining 20 samples fell into five haplotypes: (1) Haplotype B: *F. p. tundrius* SAS229, *F. p. minor* ZFC2 and ZFC4, *F. p. macropus* DS1, and *F. p. anatum* JP14 and 2H, from North America, Africa, and Australia; (2) Haplotype D: *F. p. anatum* DS5, DS7, and LB3, and *F. p. pealei* WN29, from North America; (3) Haplotype E: *F. p. cassini* ALB1, *F. p. pelegrinoides* LO2, *F. p. minor* ZFC1, *F. p. tundrius* LAB4, and *F. p. anatum* MG6, from South America, Middle East/Africa, and North America; (4) Haplotype I: *F. p. tundrius* MG2 and MG5, and *F. p. brookei* A8, from North America and Europe; (5) Haplotype K: *F. p. minor* RH6 and *F. p. tundrius* LAB1, from North America and Africa.

These haplotypes reflect neither taxonomic designation nor geographic origin (Tables 1 and 2). Haplotypes B, D, and I differed from haplotype E by a single substitution, whereas haplotype I differed by seven substitutions. The three Taita Falcon samples had a unique haplotype (Haplotype R, Table 2).

Phylogenetic Inference. There was no significant base composition heterogeneity among the 45 initial taxa. For the phylogenetic analysis, we eliminated redundant taxa, yielding a final matrix with 28 taxa and 1044 characters. Phylogenetic inference yielded 300 trees with length 551 steps (Consistency Index = 0.5699 and Retention Index = 0.6981).

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Table 2. Eighteen mitochondrial DNA haplotypes observed among Peregrine Falcon (A-Q) and Taita Falcon (R) samples. Vertical numbers refer to positions of variable nucleotides within 1044 bp of cyt *b* sequence, corresponding to the published mitochondrial genome of *Falco peregrinus* (haplotype A, GenBank Accession No. AF90388). Dots under nucleotide positions indicate an identical nucleotide as given with Haplotype A. See Table 1 for haplotype assignments by specimen.

HAPLOTYPE	13816	13840	13858	13997	14104	14155	14188	14203	14236	14258	14284	14348	14423	14428	14458	14501	14626	14628	14629	14638	14705
A	T	A	T	A	C	T	C	A	A	C	C	A	T	G	A	T	G	G	T	T	A
B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.
C	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	C	.	.	C	C	.
D	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	C	C	.
E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.
F	.	.	.	G	.	C	.	.	.	.	T	.	.	C	.	C	.	.	.	.	G
G	.	.	.	.	.	C	A	.	.	.	.	.	.	.	C	.	.	.	C	C	.
H	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	C	C	.
I	.	.	.	.	.	C	.	.	.	.	T	.	.	C	.	C	.	.	.	.	G
J	.	.	.	.	.	C	.	.	.	.	T	.	.	C	.	C	.	.	C	C	.
K	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.
L	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	C	C	.
M	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	A	C	C	.
N	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.
O	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	C	.	.	.	.	G
P	.	.	.	.	A	C	.	.	.	.	T	.	.	C	.	C	.	.	.	.	G
Q	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.
R	.	.	C	.	.	C	.	.	.	T	.	G	.	C	.	C	A	.	.	.	G

The majority-rule consensus tree showed that the Peregrine Falcon subspecies and the Taita Falcon formed a single clade (Fig. 1), which was noteworthy because the Taita Falcon did not group with any of the smaller-sized falcons tested here: Greater Kestrel (*F. rupicoloides*), Eurasian Hobby (*F. subbuteo*), Red-footed Falcon, Aplomado Falcon (*F. femoralis*), and American Kestrel.

Relationships of the taxa within the Peregrine Falcon/Taita Falcon clade were unresolved. Five haplotypes were shared among multiple subspecies of Peregrine Falcon (Fig. 1). The minimum spanning tree inferred from the estimation of haplotype relationships provided more structure (Fig. 2); however, there was no clear biogeographic signal. Haplotype E included sequences from four specimens of known origin in Africa, South America, and North America. Another specimen in this group, *F. p. pelegrinoides*, was of unknown origin, but the subspecies range includes northern Africa and the Middle East. We found Haplotype B in samples from the Canadian arctic, South Africa, Australia, and the Pacific coast of North America. Haplotypes were shared among widely disparate geographic regions; e.g., three haplotypes found in the North American arctic and sub-Saharan Africa were shared.

We also found unique haplotypes in widely disparate geographic regions. North American samples yielded five unique haplotypes, and we found two each in samples from Europe, sub-Saharan Africa, and Fiji. The minimum spanning tree also showed that the Taita Falcon haplotype differed by five substitutions from the closest Peregrine Falcon haplotype, found in arctic North America and Spain (Haplotype I, Fig. 2).

DISCUSSION

Our study suggests that haplotype diversity and sequence divergence in the cyt *b* mtDNA gene in Peregrine Falcons is comparable to that found in other falcons. For instance, we found 16 haplotypes in 31 specimens, and Nittinger et al. (2005, 2007) found 14 haplotypes of the CR-ps gene (456–458 bp) in 22 specimens of the Lanner Falcon from sub-Saharan Africa. Two other studies compared a 559-bp segment of the mtDNA control region of Peregrine Falcons. White et al. (2013) found 30 haplotypes in 219 individuals from 12 subspecies in 27 locations; 17 were unique haplotypes. Talbot et al. (2011) found 14 haplotypes in 65 Peregrine Falcons sampled across seven populations; 10 were private haplotypes (found in a single population).

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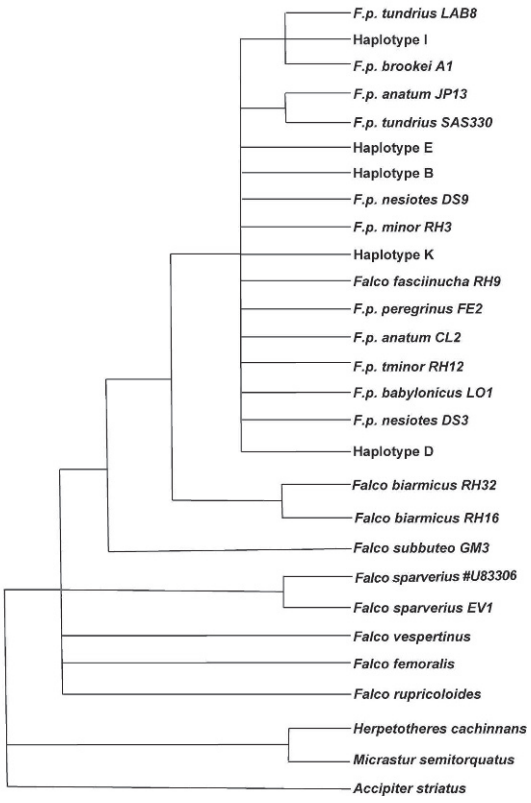


Figure 1. Strict consensus tree inferred from sequences of *Falco peregrinus* subspecies, *F. fasciinucha*, and outgroups. Terminal taxa labeled as Haplotypes B, D, E, I and K are groups of identical Peregrine Falcon sequences; refer to text for listing of samples assigned to each Haplotype. Terminal taxon labeled ''*F. fasciinucha* RH9'' includes all three identical Taita Falcon sequences. See text for details.

These two studies suggest that haplotype diversity can be quite high regionally, and show similar proportions of shared haplotypes among all individuals sampled (0.061 and 0.059, respectively).

The overall lack of concordance between mtDNA variation and taxonomic designation at the subspecies level observed here is consistent with similar studies in other falcons, including members in the hierofalco group: Lanner Falcon and Saker Falcon (*F. cherrug*; Wink et al. 2004; Nittinger et al. 2005, 2007), and Gyrfalcon (*F. rusticolus*; Nittinger et al. 2005, 2007; Johnson et al. 2007). Wink et al. (2000) found some clustering among three subspecies of peregrines, but only when using neighbor joining; maximum parsimony showed no resolution. In population genetic studies incorporating both mtDNA and microsatellite data, Brown et al. (2007) and Johnson et al. (2010) found *F. p. pealei* to be distinct from the other two North American subspecies, *F. p. anatum* and *F. p. tundrius*, with no genetic support for designating the latter two taxa as separate subspecies. In contrast, within a subspecific taxon, the northern and southern populations of the nominate *F. p. peregrinus* in Scandinavia revealed genetic distinctiveness within both contemporary (Nesje et al. 2000) and historical time frames (Jacobsen et al. 2008). White et al. (2013) confirmed a general lack of concordance between control region mtDNA variation and 12 subspecies of Peregrine Falcons, but found some evidence for the genetic distinctiveness of island populations of Peregrine Falcons, several of which are well-defined subspecies. Our results are based on 11 subspecies of Peregrine Falcons with nearly half of the samples from North America, where extensive reintroduction efforts with nonnative subspecies was accomplished in the eastern and midwestern United States (Tordoff and Redig 1997, 2001). Some of the haplotype diversity revealed here may have resulted from admixture of genotypes, which would obscure phylogenetic patterns (but see below). Greater density sampling of Peregrine Falcon subspecies will be necessary to fully understand the systematics of this species at both the population and taxonomic level.

Lack of concordance between morphological and genetic data implies that differential rates of evolution occur between phenotypic characters and genetic markers. Genetic evidence suggests that the Peregrine Falcon is a recently diverged species (Nittinger et al. 2005, White et al. 2013). So for this species, morphological differentiation, as defined by subspecific variation, may proceed at rates faster than mtDNA sequence evolution (see also White et al. 2013). This could be seen as an adaptive response to varied environmental conditions. Kruckenhauser et al. (2004) showed that rapid differentiation in 92 morphological characters in several western Palearctic buzzard species in the genus *Buteo* was not accompanied by mitochondrial genome differentiation. Rapid morphological change in response to anthropogenic influences, occurring on the order of a century, also has been demonstrated in some raptors (Pereva and Grazhdankin 1994). Thus, it is feasible that widespread phenotypic differentiation, as seen in the 16–19 subspecies of Peregrine Falcon, albeit occurring on the order of thousands of years, may reflect an adaptive response to the wide

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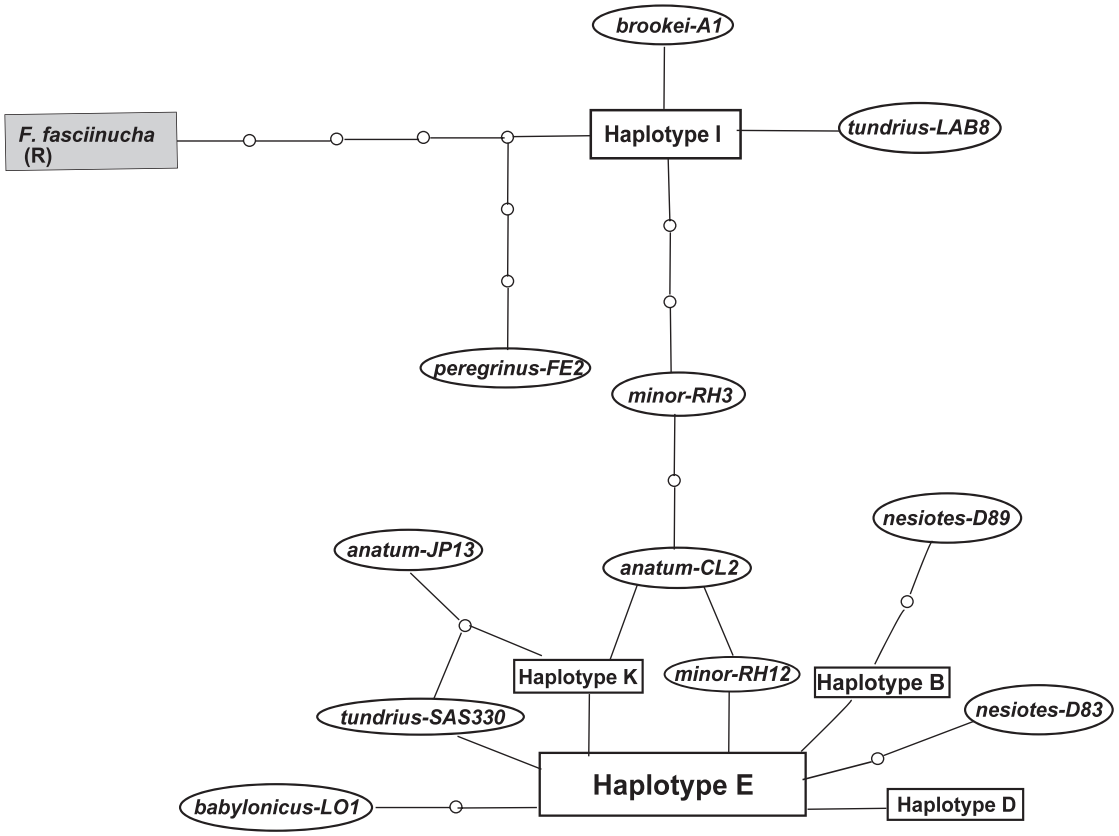


Figure 2. Minimum-spanning network of *Falco fasciinucha* and 16 haplotypes of *Falco peregrinus* subspecies. The haplotypes displayed as squares represent shared haplotypes; refer to text for listing of samples assigned to each haplotype. The square labeled *F. fasciinucha* represents identical Taita Falcon sequences. Refer to Table 1 for a complete listing of haplotypes.

range of environmental conditions faced by this circumpolar species.

We identified two private haplotypes of cyt *b* in *F. p. nesiotes*, the subspecies of Peregrine Falcon found in the Fiji Islands of the South Pacific (White et al. 1998). Members of this subspecies exhibit near-identical morphology and have high genetic similarity based on DNA fingerprinting (White et al. 1988, 1993), microsatellite loci, and control region mtDNA (Talbot et al. 2011). In contrast to our cyt *b* results, Talbot et al. (2011) found a single haplotype in the mtDNA control region in *F. p. nesiotes*. This haplotype was neither private nor did it originate from one of the neighboring subspecies of Peregrine Falcon, *F. p. macropus* of Australia. As an explanation for the overall low genetic polymorphism in *F. p. nesiotes*, Talbot et al. (2011) could not differentiate between bottleneck effects or sustained isolation through evolutionary time, partly due to a lack of museum reference specimens. To date, genetic signatures resulting from the DDT-era induced population bottlenecks in Peregrine Falcons have not been clearly detected (Brown et al. 2007, Jacobsen et al. 2008). Further sampling of island populations of Peregrine Falcons (e.g., *F. p. ernesti, F. p. furuitii, and F. p. madens*) may shed light on levels of polymorphism in island forms.

Our analysis of sequence variation in cyt *b* did not recover any phylogeographic pattern. Two hypotheses, not necessarily exclusive, could account for this: historical dispersal followed by incomplete lineage sorting with retention of ancestral polymorphisms (Johnson et al. 2007) or contemporary (ongoing) dispersal of maternal lineages worldwide. Identical haplotypes found in samples of morphologically

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distinct subspecies of Peregrine Falcons from North America, South America, Australia, Europe, and Africa support the concept of incomplete lineage sorting of ancestral haplotypes, as does the phylogeographic structure unveiled by microsatellite DNA analysis of Peregrine Falcons in Scandinavia (Nesje et al. 2000). However, the sharing of some haplotypes on a global basis may be more reflective of contemporary dispersal, whether natural or human-mediated through recovery efforts, which would erase the relationship between population-level haplotype genetic distance and geography (Neigel and Avise 1993, Oomen et al. 2011). The Peregrine Falcon does exhibit maternal-biased dispersal (Mearns and Newton 1984, Tordoff and Redig 1997, Dennhardt and Wakamiya 2013, Faccio et al. 2013) and a remarkable ability to reach all corners of the globe, whether during migration (e.g., from Greenland to southern Chile; del Hoyo et al. 1994) or as pioneering dispersers (e.g., a nestling banded at Lake Powell in the southwestern United States was later recovered in Japan; B. Anderson, Falcon Research Group, Bow, Washington, U.S.A. pers. comm.). Although most of the samples analyzed here originated from source populations that were acquired at the outset of recovery efforts, we cannot rule out genetic admixture via anthropogenic-induced dispersal and manipulation through Peregrine Falcon recovery efforts (Nesje et al. 2000, Brown et al. 2007, Jacobsen et al. 2008, Johnson et al. 2010). We hypothesize that historical and recent dispersal combined with rapid morphological evolution explains the lack of concordance between variation in cyt *b* mtDNA sequences and phylogeography in the Peregrine Falcon. Further work will be required to decipher the relative contribution of historical versus contemporary dispersal in haplotype sharing.

The percent sequence divergence between the Taita Falcon and Peregrine Falcon (0.4–1.2%) overlapped the range of divergence among Peregrine Falcon subspecies (0.0–1.0%). This close genetic relationship and the clustering of the Taita Falcon within the Peregrine Falcon clade is consistent with the results derived from studies based on the mtDNA control region (White et al. 2013) and major histocompatibility complex (MHC) genes (Gangoso et al. 2012). These data suggest very close genetic affinity of the Taita Falcon with the Peregrine Falcon. Although the Taita Falcon is approximately half the size of the Peregrine Falcon (Ferguson-Lees and Christie 2001), its proportions and behavior have been categorized as peregrine-like (Cade 1982). The two species breed sympatrically in sub-Saharan Africa (Brown 1971, Hartley 2000) and nest in close proximity to one another. In the Zambezi River Gorge on the Zambia/Zimbabwe border, the Taita Falcon exhibits strong interspecific aggression toward Peregrine Falcons (Dowsett 1980). Interestingly, some naive Peregrine Falcons (i.e., those with no prior contact with Taita Falcons) react with recognition behavior upon seeing a Taita Falcon. For example, a male Taita Falcon flown for falconry in North America elicited courtship/recognition behavior from wild female Peregrine Falcons (H. Peeters pers. comm.) and a captive *F. p. nesiotes* × *macropus* (South Pacific/Australia; D. Bell unpubl. data). Regardless of taxonomic status, the time since divergence between these two species, assuming mtDNA evolves at a constant rate of 2% per million years (Johnson and Cicero 2004), would have occurred at least 250,000 years ago. This time frame is consistent with other studies suggesting a recent origin for the Peregrine Falcon (Nittinger et al. 2005, White et al. 2013). This period corresponds with the warm Holstein interglacial, when tundra was restricted and fragmented (Newton 2003). Such conditions may have been conducive to rapid global dispersal in the Peregrine Falcon.

This study compared sequences from only a few small falcons, from which the Taita Falcon clearly diverged: Eurasian Hobby, Greater Kestrel, Red-footed Falcon, American Kestrel, and Aplomado Falcon. Additional comparative genetic work on a wide range of falcon species is required to further clarify the evolutionary relationships between the Taita Falcon and Peregrine Falcon.

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