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CLOSE INBREEDING IN PEREGRINE FALCONS IN MIDWESTERN UNITED STATES

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Selection against inbreeding is usually assumed to be an important factor in the evolution of dispersal patterns in animals (Thornhill 1993), because close inbreeding increases the probability of expression of deleterious recessive genes. We have identified several cases of close inbreeding (here defined as mating between siblings, half-siblings or parents and offspring) in Peregrine Falcons (*Falco peregrinus*) in the midwestern United States. This paper discusses the possible causes and consequences of these inbreeding events.

The current midwestern peregrine population originated from 857 captive-bred falcons released since 1982 as a part of the continent-wide effort to reestablish populations of the species in areas where they had been eliminated or reduced by poisoning by DDT and related compounds. Midwest as here used includes Minnesota, Wisconsin, Michigan, Nebraska, Iowa, Illinois, Indiana, Ohio, Kansas, Missouri, Kentucky, southeastern Manitoba and the Lake Superior basin of Ontario. We have already shown for this new population (Tordoff and Redig 1997), numbering 99 territorial pairs in 1998, that: 72% nest on man-made structures and 28% on cliffs. First breeding is usually at age two, although some females and fewer males begin at one year of age. First-year survival is probably close to 40% and annual survival of adults is 86%. Dispersal from hack or natal sites has huge variation (range 0–>1500 km for both sexes, but mean dispersal of females (323 km) is about twice that of males (176 km).

Peregrines released in the restoration effort have passed through three bottlenecks, each of which must have reduced genetic variation in the population. The first was the pesticide-induced reduction in size of wild populations from which captive birds were drawn. Second, captive-breeding peregrines represented a small sample of the wild populations from which they were taken. The number of true founders (unrelated ancestors brought in from the wild for captive breeding) for the new midwestern population was 70–80 individuals. Third, a founder's contribution of genetic material to the wild population is determined by differential reproduction in captivity, which is probably more pronounced than in the wild.

Only about one-fourth of fledged young, released or wild-produced, actually become breeders in the wild. Through 1996, 1383 peregrines were known to have fledged in the Midwest (757 hacked, 626 wild); through 1998, about 290 (21%) of these were known to have become breeders, although some additional birds fledged

Table 1. Close inbreeding in nesting (eggs laid) midwestern Peregrine Falcons.

FEMALE	MALE	RELATIONSHIP AND PLACE OF FLEDGING	NESTING LOCALITY
Mae 31T	13T	Half-siblings from different wild broods, same mother, different fathers; Minneapolis MN	NSP King, Bayport MN
Mae 31T	Jim 51Z	Mother, son, both wild fledged; Minneapolis and Bayport MN	NSP King, Bayport MN
Mae 31T	Caesar 49Z	Full siblings from different wild broods; Minneapolis MN	NSP King, Bayport MN
Skywalker U/R	55X	Half-siblings from different wild broods, same mother, different fathers; St. Paul MN	NSP Black Dog, Eagan MN
Sunrise 55R	Cinder 5/C*	Mother, hacked Cincinnati OH, 1-yr old son, wild Detroit MI	Whittier Apartments, Detroit MI
Carmen D/N	C/U	Full siblings from different wild broods, Milwaukee WI	Commodore Perry, Toledo OH
Suzy Q 52P	Doc 55Y	Full siblings, same age, hacked together at Grand Rapids MI	U.S. Steel, Gary IN

* Two captive-produced young added to nest fledged.

in 1996 or earlier will still enter the breeding population in future years. Given first-year survival of 40% and annual survival of territorial adults of 86%, one would expect 34% of fledged peregrines to survive to the end of their second year, 30% to the end of the third year. The discrepancy between the observed 21% that became breeders and the predicted 30% that survived to age three showed that living to adulthood was not a guarantee of becoming a breeder. It is still necessary to find a territory and a mate. Further, the 86% annual survival of territorial adults probably overestimates survival of nonterritorial adults, which have to cope daily with unfamiliar surroundings (Ratcliffe 1980).

We identified 17 nestings (4% of a total of 454 from 1987–98) by seven pairs of peregrines in the Midwest in which the adults (5 females, 7 males) were related as half-siblings, full siblings or mother and son (Table 1). What behaviors in peregrines act to minimize inbreeding? Two obvious possibilities are dispersal tendencies and avoidance of potential mates known from memory to be close relatives. Peregrines are highly mobile and capable of long distance dispersal. Since dispersal directions of individuals fledging from the same site are generally random, the dispersal distances typical of midwestern peregrines should minimize incestuous pairings. Further, females disperse on average about twice as far as males, increasing the odds against sibling matings. The short dispersal distances of some individual midwestern peregrines early in the restoration program reflected the lack of competition for suitable breeding sites in a growing population. As the peregrine population approaches carrying capacity and suitable territories become more difficult to find, the opportunity for short distance dispersal between natal and subsequent breeding site should diminish.

Can peregrines recognize same-age siblings, offspring and previous mates? Is their memory good enough to permit recognition of these relatives from one year to another? Might peregrines recognize in some way close relatives that they have not previously encountered, such as older or younger siblings? These questions cannot be answered convincingly with the evidence available, but some comments seem justifiable. The long-term memory of peregrines, like that of other migratory birds, is clearly adequate for performing impressive feats of migration Many western hemisphere peregrines move over half the globe, from Alaska and Greenland to southern South America. Recognition of landmarks, however, does not necessarily guarantee recognition of individuals. Territorial peregrines obviously recognize their current mates visually (and probably vocally) and respond to intrusions of strange peregrines at substantial distances. Further, it is clear that peregrines can easily recognize the sex of other peregrines, much more efficiently than can experienced human observers. On territory, females usually chase out intruding females and males likewise usually chase males. Territorial adults appear to recognize intruders as such, but usually refrain from aggressive challenges of intruders of the opposite sex. Unpaired adults on territory seem willing to accept any adult of the opposite sex. No conclusive evidence exists either way that pairs from the previous year, separated over winter, recognize each other at reunion. In at least a dozen cases in the Midwest, we have identified occupants of territories in early spring to comprise one bird from the previous year and a new individual. Usually, the other bird from the previous year has returned and evicted the new bird. If the first bird from the previous year favored either of the struggling birds, it was not obvious.

Parental peregrines in captivity and in the wild accept their own young and augmented young without prejudice, even up to the early days after fledging. Even young

of inappropriate age are usually accepted, such as 10-d-old young given to adults in place of a clutch of only partially incubated eggs. Young in a brood, whether wild birds or young being hacked, seem to discriminate among members of their group, acting aggressively toward some individuals, friendly toward others and submissive to some. Despite the subjectivity of these observations, it seems fair to conclude that peregrines of all ages have the ability to recognize and discriminate among other individuals over the short term, although parental behavior may override such recognition in favor of guaranteed care of all young in a nest. Selection to identify own nest contents by breeders would not exist because mixing does not occur in nature. Whether short-term ability to recognize other individuals carries over from year to year and might be useful in avoiding close relatives as mates is less obvious.

Pairings of full siblings or half-siblings from different broods (Bayport, Eagan and Toledo pairs, Table 1) without prior contact seem to be matters of mere chance. Avoidance of pairings between siblings from the same brood would require individual recognition persisting over a year or more. There is no evidence that peregrine siblings remain together through the winter. Similarly, avoidance of parent-offspring pairings (Bayport) would require long-term memory of individuals (assuming separation over winter), which, if present in peregrines, is clearly not wholly effective in eliminating such incestuous relationships. In Detroit, Sunrise 55R paired in 1997 with an unbanded male and fledged one young, a male that remained with her on the nesting territory through the winter, mated with her in 1998, and fledged two young (J. Yerkey, unpubl. data), suggesting that even recognition of the parent-offspring relationship by both birds was not a deterrence to mating. Finally, siblings released at hack sites (Gary pair) experienced enough disrupted interactions with their own parents and enforced interactions with nonrelatives before release to make futile any effort to understand the effect of long-term memory on their later pairing propensities. So far, we have seen no instances of full sibling wild brood mates pairing in later years, but this may be simply a matter of small sample size.

These instances of inbreeding suggest that avoidance of incest by recognition of close relatives is ineffective and that dispersal behavior is the primary, perhaps exclusive, mechanism for avoidance of close inbreeding in Peregrine Falcons.

In none of the close-inbreeding pairings described here was there any obvious indication of genetic problems in the offspring which might have been expressed through exposure of deleterious recessive alleles. All 37 young appeared to be normal and breeding success did not differ from the rest of the population (2.2 young per nesting for the inbreeding pairs, 2.1 young per nesting for the whole population). The fact that the new population has passed through three bottlenecks ensures loss of some genetic variability, including deleterious alleles as well as normal ones. Further, like all organisms, peregrines are routinely subject to rigorous selection against alleles that might impair their fitness. Although the global population of peregrines is large, they occur mostly at low density, lowering the effective population size despite their mobility. This would favor, by fostering inbreeding, the expression of and consequent selection against deleterious recessive alleles. All these factors may have functioned to minimize levels of deleterious alleles in peregrine populations, which would result in less rigorous selection against close inbreeding.

RESUMEN.—En el oeste medio de los Estados Unidos, 17 eventos de entrecruzamientos cercanos (copulas entre hermanos, medio-hermanos y padres e hijos) de halcones peregrinos (*Falco peregrinus*) han sido documentados. El evitar el entrecruzamiento en esta especie parece ser el resultado del comportamientos de dispersión (a la suerte en dirección, la media de la distancia de dispersión de las hembras es el doble de la de los machos) mas que la memoria a largo plazo y el reconocimiento de parientes cercanos.

[Traducción de César Márquez]

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