
Role of Genetic Background in the Success of Reintroduced Peregrine Falcons

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Abstract: *Peregrine Falcons (Falco peregrinus) of seven subspecies from four continents were bred in captivity, and approximately 1173 of their progeny were released in the midwestern United States and adjacent regions of Ontario and Manitoba in an attempt to replace the original population that was extirpated by chlorinated hydrocarbon poisoning in the 1950s. We analyzed the success of individuals of the different subspecies introduced to the Midwest. Five of the seven subspecies released have contributed to the current breeding population. Subspecies of breeding Peregrine Falcons were equally represented when breeding birds of high productivity were compared with less prolific breeders. The subspecific makeup of the breeding population did not differ significantly from that of the released population, suggesting that adaptability in this species was sufficient to override genetic differences between subspecies. Peregrines of widely different genetic stocks have thrived after release, making substantial genetic contributions to the new population.*

Papel de la Condición Genética en el Exito de Halcones Peregrinos Reintroducidos

Resumen: *Halcones peregrinos (Falco peregrinus) de siete subspecies de cuatro continentes fueron reproducidos en cautiverio y aproximadamente 1173 de sus descendientes han sido liberados en el oeste medio de los Estados Unidos y regiones adyacentes de Ontario y Manitoba en un intento por reemplazar a la población original que fue extirpada por envenenamiento con hidrocarburos clorinados en los años 50. Analizamos el éxito de individuos de las diferentes subspecies introducidas en el oeste medio. Cinco de las siete subspecies liberadas han contribuido a la población reproductora actual. Las subspecies de halcones reproductores estuvieron igualmente representadas cuando las aves de alta productividad fueron comparadas con los reproductores menos prolíficos. La composición subspecifica de la población reproductora no difirió significativamente de la población liberada, sugiriendo que la adaptabilidad de esta especie fue suficiente como para contrarrestar las diferencias genéticas entre subspecies. Los halcones peregrinos de grupos ampliamente diferentes han proliferado después de la liberación, aportando contribuciones genéticas sustanciales a la nueva población.*

Introduction

The present population of Peregrine Falcons (*Falco peregrinus*) breeding in the United States east of the Great Plains was established by release of approximately 2500 captive-produced birds, 1173 in the Midwest and 1300 in the East, following extirpation of the original population. Ecosystem-wide chlorinated hydrocarbon poison-

ing, which began in the late 1940s, caused the extirpation. By 1964 no territories of the original population breeding east of the Great Plains and south of the Arctic were known to be occupied (Berger et al. 1969). Use of DDT and its relatives was curtailed in Wisconsin in 1969, in Canada in 1970, and in the rest of the United States in 1972 (Hickey 1988). T. Cade and colleagues began captive breeding of Peregrine Falcons with the goal of reintroduction (The Peregrine Fund), and the first releases in the East were made in 1974 (Barclay 1984). In the Midwest (here defined as Minnesota, Wisconsin,

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Michigan, South Dakota, Nebraska, Iowa, Illinois, Indiana, Ohio, Kansas, Missouri, Kentucky, the Lake Superior basin of Ontario, and southeastern Manitoba) a separate program began in 1982. We released 972 falcons in the United States part of the Midwest from 1982 through 1998. Released falcons were supplied by 32 private falcon propagators; just three of these propagators produced 566 birds, more than half of the total. An additional 201 falcons, provided by the Canadian Wildlife Service, were released in western Ontario and southeastern Manitoba. Also, 998 young were fledged in the wild in the Midwest from 1987 through 1998 by released birds or their progeny. In 1998 at least 99 pairs of Peregrine Falcons held territories in the Midwest; 84 of these are known to have nested, fledging 205 young.

Reintroduction of captive-bred individuals provides one important component of species conservation. In some cases, parents used for captive breeding are determined simply by the scarcity of potential breeders. In others, genetic methods are used to pair individuals to minimize inbreeding effects. Alternatively, individuals used in captive breeding programs might be from different geographic areas (Temple & Cade 1988). This ensures the "unrelatedness" of parents. If parents were from sufficiently different ecological regions, however, their offspring might be at a disadvantage because local parental adaptations might be inappropriate for the environment at the release site.

Background Information

Peregrine Falcon restoration in the Midwest was initiated in Minnesota and coordinated for the region by P.T.R. and H.B.T. We received young falcons at the University of Minnesota from the propagators, checked their physical condition, took blood samples, banded them with U.S. Fish and Wildlife Service bands and field-readable color bands, and sent them to various Midwestern sites for release. We maintained a central database on all birds released, in which we also recorded subsequent sightings and nestings.

The captive-produced Peregrines were released by hacking, the release of free-flying young birds at a site where food is provided until independence. Individual adult Peregrines were identified in the field by several dozen observers reading leg bands in each of the 12 states and two provinces in the Midwest. Over two-thirds of the current Midwestern Peregrine pairs live in cities, using human-made structures for nesting sites. Many of these pairs are seen daily at close range by persons working in nearby offices. The combination of a heavily urban population of Peregrines, many observers, a central database for recording observations, and regular reports sent to all participants has made it possible to monitor the Midwest population closely.

To illustrate the degree of coverage of this population in 1998, 175 of the 205 young known to have fledged in the wild from 84 nesting pairs were banded before fledging. Of the 168 breeding adults, 107 were banded and individually identified, 16 were banded but not further identified, 19 were not banded, and the banding status of 26 was not determined. We estimate that, in addition to the known nestings, about 10%–20% of the current population in the Midwest is nesting undetected. These undiscovered nestings are, of course, a source of unbanded adults, in addition to unbanded young fledged from known sites.

Each Peregrine coming from the wild to the captive breeding population was referable by its geographic origin to a single subspecies. Birds of different subspecies were frequently interbred in captivity by the U.S. falcon propagators. As a result, Peregrines released in the Midwest were diverse in their ancestry; some were from a single subspecies, others had from two to four subspecies as ancestors. No bird released in the Midwest had any ancestor's subspecies diluted to less than one-fourth, which implies one or two generations in captivity. The subspecific identity, when known to us, of all birds released was entered into the central database, and this provided the basis for calculating the success of the different genetic stocks released. For example, pairing a female of the subspecies *F. p. anatum* with a male whose father was *F. p. pealei* and mother *F. p. tundrius* produces young that are 50% *anatum*, 25% *pealei*, and 25% *tundrius*. The percentages of the various subspecies in the released population and in the population of breeding birds were calculated by extension of this procedure.

Parents of the released falcons came from captive stock derived from North America, Europe, South America, and Australia. The differences among populations from these areas are reflected in the fact that the parents represented seven different subspecies. These were described on the basis of geographic variation in size, color, and proportion and have been historically thought to represent local adaptations to different environments.

Five subspecies are represented in the current population of breeding Peregrines in the Midwest. *F. p. anatum* applied in part to the original population in eastern North America that was extirpated by pesticides by about 1965 (Berger et al. 1969). These "Rock Peregrines" or "Duck Hawks" were large birds able to deal successfully with Great Horned Owls (*Bubo virginianus*) at their cliff nests. They fed on a wide range of prey, from small passerines to ducks. The captive-bred *anatum* Peregrines released in the Midwest came primarily from interior northwestern Canada, interior Alaska, and the western United States. They are smaller on average than the eastern "Rock Peregrines" and therefore differ genetically to an unknown extent, but they are similarly adapted for feeding on a wide range of prey (Bent 1938). About 526

"pure" *anatum* were released in the Midwest, along with many whose mixed ancestry included *anatum*.

F. p. pealei breeds on the coastal cliffs of British Columbia, southeastern Alaska, and the Aleutian Islands. They are the largest Peregrines, generally nonmigratory as adults. They feed mainly on small alcid captured over the open ocean, the smallest average prey taken by the largest Peregrines, suggesting that their large size is an adaptation to life in a cold and frequently stormy environment (Nelson 1988; Sherrod 1988). About 80 pure *pealei* were released in the Midwest, but many more had *pealei* heritage in their mix of ancestors.

F. p. peregrinus breeds over much of northern and western Europe; the captive *peregrinus* stock came from Scotland. Falcons of this subspecies are large, but not as large as *pealei*. They feed on a wide range of prey, from seabirds to passerines. Inland populations in Great Britain prey heavily on pigeons (Cramp & Simmons 1980; Ratcliffe 1980). No pure *peregrinus* were released in the Midwest.

F. p. brookei resides throughout much of southern Europe. The captive stock came from Spain. These are medium-sized Peregrines, adapted for life on river cliffs, sea coasts, and ruins, and for capturing a wide range of small to medium-sized birds (Cramp & Simmons 1980). Two pure *brookei* were released in the Midwest; one of these survived to breed.

F. p. tundrius breeds in the Arctic of North America and Greenland and winters in Central and South America. They are medium-sized, with the long wings characteristic of long-distance migrants. Some *tundrius* falcons feed mainly on seabirds in summer; others at interior sites rely mostly on small passerines and shorebirds. At other times of the year, they are generalists, taking a variety of prey (Sherrod 1988). No pure *tundrius* were released in the Midwest.

At the beginning of the restoration effort in eastern North America, the number of Peregrines available for captive breeding was limited. Because the distinctive original population of "Rock Peregrines" was extinct and not available for reintroduction, falcons from a variety of subspecies were used as parents in the captive breeding program, in the expectation that natural selection would then have abundant genetic variation from which to produce a new population adapted to present conditions (Barclay & Cade 1983). This decision was opposed by some who argued that introduction of nonindigenous subspecies in this area was inappropriate. Even if captive breeding had been delayed long enough in the East to build up a stock of breeders of *anatum* ancestry, they would still have differed genetically and morphologically from the original extirpated eastern population, individuals of which averaged larger than *anatum* from western and northwestern parts of the range of the subspecies. In the end, a mixture of subspecies was used for the captive breeding programs producing Peregrines for

release in the eastern and midwestern United States. In the western United States and Canada, where remnants of the original *anatum* stock persisted, only birds of *anatum* ancestry were propagated for release.

We analyzed the success of each Peregrine subspecies, with its own range of adaptations, when it was introduced into the Midwest. We discuss the merits of the use of nonindigenous individuals for reintroductions.

Methods

We compared the subspecific makeup of the Peregrines released in the Midwest, from the beginning of the program in 1982 through the end of substantial releases in 1995, with that of the breeding population, from the first successful nest in 1987 through 1998. The breeding population included Peregrines originally released by hacking and their wild-produced descendants (57% and 43%, respectively, of the 195 individually identified breeders, 1987 through 1998; about 95 additional breeders were not individually identified). This comparison provides a general picture of the relative success of birds of various subspecific ancestries in surviving to reproduce in new environments.

We sampled the 921 Peregrines released in the Midwest through 1995 (birds released after 1995 were not included because most would not have entered the breeding population by 1998) by counting every second bird in the database for which we knew the subspecies ($n = 358$). We then determined the subspecific makeup of the most prolific breeders (living or dead, those fledging 12 or more young) of the new population ($n = 42$). We did the same for breeders (only those known or presumed dead) that had fledged eight or fewer young in their lives ($n = 31$) to see if fecundity might be related to subspecific ancestry.

Results and Discussion

The contributions of the various subspecies to the gene pool of the 921 Peregrines released in the Midwest were *anatum*, 57%; *pealei*, 27%; *peregrinus*, 6%; *brookei*, 6%; and *tundrius*, 4%. In contrast, the 758 captive-reared Peregrines released from 1975 through 1985 in the eastern United States by The Peregrine Fund were a very different mix: *tundrius*, 46%; *anatum*, 18%; *brookei*, 18%; *pealei*, 9%; *cassini*, 4%; and "others," 4% (Temple 1988; percentages estimated from histogram, p. 847).

The only pure birds released in the Midwest were 526 *anatum*, 80 *pealei*, and 2 *brookei* mentioned earlier; the rest were any of about 26 different combinations of

Table 1. Subspecies of Peregrines breeding in the midwest, 1987–1998.*

Gene pool	Subspecies (%)				
	anatum	pealei	peregrinus	brookei	tundrius
Prolific breeders ($n = 42$)	55	21	9	10	5
Less prolific breeders ($n = 31$)	53	23	9	9	6

*Midwest defined as Minnesota, Wisconsin, Michigan, South Dakota, Nebraska, Iowa, Illinois, Indiana, Ohio, Kansas, Missouri, Kentucky, northwest Ontario, and southwest Manitoba; $\chi^2 = 0.27$, $df = 4$, $p = 0.99$.

the five subspecies, in various proportions, one-fourth, one-half, or three-fourths.

No significant difference occurred in proportions of subspecies represented in the population of prolific breeders (12 or more young fledged) versus the less prolific breeders (8 or fewer young) (Table 1). Combined (Table 2), the breeders ($n = 73$) were *anatum*, 54%; *pealei*, 22%; *peregrinus*, 9%; *brookei*, 10%; and *tundrius*, 5%. Most (44) were of mixed ancestry, but 25 breeders were pure *anatum*, 3 were pure *pealei*, and 1 was pure *brookei*.

When we compared released Peregrines with the breeders (Table 2), no statistically significant difference existed in their subspecific makeup. Of the five subspecies, one might have predicted that *pealei*, a maritime race, would be the least well preadapted for life in the Midwest. Considering latitude, climate, and general habitat, heavily populated by humans, of the ancestral Spanish home of *brookei*, this race might have been expected to do well in the Midwest. Perhaps it is too early to expect adaptive differences among the five subspecies to have emerged at a statistically significant level. The majority (57%) of the current breeding adult Peregrines were reared in captivity. About one in six of the Peregrines hacked in the Midwest have become breeders. Most of the wild-produced adults are the first generation beyond captivity. Only a few breeders represent the second or third generations in the wild.

The most important conclusion is that Peregrines of widely different genetic stocks, and their hybrids, have done well in the Midwest (Table 2). Five of the seven subspecies released have made substantial genetic contributions to the new population. The new population in the Midwest differs dramatically from the original cliff-nesters in that 72% now nest on human-made structures, most in urban areas. The challenges provided by

the new niches being used today by the midwestern Peregrines and the diverse genetic stocks they represent should provide ample opportunity for natural selection to proceed.

The Peregrine Falcon's cosmopolitan distribution apart from the polar regions, versatility in use of nest sites despite lack of ability to build its own nests, use of ubiquitous avian prey, persistence over the centuries in the face of heavy human persecution, and possession of genetic stocks from strikingly different habitats that can thrive when introduced together into new areas are all testimony to the adaptability of the species. The Peregrine's Achilles' heel is a sensitivity to chlorinated hydrocarbon pesticides that led to the threat of world-wide extinction and to the actual extirpation of regional populations, which have now been restored, albeit with birds of diverse genetic backgrounds.

The Peregrine Falcon project provided valuable experience and techniques for restoration of other avian species. The Peregrine Fund, in particular, has employed these lessons in work with California Condors (*Gymnogyps californianus*), Mauritius Kestrels (*Falco punctatus*), Aplomado Falcons (*Falco femoralis*), and a variety of other species (see annual reports of The Peregrine Fund, Boise, Idaho). The first question to be asked in deciding whether to attempt reintroduction to replace an extirpated population is whether the cause of extinction can be identified and corrected. If not, restoration efforts are likely to be futile. When the vacant habitat is judged capable of supporting a new population, what factors should govern the choice of candidates for reintroduction? The goal should be restoration with individuals of the same or most similar genotype. Usually, the genotype is not known directly but is inferred through morphological or ecological traits. In the absence of better criteria, geographic distance can be useful on the as-

Table 2. Peregrine subspecies in the midwest, hacked versus breeders.*

Gene pool	Subspecies (%)				
	anatum	pealei	peregrinus	brookei	tundrius
Hacked (years) United States 82–92;					
Ontario, 89–95 ($n = 358$)	57	27	6	6	4
Breeders, 87–98 ($n = 73$)	54	22	9	10	5

*Midwest as defined in footnote to Table 1; $\chi^2 = 2.3$, $df = 4$, $p = 0.68$.

sumption that nearby populations are more likely to be similar genetically than more distant populations, as shown for the Red-cockaded Woodpecker, (*Picoides borealis*) (Haig et al. 1994, 1996). Behavioral and ecological criteria must also be considered. For example, hindsight tells us that the predominantly urban population of Peregrines in the Midwest might better have been established with birds of nonmigratory ancestry. Midwestern cities provide adequate food for Peregrines in winter. An adult that leaves its territory in winter in response to its ancestral urge to migrate is likely to find its territory taken over in its absence by a new bird, resulting in a dangerous fight (Tordoff & Redig 1999). Each case of potential restoration must be considered individually. The Peregrine example shows that different genotypes of adaptable species may thrive when introduced into new habitats, but probably few species match the Peregrine Falcon in adaptability.

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Literature Cited

Barclay, J. H. 1984. Eastern Peregrine Falcon reintroduction program. Summary report. Cornell University Laboratory of Ornithology, Ithaca, New York.

- Barclay, J. H., and T. J. Cade. 1983. Restoration of the Peregrine Falcon in the eastern United States. Pages 3–37 in S. A. Temple, editor. *Bird Conservation*. University of Wisconsin Press, Madison.
- Bent, A. C. 1938. Life histories of North American birds of prey (part 2). *U.S. National Museum Bulletin* 170:43–67.
- Berger, D. D., C. R. Sindelar Jr., and K. E. Gamble. 1969. The status of breeding Peregrines in the eastern United States. Pages 165–173 in J. J. Hickey, editor. *Peregrine Falcon populations: their biology and decline*. University of Wisconsin Press, Madison, Wisconsin.
- Cramp, S., and K. E. L. Simmons. 1980. *Handbook of the birds of Europe, the Middle East and North Africa*. Volume 2. Hawks to bustards. Oxford University Press, Oxford, United Kingdom.
- Haig, S. M., J. M. Rhymer, and D. B. Heckel. 1994. Population differentiation in randomly amplified polymorphic DNA of Red-cockaded Woodpeckers. *Molecular Ecology* 3:581–595.
- Haig, S. M., R. Bowman, and T. D. Mullins. 1996. Population structure of Red-cockaded Woodpeckers in south Florida: RAPD's revisited. *Molecular Ecology* 5:725–734.
- Hickey, J. J. 1988. Some recollections about eastern North America's Peregrine Falcon population crash. Pages 9–16 in T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund, Boise, Idaho.
- Nelson, R. W. 1988. Do large natural broods increase mortality of parent peregrine falcons? Pages 719–728 in T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund, Boise, Idaho.
- Ratcliffe, D. 1980. *The Peregrine Falcon*. Buteo Books, Vermillion, South Dakota.
- Sherrod, S. K. 1988. Behavioral differences in Peregrine Falcons. Pages 741–748 in T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund, Boise, Idaho.
- Temple, S. A. 1988. Future goals and needs for the management and conservation of the Peregrine Falcon. Pages 843–848 in T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund, Boise, Idaho.
- Temple, S. A., and T. J. Cade. 1988. Genetic issues associated with recovery efforts for three endangered raptors. Pages 17–29 in D. K. Garcelon and G. W. Roemer, editors. *Proceedings of the International Symposium on Raptor Reintroduction, 1985*. Institute for Wildlife Studies, Arcata, California.
- Tordoff, H. B., and P. T. Redig. 1999. Two fatal Peregrine Falcon territorial fights. *Loon* 71(4):182–186.

