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MIDWEST PEREGRINE FALCON DEMOGRAPHY, 1982–1995

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ABSTRACT.—Peregrine Falcon (*Falco peregrinus*) restoration in the midwestern U.S. has resulted in a growing population estimated in 1995 to consist of 67 pairs. Dispersal from hack or natal sites has huge variation, but mean dispersal distance of females (320 km) is about twice that of males (176 km). Minimum first-year survival is 23% but actual first-year survival probably exceeds 30%. Annual survival of territorial adults is 86% (93% for females and 79% for males). Age at first breeding is usually two years although some females and a few males begin breeding at one year of age. Peregrines seem not to delay first breeding beyond two years by choice. Only a small proportion of birds fledged become breeders. Successful individuals vary greatly in productivity, which is correlated with life span. Fidelity to territory is strong, but territorial shifts do occur. Mate fidelity appears to be a by-product of territorial fidelity. The midwestern population of peregrines appears to be secure. Reproduction and survival are adequate to permit growth to current carrying capacity although 80% of the peregrines nest on man-made structures and only 20% on cliffs.

KEY WORDS: *peregrine falcon*; Falco peregrinus; *midwest U.S.*; *natal dispersal*; *survival*; *productivity*; *nest-site fidelity*.

Demografía del *Falco peregrinus* en el oeste del medio, 1982–95

RESUMEN.—Restauración de *Falco peregrinus* en el oeste del medio en EEUU e resultado en aumento de población estimado en 1995 que consistio de 67 pares. Dispersión natal de sitios naturales o no-naturales tiene variación grande, pero la distancia promedio de dispersión de hembras (320 km) es doble eso de machos (176 km). El supervivencia minimo de el primer año es 23%, pero supervivencia actual de primer año problamente sobrepaso 30%. Supervivencia actual del adultos territorial es 86% (93% para hembras y 79% para machos). Edad de la primer cría es por lo general dos años aunque unas hembras y unos cuantos machos empiezan crías en el primer año de edad. *Falco peregrinus* parcen no demora la primer cría despues de dos años por decisión. Nomas un proporción pequeño de los pajaritos se hacen criadores. Individuales con exito varia mucho en productividad que esta correlacionado con la duracion de la vida. Fidelidad al territoria es fuerte, pero movimiento en el territorio si ocure. Fidelidad del par es un producto del fidelidad territorial. La población de *Falco peregrinus* en el oeste del medio parece ser seguro. Reproducción y supervivencia es suficiente para permitir crecimiento a la capacidad de carga aunque 80% de los *Falco peregrinus* anidaban en estructuras hechas con manos de hombre y nomas 20% en precipicios.

[Traducción de Raúl De La Garza, Jr.]

The worldwide devastation of Peregrine Falcon (*Falco peregrinus*) populations by pesticides and the subsequent recovery by restriction of pesticide usage is now a familiar story. In the eastern and midwestern U.S., breeding peregrines were extirpated. We coordinated the restoration of the peregrine population in the Midwest by release of captive-reared falcons under the supervision of the USFWS Eastern Peregrine Falcon Recovery Team. In this paper, we present current information on dispersal, first-year survival, survival of territorial adults, age of first breeding, longevity, lifetime reproduction, and fidelity to mates and territories for the expanding Midwest peregrine population.

METHODS

Due to restoration efforts in the Midwest, the Peregrine Falcon population was estimated at 67 territorial pairs of which 53 pairs produced eggs in 1995. From 1982–95, 747 captive-produced ("hacked") young were released. In addition, at least 493 wild-produced ("wild") young were produced by the new population. Each year an effort is made to identify all breeding birds and band all young, with the result that most of the new population is banded. In 1995, for example, only seven of 90 breeding peregrines were unbanded (at eight additional territories where eggs were laid the banding status of the 16 breeders was not determined) (Table 1). The combina-

Table 1. Peregrine Falcon population growth and productivity in the U.S. Midwest. Young fledged includes all young surviving to first flight from nest.

YEAR	HACKED YOUNG	TERR. PAIRS	NESTING PAIRS	SUCCESS PAIRS	YOUNG FLEDGED	YOUNG/ TERR. PAIR	YOUNG/ NESTING PAIR	YOUNG/ SUCCESS PAIR
82–86	102	4	1	0	0	0	0	0
1987	68	6	3	1	1	.17	.33	1.0
1988	84	13	8	6	12	1.1	1.5	2.0
1989	116	16	12	9	22	1.4	1.8	2.4
1990	83	23	16	13	33	1.4	2.1	2.5
1991	110	30	22	17	36	1.2	1.6	2.1
1992	104	37	32	23	68	1.8	2.1	3.0
1993	20	53	43	33	87	1.6	2.0	2.6
1994	42	62	51	41	116	1.9	2.3	2.8
1995	18	67	53	43	118	1.8	2.2	2.7
Totals:	747	311	241	186	493	1.6	2.0	2.7

tion of a high proportion of banded birds and a region-wide network of observers has made it possible to obtain more data on several topics than previously available (Ratcliffe 1980, Newton 1988).

Herein, we use the term "Midwest" to include Minnesota, Wisconsin, Michigan, Nebraska, Iowa, Illinois, Indiana, Ohio, Kansas, Missouri, Kentucky, the Lake Superior shore of Ontario and southeastern Manitoba.

RESULTS AND DISCUSSION

Dispersal. We measured natal dispersal, as defined by the straight-line distance from hack or natal site to first breeding site, for 73 male and 67 female peregrines. Natal dispersal showed huge individual variation, with individuals of both sexes moving short distances or even settling at the hack or natal site, while others moved >100 km (Fig. 1). Longest dispersal movements were by two peregrines in Canada that moved into the Midwest. One was a hacked male that moved 1520 km from Cap Tourmente, near Quebec City, Quebec to Duluth, Minnesota, and a hacked female that moved 1760 km from Blomidon, Bay of Fundy, New Brunswick to the Porcupine Mountains, western upper peninsula of Michigan.

Despite the great individual variation, female peregrines consistently moved about twice as far as males, 354 km vs. 174 km (Fig. 1, $\chi^2 = 79.1$, df = 1, $P < 0.001$). Hacked birds ($N = 152$) and wild birds ($N = 38$) do not differ significantly in distance of dispersal ($\chi^2 = 2.46$, df = 1, $P > 0.05$). Dispersal direction appeared to be random (Rayleigh's test; $Z = 0.976$, $P > 0.05$, $r = 0.088$), although many pairs (34 of 67 in 1995) settled within sight of the Great Lakes, demonstrating a tendency of peregrines to remain near large bodies of water.

Greater dispersal of females than males has been reported for other populations of peregrines. In Alaska, Ambrose and Riddle (1988) reported natal dispersal of 20 females to average 121 km (range = 2–370 km, SD = 87 km) and of 6 males to average 69 km (range = 4–206 km, SD = 74 km). Newton and Mearns (1988) reported greater natal dispersal distances for 15 female peregrines in Scotland (median = 68 km, maximum = 185 km) and smaller distances for 24 males (median = 20 km, maximum = 75 km). Midwestern peregrines dispersed farther than Alaskan birds, perhaps because suitable cliffs are more readily found in Alaska than are either cliffs or tall buildings in the Midwest. If Scottish peregrines dispersed as far as midwestern birds, many would find themselves at sea.

First-year Survival. Survival from fledging through the first year is more difficult to measure. First-year survival has previously been reported to be 30% for North America (Enderson 1969), 29% and 44% for Finland and Germany, respectively (Mebs 1971), and 41% for Sweden (Lindberg 1977). Newton and Mearns (1988) calculated survival between fledging and recruitment into the breeding population at 44% for Scotland.

We are able to give minimum survival figures for midwestern peregrines, based on the number of positively identified individuals seen alive after 1 January following their hatching year (1 January was chosen arbitrarily because actual birthdays of

Table 2. Territorial shifts in midwestern Peregrine Falcons.

INDIVIDUAL	SITE 1 DATES, MATE	SITE 2 DATES, MATE	DISTANCE SITE 1 TO SITE 2	POSSIBLE CAUSE	COMMENT
F Marla 81V	Colonnade, Mpls MN, 1992–94. M Kato 31T	Multifoods, Mpls MN, 1995. M Will 04Y	6.4 km	Preferred taller building: Colonnade nest 15th fl, Multifoods nest 50th fl	Marla killed MF-1, 9-year-old incumbent female at Site 2 in takeover
M Will 04Y	Multifoods, Mpls MN, 1989–93, F MF-1. 1995, F Marla 81V	City Hall, Mpls MN. 1994. F Rusty	1 km	Previous mate F MF-1 gone in 1994; male moved to site already occupied by replacement F Rusty	F Rusty visited and rejected nest site at Multifoods Tower in 1994
M Maverick 05T	NCL Tower, St. Paul MN. 03/90–04/08/90. F Meg 12R	Ward Tower, St. Paul MN. 1990–93. F Comet 11V	5.6 km	NCL incumbent M Beaner returning from winter, evicted M Maverick in fight 04/08/90	1990 NCL eggs already laid on 04/08/90; M Beaner helped F Meg raise Maverick's young (Tordoff et al, 1993)
M bl 1/X	Univ. Manitoba, Winnipeg. 1991, F 52V; 1992–94, F red E/H	Delta Winnipeg Hotel, Winnipeg MB. 1995. F 52V	11 km	Taller building, previous male gone, territory vacant	Reunion with former mate, see next entry
F 52V	Univ. Manitoba, Winnipeg MB, 1991, M bl 1/X	Delta Winnipeg Hotel, Winnipeg MB. 1992–94, M red 5P9; 1995, M bl 1/X	11 km	Taller building, previous female gone, territory vacant	Reunion. M 1/X and F 52V paired at Site 1 in 1991 and at Site 2 in 1995
M Spanky 04T	Control Data, Bloomington MN. 1990–91. F Rambo 08V	NCL Tower, St. Paul MN. 1992–95, F Meg 12R	14 km	Taller building, previous mate F Rambo gone, male at NCL gone, territory vacant	Left viable nest site
M red 6P3	Bong Bridge, Duluth MN. 1991–92. F 34R	Blatnik Bridge, Duluth MN. 1993–94. F 85R	4 km	Failed nests at Site 1 both years	Left living female and questionable nest site
M Solo 20Y	Detroit MI, 1988. F Bogey; 1989, new unid. F; 1990, new unid. F	Toledo OH. 1991–93. F Nellie red 3C7	75 km	Nests failed all 3 years in Detroit	
F Sunrise 55R	Fisher Building, Detroit MI. 1993. M Pop	Terminal Tower, Cleveland OH. 03/24/94–04/02/94. M Szell 67Z	160 km	Failed nest in 1993 in Detroit, moved to Cleveland, lost fight 04/02/94 to returning incumbent F Zenith 23W, returned to Detroit by 04/12/94	1993 mate Pop paired bigamously. F Sunrise 55R was given little attention, her nest failed
F Blueberry M Oly	Cliff near Finland MN. 1990	Cliff at Kennedy Creek, Little Marais MN. 1991–95	3 km	Moved as a pair from good cliff on a small lake to small cliff on Lake Superior	Perhaps best viewed as move from one nest site to another within a large territory

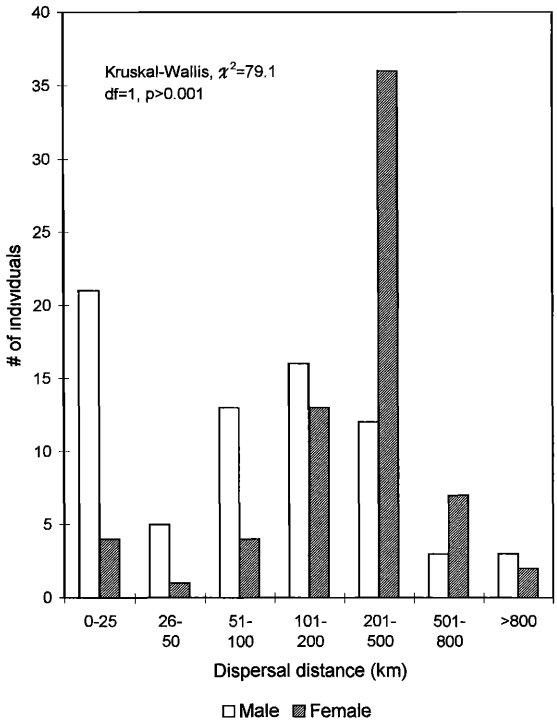

Figure 1. Natal dispersal distances of 140 midwestern Peregrine Falcons from hack and natural sites.

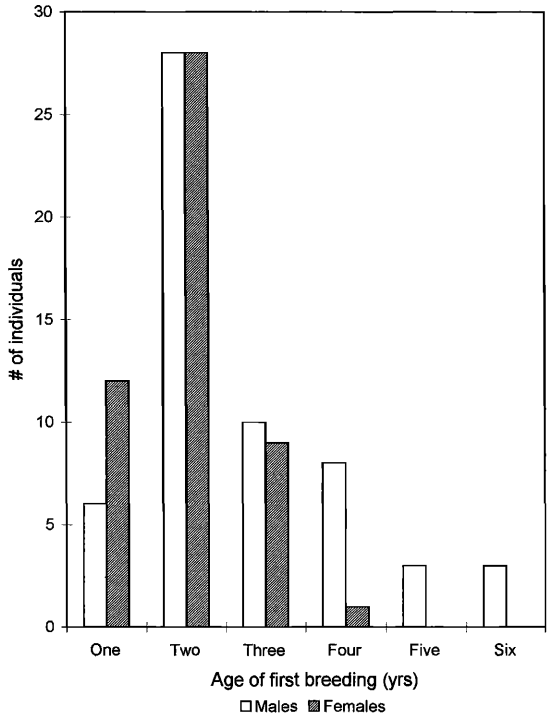

Figure 2. Age at first breeding of 108 midwestern Peregrine Falcons.

individual birds of a given cohort varied by as much as three months, and because most first-year mortality occurs in the first few months after fledging or release). Therefore, our figures are not exactly comparable with previous estimates. Captive-produced birds were considered hacked when the hack box was opened, not when they became independent; wild-produced birds were considered fledged if they lived to fly from the nest. In some cases, no information about survival in the nest after three wk of age was available. For these, we assumed that all of the falcons fledged because mortality during the last three wk young were in nests was very low.

Significantly more hacked males (76 of 417, 18%), were seen alive after 1 January than were wild males (23 of 191, 12%) (χ^2 = 3.23, df = 1, P = 0.07). Of all the males we observed, 99 of 608 (16%) were known to have survived their first yr. We also found that hacked females (59 of 311, 19%) survived significantly more than did wild females (25 of 196, 13%; χ^2 = 2.93, df = 1, P = 0.09) and overall females showed a 17% survival rate (84 of 507).

Combining sexes, a greater number of hacked birds (135 of 728, 19%) survived than did wild birds (48 of 387, 12%; χ^2 = 6.5, df = 1, P = 0.01). Combining sexes of hacked and wild birds, 183 of 1115 (16%) were known to have survived beyond the end of their yr of hatching. The fact that hacked birds were fed to repletion until independence probably increased their survival enabling them to fledge at near optimum weights. A positive relationship between weight at fledging and first-year survival has been demonstrated for numerous raptors (Newton 1979).

It could be argued that because 79% of the peregrines in the Midwest were hacked in cities or fledged from wild pairs in cities, survival estimates for these individuals would be higher because city-reared peregrines are more likely to be seen, making the differential survival of hacked versus wild birds perhaps more apparent than real. To test this, we compared survival of 535 birds hacked from buildings (20%) with survival of 277 birds fledged wild from buildings (14%); again, the

hacked birds survived better ($\chi^2 = 3.95$, df = 1, $P = 0.047$).

Actual first-year survival is, of course, better than the minimum figures we report. The question is, how much better? Some peregrines survive and are reported as seen but not individually identified. We did not count these. Others survive and go unreported; this group may equal or surpass those birds individually identified even in an area such as the Midwest.

In early spring 1992, we tried to account for every individual midwestern peregrine reported alive at least to 1 January following hatch whether it was banded or not. Of 93 such individuals, 70 were individually identified by their bands, leaving 23 either unbanded or not identified if banded. This suggested that about a third more survivors are seen and reported than are individually identified by their bands. Based on this, the overall first-year survival of 16% that we calculated should be increased to about 23%.

Survival of Territorial Adults. We measured annual survival of individually identified territorial adult peregrines through 251 "territory years." A territory year is the record of one territorial adult from one breeding season to the start of the next. Adults are assumed dead if they did not return, unless positively known to have moved to another territory. Between-territory shifting was rare in our population so it was not a likely source of error in our calculations of annual adult survival.

From 1987–95, 115 male territory years were counted. During this time, 24 individuals died for an average annual survival of 79%. Annual survival of territorial males varied from 71% (1992–93) to 83% (1990–91, 91–92, 94–95). In the same period, 136 female territory years were counted. Only 10 individuals died for an average annual survival of 93%, higher than reported for most other peregrine populations. Annual survival of territorial females varied from 80% (1988–89) to 100% (1989–90, 90–91). The difference in annual survival of males (79%) compared with females (93%) was significant ($\chi^2 = 8.60$, df = 1, $P = 0.0034$). Combining sexes, there were 34 deaths over the 251 peregrine territory years for average annual survival of territorial adults of 86% in this midwestern population.

Estimates of survival of territorial adults in other populations, all based on smaller samples, are 75% for eastern U.S. prior to 1953 (Enderson 1969), 79% for Colorado (Enderson and Craig 1988), 68% for British Columbia (Nelson 1988), 81% and 72% for Finland and Germany, respectively (Mebs 1971), 68% for Sweden (Lindberg 1977), 89% for Scotland (Newton and Mearns 1988) and 95% for southeastern Australia (Olsen and Olsen, 1988). The 86% annual survival of adult territorial peregrines in the current midwestern U.S. population is exceeded only by the Scottish and Australian populations.

Peregrine populations typically include nonterritorial adults and immatures. Evidence for the nonbreeding segment of the population comes mainly from recorded incidences when territorial adults are killed and rapidly replaced, sometimes within hours, by new adults. The size and annual survival of the nonterritorial segment are usually impossible to measure but, based on reproduction and survival estimates for an expanding population in Scotland, the nonbreeding segment should stabilize at a minimum of three birds per breeding pair (Newton 1988). Hunt (1988) pointed out that adults should refrain from attempting to breed, even if only substandard sites are available, if this delay results in an individual producing a greater number of surviving offspring during its lifetime. Ratcliffe (1980) suggested that mortality was higher for peregrines not established on a territory because of their daily need to deal with unfamiliar surroundings. In addition, nonterritorial birds face a substantial risk of injury or death as they test the occupancy of territories. In the Midwest, incapacitating injuries or deaths inflicted in peregrine territorial encounters have involved at least 10 birds and are an important source of mortality (Tordoff and Redig, unpubl. data).

Age of First Breeding. One difficulty in determining age at first breeding is confirming that the first observed nesting of a peregrine is in fact its first breeding attempt. Because the midwestern population is watched closely and almost all of the population is banded, it is unlikely that any individuals breed unobserved elsewhere before appearing on their known territories.

Our observations for 108 peregrines showed that, although most peregrines begin nesting at age two, females often start at age one while only a few males breed at age one (Fig. 2). Although adults are first reported breeding at ages three or older (10 females, 9%; 24 males, 22%), we think that these were birds that tried and failed in earlier attempts or were unable to locate suitable nesting sites or mates. Although most of these late breed-

ers were undetected in their first two yr of life, for several of them we know their individual histories.

Female 31R, Monticello, MN, first bred at age four but was present on the same territory at age two, paired bigamously with a male from an adjacent territory but did not breed. At age three, this female was present intermittently through summer but failed to find a mate.

Male Beaner 848, St. Paul, MN, first bred in 1991 at age five. In 1988 at age two, this bird occupied a cliff territory with a juvenile female at Hastings, MN, but she did not lay eggs. In 1989, Beaner 848 moved 18 miles to a smokestack at Bayport, MN and remained unmated until a male with fledged young in St. Paul was killed in July in a collision with an airplane. Within eight hr, Beaner 848 took over the newly-vacant St. Paul territory, 16 miles west of Bayport, and mated with the incumbent female Meg 12R. In April 1990, Beaner 848 returned late, displaced a new male (Maverick 05T), and with Meg reared young fathered by Maverick 05T (Tordoff et al. 1993). It was not until 1991 that Beaner 848 actually sired its own young.

Male Calvin 28T, Madison, WI, first bred in 1995 at age six. This male was released in Madison in 1989. It was trapped and released at Padre Island, TX on 14 April 1990. Calvin 28T replaced male Jade 72T in Madison in mid-June 1992. In 1993 and 1994, Calvin returned in mid-April, courted many females but remained unpaired. In 1995, Calvin 28T mated with a female (Anita 74R), nested for the first time and fledged three young.

Male Szell 67Z, Cleveland, OH, first bred in 1993 at age five. From 1990–93, this male paired with an escaped female hybrid Peregrine x Prairie Falcon (*Falco mexicanus*) but no eggs were laid. In 1993, the hybrid female was trapped and removed, and was replaced by a juvenile female (Zenith 23W from Omaha, NE) and the pair bred.

These examples suggest that midwestern peregrines are capable of breeding at two yr of age if not at one, if the conditions allow. We think that no peregrines in our area delay first nesting beyond age two.

When an individual peregrine first breeds depends not only on its state of physiological maturation but also on its social environment. For example, female MF-1 hacked at the Multifoods Tower, Minneapolis, MN in 1986 was identified by her band at Fargo, ND in September 1986. In April 1987, this bird returned to its hack site and bred with the 4-yr-old male that held the territory.

In the early years of the midwestern restoration effort, when the whole countryside was open to peregrines searching for nest sites, 1-yr-olds nested more frequently. In the past few years, with the best territories already occupied, more first-time breeders and replacement breeders have been adults. From 1987–92, in 87 nesting pairs, 20 of the 174 breeders (11%) were 1-yr-olds. From 1993–95, in 123 nesting pairs, only 13 of the 246 breeders (5%) were 1-yr-olds.

Longevity. The oldest peregrines in the new midwestern population, all still living in January 1996, were a 10-yr-old female, two females that are nine, and two 9-yr-old males. It is too early to see maximum life spans in this population but, given a population of 100 birds at age one with an annual survival of 86%, six birds would be expected to reach 20 yr of age, making the unlikely assumption that senescence has no effect on annual mortality (Newton et al. 1997). Captive peregrines may live to about age 20. In 1995, six captive females and 12 males were still alive at age 15, two males at 16 and one male at 17 (Peregrine Fund Operation Report 1995) suggesting that the higher mortality of male peregrines in the wild may be involved with hunting and defense of their territories. The oldest wild peregrine reported was the Sun Life female in Montreal, Quebec, that lived to age 18 (Hall 1970).

Lifetime Reproduction. Although it is too early to measure definitive lifetime reproduction in midwestern peregrines, where the oldest individual will be 11 years old in 1996, some interesting information is already available. Of those birds that bred at least once and are already dead, 31 males (average age at death = 4.0 yr) fledged 143 young, or 4.6 young/male (including 17 augmented young). Eighteen females (average age at death = 2.7 yr) fledged 75 young, 4.2 young/female (including 12 augmented). One 9-yr-old female (MF-1) fledged 25 young, including five augmented, before being killed by another peregrine in 1995. Deleting her third of the total, 17 females fledged 50 young, 2.9 young/female.

Thirty-one males still alive (average age in 1995 = 4.6 yr) have already fledged 238 young for an average of 7.7 young/male (including 18 augmented young). Thirty-six living females (average age in 1995 = 5.1 yr) have fledged 355 young, 9.9 young/female (including 28 augmented young).

One male, Will 04Y, Minneapolis, MN, has fledged 22 young, including two augmented. Male

Bill 74T, Milwaukee, WI, has fledged 17, one augmented. Female Meg 12R, St. Paul, MN, has fledged 24 young. Female Sibella 20V, Milwaukee, WI, has fledged 23, one augmented. The four living females (ages 9, 9, 9 and 7 yr) each with 20 or more young to their credit have fledged 87, a quarter of the total. Fridge 43R, a cliff-nesting female, in eight years and with four mates, has fledged 20 young at Palisade Head on Lake Superior. This bird killed about two dozen Ring-billed Gulls (*Larus delawarensis*) to feed its young in 1990, the only year it raised a brood of four young.

Although the midwestern peregrine population cannot yet be subjected to a detailed analysis of lifetime productivity, it is already clear that in populations of Peregrine Falcons, as in populations of Sparrowhawks (*Accipiter nisus,* Newton 1989a), Ospreys (*Pandion haliaetus,* Postupalsky 1989), and an array of other species, a large fraction of all fledglings produced die before they can breed, not all the individuals which survive to attempt breeding subsequently produce offspring, and successful individuals vary greatly in productivity, which is correlated with life span (Newton 1989b).

Fidelity to Mates and Territories. Midwestern Peregrine Falcons show strong fidelity to nesting sites as do peregrines elsewhere. Many midwestern peregrines move several times before settling down to breed for the first time, but once they establish a territory they seldom move to new territories. Of 241 nestings through 1995, only ten involved adults moving from a former nesting territory to a new one (Table 2). Seven moves involved leaving territories where breeding had been unsuccessful or where a mate had disappeared. Four moves occurred where a bird abandoned a successful territory for a better one, and three involved evictions by fights (categories not mutually exclusive).

Fidelity to territory in peregrines is clearly strong and probably accounts for the apparent year-to-year durability of pair bonds. We think that fidelity to mates, independent of mutual attraction to the same territory, may be weak or absent. Territorial adults seem willing to accept any bird of the opposite sex as a mate if it finds the territory acceptable. Territorial males appear ready to copulate with any willing females. Over two seasons in Madison, WI, Tim and Mary Ellestad saw courtship feedings and some copulations between Calvin 28T and at least eight migrating females, each pausing for a day or two before heading north. Similarly, in Milwaukee, WI, Greg Septon and Jim Marks noted that territorial male Leopold C/D attracted at least five females in sequence in one season. Some may have been migrants but the fourth had fledged wild in Chicago in 1993. It was replaced by an aggressive unbanded juvenile female that remained a month but did not breed. Evidently, both courtship feeding and copulations occur as a part of early courtship, even in the absence of an enduring pair bond.

CONCLUSION

Prospects for the Future of Midwestern Peregrines. Annual increases in peregrine pairs from 1987–95 show rapid growth earlier and recent leveling off in percent annual increase, but absolute annual increase remains strong. Releases of captive-produced peregrines from 1989–92 averaged 104/yr, accounting for the big increase in pairs in 1993. Numbers of wild-produced young from 1993–95 have averaged 107/yr. Wild peregrines now produce more young each year than were hacked in the peak years of releases.

It has been estimated that peregrine populations would go extinct with a first-year survival of 10%, would persist at a low level for 50 years with first-year survival at only 20% and would grow at 25% (Grier and Barclay 1988). This later estimate is well below our first-year survival estimate of 30% survival. Based on our estimates that first breeding occurs at 2 yrs, 60% of adult females fledge young, production averages 2.6 young/successful female, and there is a 14% annual mortality of adults, this population should continue to show steady growth to its current carrying capacity based on "serviceable breeding locations" (nesting territories) (Hunt 1988). It is difficult to predict current carrying capacity because of the unprecedented heavy use by restored peregrines of human-made structures for nesting and their inability, thus far, to nest successfully on the traditional cliffs along the Mississippi River and its tributaries. We venture a guess that the new population will level out at 80 to 100 territorial pairs, which would be about twice the estimated size of the original cliff-nesting population. The future of the restored peregrine population in the Midwest appears secure, assuming no new threats to the population develop in coming years.

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LITERATURE CITED

AMBROSE, R.E. AND K.E. RIDDLE. 1988. Population dispersal, turnover, and migration of Alaska peregrines. Pages 677–684 *in* T.J. Cade, J.H Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

ENDERSON, J.H. 1969. Peregrine and Prairie Falcon life tables based on band-recovery data. Pages 505–508 *in* J.J. Hickey [ED.], Peregrine Falcon populations: their biology and decline. Univ. Wisconsin Press, Madison, WI U.S.A.

——— AND G.R. CRAIG. 1988. Population turnover in Colorado peregrines. Pages 685–688 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

GRIER, J.W. AND J.H. BARCLAY. 1988. Dynamics of founder populations established by reintroduction. Pages 689–700 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

HALL, G.H. 1970. The story of the Sun Life falcons. *Can. Field-Nat.* 84:209–30.

HUNT, W.G. 1988. The natural regulation of Peregrine Falcon populations. Pages 667–676 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine Falcon populations; their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

LINDBERG, P. 1977. The Peregrine Falcon in Sweden. Pages 329–338 *in* R.D. Chancellor [ED.], Proc. ICBP World Conference on Birds of Prey. Intern. Council for Bird Preservation, London, UK.

MEBS, T. 1971. Todesursachen und mortalitatsraten beim Wanderfalken (*Falco peregrinus*) nach den Wiederfunden deutscher und finnischer Ringvogel. *Vögelwarte* 26:98–105.

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 [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.

———. 1988. Population regulation in peregrines: an overview. Pages 761–770 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

———. 1989a. Sparrowhawk. Pages 279–296 *in* I. Newton [ED.], Lifetime reproduction in birds. Academic Press, London, UK.

———. 1989b. Synthesis. Pages 441–469 *in* I. Newton [ED.], Lifetime reproduction in birds. Academic Press, London, UK.

——— AND R. MEARNS. 1988. Population ecology of peregrines in south Scotland. Pages 651–665 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

———, P. ROTHERY AND I. WYLLIE. 1997. Age-related survival in female Sparrowhawks *Accipiter nisus*. *Ibis* 139: 25–30.

OLSEN, P.D. AND J. OLSEN. 1988. Population trends, distribution, and status of the Peregrine Falcon in Australia. Pages 255–274 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine Falcon Populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

POSTUPALSKY, S. 1989. Osprey. Pp. 297–313 *in* I. Newton [ED.], Lifetime reproduction in birds. Academic Press, London, UK.

RATCLIFFE, D. 1980. The Peregrine Falcon. Buteo Books, Vermillion, SD U.S.A.

TORDOFF, H.B., S.M. MOEN, P.T. REDIG, J.L. LONGMIRE AND D. FOSTER. 1993. Peregrine paternity case. *Loon* 65:107–110.

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