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Author: Faccio, Steven D.

Source: Journal of Raptor Research, 47(3) : 246-261

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/JRR-12-21.1>

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MOVEMENT PATTERNS, NATAL DISPERSAL, AND SURVIVAL OF PEREGRINE FALCONS BANDED IN NEW ENGLAND

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ABSTRACT.—Knowledge of dispersal patterns and survival rates is essential to understand population dynamics and demography, and to develop effective long-term management strategies for species of conservation concern. In New England, Peregrine Falcons (*Falco peregrinus*) were extirpated as a breeding species in the 1960s. Following a captive breeding and release program, the population subsequently underwent a rapid, dispersal-based expansion into its former range, particularly during the last two decades. Use of buildings, bridges, and other human-made structures for nesting has become widespread in urban areas, where the species only infrequently nested prior to reintroduction. We analyzed encounters of Peregrine Falcons banded as nestlings in the six New England states between May 1990 and June 2009 to determine: (a) differences in dispersal patterns (distance and direction) by sex; (b) differences in movement and natal dispersal among birds from cliff and artificial nest sites; (c) causes of mortality; and (d) effects of sex, age, and natal habitat type on survivorship. Of 986 Peregrine Falcons banded, 24% were encountered again at least once by December 2009. Although most encounters (76%) occurred within the study area, 24% were outside New England in eight other eastern states, three Canadian provinces, Cuba, and Nicaragua. Five percent of the marked population was later confirmed at breeding territories in the eastern U.S.A., primarily in New England. Females dispersed greater distances (natal dispersal = 152.6 km; range = 70.2–853.5 km; $n = 28$) than males (88.0 km; range = 0.03–1009.7 km; $n = 22$). New England peregrines showed a strong tendency to settle at nest types similar to those on which they were raised (rural cliff vs. urban structures); however, we documented movement from urban to rural habitats and vice versa in equal proportions. The causes of mortality for 122 recovered birds included unknown (61%), collisions with aircraft (11%), collisions with stationary objects (8%), falling from nest site (8%), collisions with vehicles or trains (7%), gunshot wounds (2%), entanglement in fishing gear (1%), and poisoning (1%). Most deaths occurred among first-year (68%) and second-year (11%) birds, with first-year peregrines experiencing significantly higher mortality than other age classes. The estimated annual survival rate for second-year and adult falcons combined was 81%, whereas our estimate for first-year birds was only 9%; however, the latter rate likely is a significant underestimate. We found no effect of natal habitat or sex on survival.

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KEY WORDS: *Peregrine Falcon*; *Falco peregrinus*; *band recovery*; *dispersal*; *mortality*; *New England*; *survivorship*.

PATRONES DE MOVIMIENTO, DISPERSIÓN NATAL Y SUPERVIVENCIA DE INDIVIDUOS DE *FALCO PEREGRINUS* ANILLADOS EN NUEVA INGLATERRA.

RESUMEN.—El conocimiento de los patrones de dispersión y de las tasas de supervivencia es esencial para entender la dinámica de poblaciones y la demografía, y para desarrollar estrategias de manejo a largo plazo para especies de interés de conservación. En Nueva Inglaterra, *Falco peregrinus* desapareció como especie reproductiva en la década de 1960. Tras un programa de reproducción en cautiverio y liberación, la población experimentó subsecuentemente una rápida expansión dispersándose dentro de su antigua área de distribución, particularmente durante las últimas dos décadas. El uso de edificios, puentes y otras estructuras artificiales como sitios de anidamiento se volvió frecuente en áreas urbanas, donde la especie anidaba muy poco antes de su reintroducción. Analizamos los encuentros con individuos de *F. peregrinus* anillados cuando eran pichones en los seis estados de Nueva Inglaterra entre mayo de 1990 y junio de 2009 para determinar: (a) diferencias en los patrones de dispersión (distancia y dirección) por sexo; (b) diferencias en el movimiento y dispersión natal entre aves de acantilados y sitios de anidamiento artificiales; (c) causas de mortalidad; y (d) efectos del sexo, la edad y tipo de hábitat natal en la supervivencia. De 986 individuos de *F. peregrinus* anillados, el 24% fue encontrado nuevamente por lo menos una vez hasta diciembre de 2009. Aunque la mayoría de los encuentros (76%) ocurrieron dentro del área de estudio, 24% de los mismos ocurrieron fuera de Nueva Inglaterra en otros ocho estados del este, tres provincias canadienses, Cuba y Nicaragua. Cinco por ciento de la población marcada fue confirmado luego en territorios reproductivos en el este de Estados Unidos, principalmente en Nueva Inglaterra. Las hembras se dispersaron a mayores distancias (dispersión natal = 152.6 km; rango = 70.2–853.5 km; $n = 28$) que los machos (88.0 km; rango = 0.03–1009.7 km; $n = 22$). Los individuos de *F. peregrinus* de Nueva Inglaterra demostraron una fuerte tendencia a establecerse en tipos de nidos similares a aquellos en los que se criaron (acantilados rurales vs. estructuras urbanas). Sin embargo, documentamos movimientos desde hábitats urbanos a hábitats rurales y viceversa en proporciones iguales. Las causas de mortalidad para 122 aves recuperadas incluyeron razones desconocidas (61%), colisiones con aviones (11%), colisiones con objetos estacionarios (8%), caídas desde el sitio de anidamiento (8%), colisiones con vehículos o trenes (7%), heridas de balas (2%), enredamiento con equipos de pesca (1%) y envenenamiento (1%). La mayoría de las muertes ocurrió entre aves del primer año (68%) y del segundo año (11%), con individuos del primer año experimentando una mortalidad significativamente mayor que los de otras clases de edad. La tasa de supervivencia anual estimada para los halcones de segundo año y los adultos combinados fue de 81%, mientras que nuestra estimación para aves del primer año fue de sólo 9%; sin embargo, la última tasa es probablemente una subestimación significativa. No encontramos efectos del hábitat natal o del sexo en la supervivencia.

[Traducción del equipo editorial]

Knowledge of regional dispersal patterns and survival rates is essential to understand population dynamics and demography, and to develop effective, long-term management strategies for species of conservation concern. Dispersal is among the most important and least-understood facets of population biology, and its patterns affect all aspects of a species' ecology and behavior (Walters 2000, Clark et al. 2004). Natal dispersal (here defined as the dispersal of fledged young from hatch site to eventual breeding site) can have a strong influence on survivorship, demographic patterns, population trends, and genetics (Gadgil 1971, Paradis et al. 1998, Calabuig et al. 2008). Yet relatively few studies

have investigated natal dispersal, even with the advent of satellite telemetry, which has greatly increased our knowledge of migratory pathways, stop-over sites, and connectivity between overwintering and breeding populations of large birds (e.g., ≥ 600 g; Meyburg and Fuller 2007). Among long-lived birds, survival rates often account for most of the variance of life-time reproduction and have a greater effect on population dynamics than do reproductive rates (Newton 1989).

Since its post-DDT reintroduction to the eastern and upper midwestern United States and its subsequent recovery, the Peregrine Falcon (*Falco peregrinus*) has been well studied (e.g., Cade et al. 1988,

White et al. 2002). Investigations of dispersal within and among regional populations and dispersal's influence on survivorship and population dynamics are still needed, however (White et al. 2002). Barclay (1995) investigated dispersal patterns and survival of the reintroduced peregrine population in three regions of the eastern U.S.: the Northeast, the mid-Atlantic Coast, and the southern Appalachian Mountains. That study was based on encounters of captive-reared birds released between 1974 and 1991, and their offspring banded between 1980 and 1991. The study occurred during the early years of the recovery program, however, involving early colonizing falcons, such that the dispersal and settlement patterns exhibited may not be representative of the contemporary breeding population, which has undergone a rapid expansion into its former range. For example, use of buildings, bridges, and other human-made substrates for nesting is now widespread, especially in urban areas, where the species only infrequently used such structures prior to reintroduction. Understanding the movement patterns, natal dispersal, and survival of this reestablished and still-expanding population, and determining if there are age- and sex-related differences in basic demographic parameters between urban- and cliff-nesting birds is important for the long-term management of the species and for informing restoration efforts elsewhere.

The Peregrine Falcon was extirpated as a breeding species in the eastern U.S.A. by the mid- to late-1960s (Berger et al. 1969, Fyfe et al. 1976). An intensive captive breeding and release (hacking) program commenced in 1974, and successfully reestablished the peregrine in the eastern U.S.A. (Barclay 1988). As a result, the species was removed from the federal list of endangered and threatened species in 1999 (U.S. Fish and Wildlife Service 1999).

During the 20-yr period of this study (1990–2009), the Peregrine Falcon population across New England grew substantially, from 22 territorial pairs fledging 32 young in 1991 to 114 pairs fledging 150 young in 2010 (M. Amaral, M. Fowle, T. French, C. Martin, C. Todd, and J. Victoria pers. comm.). In northern New England (Vermont, New Hampshire, Maine), most nests were located on cliffs, including human-created cliffs (e.g., road cut, quarries) in areas where natural vegetation was still the dominant land cover, whereas in southern New England (Connecticut, Massachusetts, Rhode Island), the majority of nests were located on buildings and other human-created structures, primarily in urban settings (Corser et al. 1999).

We studied movement patterns, natal dispersal, causes of mortality, and survivorship using resightings and band-recovery data for Peregrine Falcons banded as nestlings in New England (Connecticut, Massachusetts, Maine, New Hampshire, Rhode Island, Vermont) from 1990 through 2009. We evaluated (1) differences in dispersal patterns (distance and direction) by sex and age class; (2) differences in movement and natal dispersal among birds from cliff and artificial (e.g., buildings, bridges, etc.) nest sites; (3) causes of mortality; and (4) effects of sex, age, and natal habitat type on survivorship.

METHODS

Data Collection. From 1990–2009, various researchers banded Peregrine Falcon nestlings opportunistically at nest sites in all six New England states. The U.S. Fish and Wildlife Service coordinated the overall banding effort implemented by the states. Effort varied by state and year, such that states with smaller populations of mostly urban-breeding birds (e.g., Connecticut, Massachusetts, Rhode Island) banded 90–100% of the young fledged in their state in most years, whereas states with larger, primarily cliff-breeding peregrines (Vermont, New Hampshire, Maine) banded a smaller proportion of their breeding populations. Banders fitted all birds with U.S. Geological Survey (USGS) bands on the right leg and an alphanumeric color band (black/red or black/green; Acraft, Edmonton, Alberta, Canada) on the left leg.

Throughout the 20-yr study period, researchers and volunteer nest-monitors intensively monitored the Peregrine Falcon breeding population in New England, and during nest visits attempted to determine the band-status and read the color bands of all breeding falcons. Due to variable lighting conditions, falcon behavior, and habitat and viewing constraints at some breeding sites, these efforts were not always successful or consistent among sites. Therefore, collection of band-record information was largely opportunistic, based primarily on band returns, recoveries, and resightings obtained from the USGS Bird Banding Laboratory, and supplemented by data reported to us from birders and other incidental observations.

We measured Peregrine Falcon movements in ArcView 3.1 (ESRI, Redlands, California, U.S.A.) using the Animal Movement extension to calculate the straight-line distance (km) and direction from the banding site (natal nest site) to the recovery or resighting location(s). The accuracy of most

locations was high, based on known latitude-longitude coordinates of breeding sites or descriptions of recovery locations. Occasionally, where the recovery or resighting reports did not provide exact locations (e.g., “Main Street”), we estimated the location as closely as possible based on the data provided.

Because birds were banded as nestlings, we used approximate hatch date to assign birds to age classes, rather than following Bird Banding Lab convention which uses calendar year to define age class. Hatch date was defined as 25 d prior to the banding date, and age classes were first year (FY; 1–364 d old), second year (SY; 365–729 d), and adult (>730 d).

Data Analysis. *Dispersal.* We evaluated movement patterns within two classification categories: (1) all band encounters of birds >74 d of age (the average age of independence for falcons dispersing from natal sites; Barclay 1995); and (2) verified natal dispersals (birds encountered at their first known breeding sites). We made the assumption that the first known breeding site was a bird’s first breeding site, regardless of the bird’s age.

We used a Shapiro-Wilk test (Zar 1996) to evaluate deviation from normal distributions of movement distances by sex, age class, and habitat. In all cases, data were nonnormal and failed to normalize following standard transformations. Therefore, we used nonparametric tests to examine differences in movement distances between males and females (Mann-Whitney *U*-test), and among age classes (Kruskal-Wallis test). Among natal dispersers, we used nonparametric Kruskal-Wallis tests to evaluate sex-based differences in dispersal distance by category of natal nest type (i.e., natural cliff or urban artificial sites). We used a chi-square test to determine if birds fledged from a specific type of nest site were more likely to breed at a specific type of site (e.g., did birds fledged at cliffs preferentially breed at cliffs?). Using circular statistics (Zar 1996), we examined natal dispersal direction (degrees) by sex, category of natal nest type (cliff or urban), and state of origin by calculating the mean angle $\pm 95\%$ confidence intervals from natal eyrie to point of first confirmed breeding. To examine whether dispersal direction was distributed uniformly, we calculated Rayleigh’s *z* for each group (Zar 1996).

Mortality. We evaluated recoveries of dead peregrines to determine the proportional mortality of the study population and to identify causes of mortality as a relevant parameter for conservation. We assumed the probability of band recovery was con-

stant over time for each age class. We calculated proportional mortality by age by dividing the number of recoveries of dead birds in each age class by the number of that age class not recovered. We subtracted the number of peregrines recovered in previous age classes from the number not recovered in the next older age class to determine the actual number not recovered in the older age class (Harmata et al. 1999). We analyzed proportional mortality by age with linear regression and used a Studentized residual procedure (Kleinbaum et al. 1998) to identify significant outliers, which we considered indicative of age classes with significantly different mortality rates.

Apparent survival. We estimated resighting probability and apparent annual survival (apparent because the parameter confounds true survival and permanent emigration out of the study area) using the live-recapture models implemented in Program MARK (White and Burnham 1999). We estimated both parameters based on encounter histories created for 952 birds banded as nestlings between 1990 and 2008. We excluded from the analyses birds that died before fledging and birds banded in 2009 (because they had no opportunity to be resighted during a subsequent breeding season). We defined 1 April through 30 June as the “recapture” period for all marked individuals, which corresponds to the approximate duration of the breeding season, when most resighting efforts occurred. We classified any marked individual seen alive during this period as a recapture. Estimates of apparent survival, therefore, refer to the probability that a marked individual survives, and does not permanently leave the study area, from one breeding season to the next.

We modeled three factors that are potentially important for explaining variation in survival of Peregrine Falcons: age, sex, and whether an individual was fledged from a nest on an artificial structure or cliff. Despite the large number of individuals included in this study, recapture data were sparse (see Results), so we did not evaluate potential temporal variation in survival or recapture probabilities. Thus, our global model can be stated as:

$$\Phi_{age*sex*habitat}, P_{age*sex*habitat}$$

where ϕ refers to the probability that a bird alive during breeding season *i* is alive at breeding season *i* + 1; *p* refers to the probability that a bird is recaptured, or in our case resighted, given that it is alive and in the study area; and subscripts indicate which covariates are included (Lebreton et al. 1992).

Table 1. Peregrine Falcons banded as nestlings in New England from 1990–2009, by state.

STATE	NUMBER	%
Connecticut	76	8
Maine	115	12
Massachusetts	228	23
New Hampshire	293	30
Rhode Island	43	4
Vermont	231	23
Total	986	

We began by estimating parameters for models in which survival varied as a function of all possible combinations of the three covariates, while in each case modeling recapture probability as a function of age, which we considered the most likely predictor of whether an individual was seen after being marked. We used Akaike’s Information Criteria adjusted for small sample size (AIC_c; Akaike 1973, Burnham and Anderson 2003) to determine the best model in this subset. We then examined whether it was possible to improve upon this best model by adding covariates to the recapture parameter. The complete candidate set of models that we considered thus included: (a) all models in which we varied survival covariates while holding recapture probability as a function solely of age; and (b) all models in which we varied recapture covariates while holding survival probability as a function of the best combination of covariates as revealed by (a).

We examined the goodness-of-fit for the global model using the bootstrap routine implemented in Program MARK. We calculated \hat{c} , a measure of the extent of overdispersion, in two ways. First, we divided the observed deviance of the global model by the mean deviance produced by the bootstrap simulations. Second, we divided the observed \hat{c} from the global model by the mean \hat{c} from the bootstrap simulations. We then used the larger of the two estimates—a conservative approach—to adjust AIC_c values to reflect the estimated degree of overdispersion (QAIC_c).

We ranked candidate models according to QAIC_c and used the relative rank and weight (a measure of the likelihood that the model is the best of the candidate models; Burnham and Anderson 2003) of the models in the candidate set to assess the importance of the covariates qualitatively. When estimating survival and recapture probabilities, however, we used average values for all of the candidate models

Table 2. Subsequent encounter locations for Peregrine Falcons banded as nestlings in New England from 1990–2009.

LOCATION	NUMBER	%
Massachusetts	56	24
Vermont	40	17
New Hampshire	35	15
Connecticut	21	9
Rhode Island	18	8
New York	16	7
Maine	11	5
Pennsylvania	10	4
Virginia	10	4
New Jersey	9	4
Quebec	8	3
Florida	5	2
Maryland	5	2
Cuba	1	<1
Nicaragua	1	<1
New Brunswick	1	<1
South Carolina	1	<1
West Virginia	1	<1
Ontario	1	<1
Total encounters	250 ^a	
Total individuals	238	

^a Includes two separate encounters of 12 individuals in different locations.

to acknowledge model-selection uncertainty (Burnham and Anderson 2003).

We conducted all analyses, other than of survival, using SYSTAT 11 (Systat Software, Chicago, Illinois, U.S.A.) and Excel 2010 (Microsoft, Redmond, Washington, U.S.A.).

RESULTS

A total of 986 Peregrine Falcons were banded at nest sites in the six New England states from 1990–2009 (Table 1). Of these, 24% (238) were encountered at least once after banding, including 55% females and 45% males. Dead birds ($n = 122$) made up 51% of the recoveries, including 52% females and 48% males. Of the 238 encounters, 76% (181) occurred in the six New England states, including 24% in Massachusetts, 17% in Vermont, and 15% in New Hampshire; 24% (57) occurred in eight states outside of New England; and 5% (12) occurred in other countries, including 10 in Canada and one each in Cuba and Nicaragua (Table 2).

Four percent (39) of banded nestlings (19 females, 20 males) were later found breeding within the study area (Table 3). Vermont had the highest proportion of recruits (33%), followed by New

Table 3. Number (%) of Peregrine Falcons banded as nestlings in New England from 1990–2008 that were recruited back into the study area as breeders, by sex and state.

	MALE	FEMALE	TOTAL
Connecticut	1 (3)	1 (3)	2 (5)
Rhode Island	3 (8)	1 (3)	4 (10)
Massachusetts	4 (10)	4 (10)	8 (21)
New Hampshire	6 (15)	5 (13)	11 (28)
Vermont	6 (15)	7 (18)	13 (33)
Maine	0	1 (3)	1 (3)
Total	20 (51)	19 (50)	39 (4)

Hampshire (28%) and Massachusetts (21%; Table 3). Eleven individuals (nine females, two males) dispersed to breed outside of the study area, including five in Pennsylvania, three in Virginia, and one each in New Jersey, New York, and Quebec, Canada.

Sex-based Differences in Dispersal Distance. For all birds >74 d of age, the median band-encounter distance was significantly greater for females (202.3 km; range = 1.7–2102.5 km; $n = 111$) than for males (99.3 km; range = 0.03–3709.8 km; $n = 93$; Mann-Whitney $U = 6524.0$, $P = 0.001$; Fig. 1). Considering only records of natal dispersal, the results were similar. Females dispersed significantly greater distances (152.65 km; range = 70.2–853.5 km; $n = 28$) than males (88.0 km; range = 0.03–1009.7 km; $n = 22$; Mann-Whitney $U = 440.0$, $P = 0.010$; Fig. 1).

For both sexes combined, the median natal dispersal distance was 108.9 km; range = 0.03–1009.7 km). Among females, 57% (16) dispersed farther than the median, compared to 36% (8) of males (Fig. 2). A majority (59%) of male peregrines dispersed ≤ 100 km, compared to 29% of females (Fig. 2).

Age-based Differences in Dispersal Distance. For all birds >74 d of age, the median band-encounter distance was significantly different among age classes (Kruskal-Wallis = 6.6, $P = 0.037$), with FY birds encountered at greater distances (172.2 km; range = 0.03–2695.8 km; $n = 102$) than were SY birds (105.7 km; range = 14.5–3709.8 km; $n = 43$) and adults (159.2 km; range = 7.0–1305.4 km; $n = 75$). Among birds that were encountered >800 km from their banding site, 71% (12) were FY birds.

Natal Dispersal Distance Relative to Nest Type. Most of the 50 birds later resighted as breeders fledged from nests on cliffs ($n = 31$, 62%) and buildings ($n = 17$, 34%), with only two fledged from hack sites (an urban building and a rural cliff; Ta-

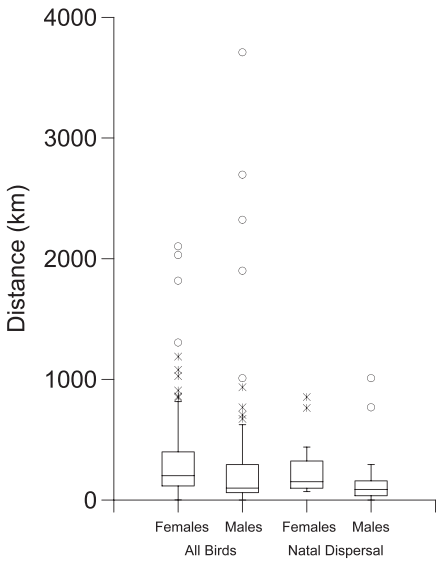


Figure 1. Variation in distances moved from natal areas, as determined from band recoveries or resightings, for male and female Peregrine Falcons banded as nestlings in New England from 1990–2009. In all cases, median values for males and females are significantly different (Mann-Whitney U -tests; $P < 0.05$).

ble 4, Appendix 1). Birds showed a distinct tendency to nest on substrates that were similar to those from which they fledged ($\chi^2_4 = 18.6$, $P = 0.001$; Table 4). Fifty-six percent of natal dispersers were found breeding on cliffs, 20% on buildings, 18% on bridges, 4% on a derelict crane, and 2% on a coastal tower platform. Among the 31 birds fledged from cliffs, 81% returned to nest on cliffs and 19% on human-made structures. Among the 17 birds fledged from buildings, 82% nested on buildings and 18% on cliffs. The two hack-site birds (one from a cliff site, one from a building site) nested together on a building. No nestlings banded on New England bridges were recovered at breeding sites.

Among birds that fledged from and nested on cliffs, females dispersed greater distances (194.3 ± 38.7 km; $n = 14$) than did males (86.6 ± 23.1 km; $n = 11$; Mann-Whitney $U = 126.0$, $P = 0.007$). Similarly, among birds that fledged from buildings (which included an urban hack-site) and later nested on buildings or other artificial structures, the median dispersal distance for females (247.4 km; range = 72.6–439.3 km; $n = 7$) was marginally greater than for males (41.4 km; range = 0.03–768.2 km; $n = 7$; Mann-Whitney $U = 38.0$, $P = 0.085$). In contrast, we found no sex-specific differences in me-

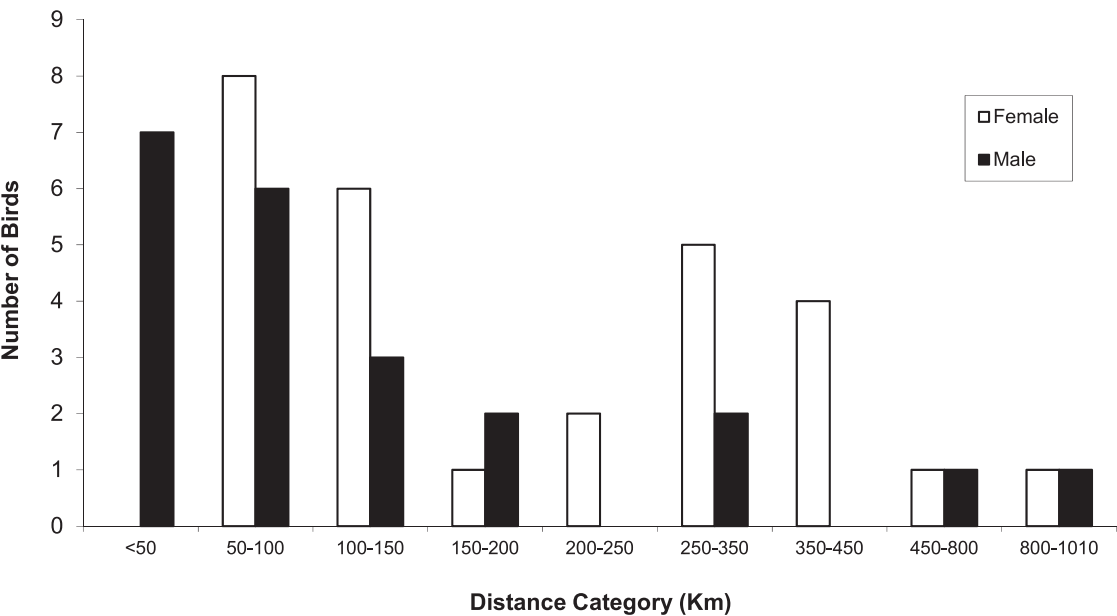


Figure 2. Natal-dispersal distance category of male and female Peregrine Falcons banded as nestlings in New England from 1990–2009.

dian dispersal distances for birds that fledged from cliffs and later nested on artificial structures (Mann-Whitney $U = 5.0$, $P = 0.14$) or for birds that fledged from buildings and later nested on cliffs (Mann-Whitney $U = 0.0$, $P = 0.22$).

Natal Dispersal Direction. Natal dispersers showed a strong tendency to disperse in a south-westerly direction from hatch sites (mean direction $\pm 95\%$ CI: $228 \pm 17^\circ$; Fig. 3, Table 5, Appendix 1). Excluding birds from hack sites and those originating from Connecticut and Rhode Island, for which sample sizes were insufficient to conduct statistical tests, all groups of interest (sexes, nest types, and states of origin) except one, showed significant, nonrandom, southwestern directionality of natal dispersal (Table 5). The exception was birds

fledged in Vermont, which showed no significant directional pattern (Table 5, Fig. 3).

Causes of Mortality. Of 238 individuals encountered after banding, 51% (122) were found dead or died from injuries shortly after being found, including 52% (63) females and 48% (59) males. The cause of death was determined for 39% of these recoveries (Table 6). Most (79%) resulted from anthropogenic causes, including aircraft collisions (30%), striking stationary objects (21%; e.g., building/window, bridge cable, etc.), and falling from nest sites (21%). Two birds found dead in New York were necropsied and submitted for toxicology screens. A 19-mo-old male from Vermont died from fenthion poisoning. A 44-mo-old female from New Hampshire that collided with a window had low

Table 4. Natal and breeding nest substrates for Peregrine Falcons banded as nestlings in New England from 1990–2009.

NATAL EYRIE	BREEDING EYRIE					TOTAL
	CLIFF	BUILDING	BRIDGE	COASTAL TOWER	INDUSTRIAL CRANE	
Building	3 (18%)	5 (29%)	7 (41%)		2 (12%)	17
Cliff	25 (81%)	3 (10%)	2 (7%)	1 (3%)		31
Cliff hack site		1				1
Urban hack site		1				1
Total	28 (56%)	10 (20%)	9 (18%)	1 (2%)	2 (4%)	50

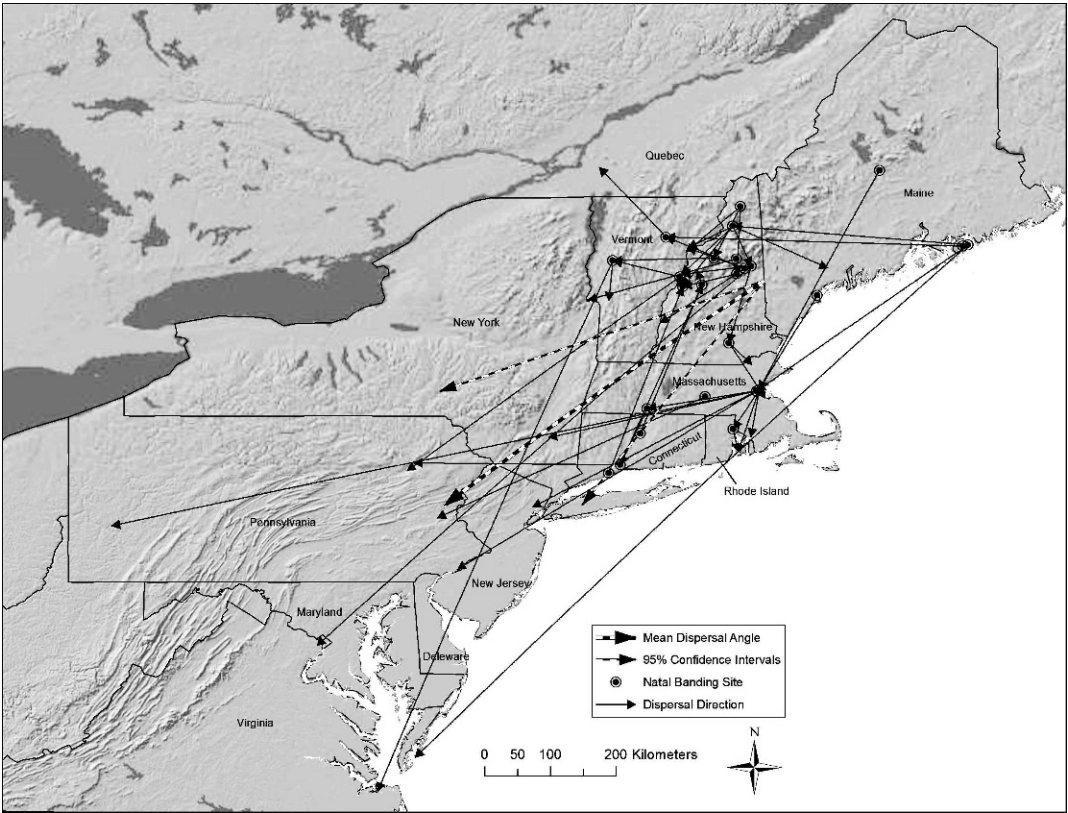


Figure 3. Pattern of natal dispersal for 50 Peregrine Falcons banded as nestlings in New England from 1990–2009 and later resighted at a breeding site, including depiction of the mean dispersal direction ($\pm 95\%$ CI) calculated using circular statistics. The origin of mean dispersal and CI lines is placed at the geographic center of the study area.

Table 5. Direction of natal dispersal by sex, natal eyrie type, and state of origin for Peregrine Falcons banded as nestlings in New England from 1990–2009.

NATAL DISPERSAL GROUP (<i>n</i>)	MEAN DIRECTION ($^{\circ}$) $\pm 95\%$ CI	RAYLEIGH'S <i>z</i>	<i>P</i>
All birds (50)	228 \pm 17	18.1	<0.001 ^a
Males (22)	206 \pm 36	5.2	<0.005
Females (28)	239 \pm 17	21.0	<0.001
Urban sites (17)	215 \pm 47	4.4	<0.05
Cliff sites (31)	236 \pm 19	14.1	<0.001
Hack sites (2)	210 ^b		
Connecticut (3)	352 ^b		
Massachusetts (11)	225 \pm 25	7.9	<0.001
Maine (6)	238 \pm 32	4.8	<0.005
New Hampshire (22)	221 \pm 27	8.0	<0.001
Rhode Island (2)	84 ^b		
Vermont (6)	227 \pm 73	2.1	>0.05

^a $P \leq 0.05$ indicates a significant directional pattern.

^b Sample size insufficient to calculate 95% CI or Rayleigh's *z*.

Table 6. Causes of mortality in Peregrine Falcons banded as nestlings in New England from 1990–2009 based on band recoveries.

CAUSE OF DEATH	NUMBER	PERCENT OF TOTAL		
		FOUND DEAD	SPECIFIC CAUSE OF DEATH KNOWN	BANDED
Unknown	56	46		6
Caught due to injury, died in captivity	17	14		2
Struck by aircraft	14	12	30	1
Struck stationary object	10	8	21	1
Fell from nest	10	8	21	1
Hit by car	7	6	15	<1
Hit by train	2	2	4	<1
Gunshot	2	2	4	<1
Found dead at nest site	2	2		<1
Entangled in fishing gear	1	<1	2	<1
Fenthion poisoning	1	<1	2	<1
Total	122	100	100	12.3

levels of PCB and mirex (W. Stone pers. comm.); however, it was unclear if either of these compounds contributed to the bird’s death.

Most deaths involved first-year (68%) and second-year (11%) birds. Proportional mortality declined significantly with age (Fig. 4) and was significantly greater for first-year birds than for other age classes ($t_{12} = 3.33$, $P = 0.005$).

Survivorship. Of the 952 individuals marked as nestlings and included in the survivorship analysis, only 61 were resighted during a subsequent breeding season. The global model provided an adequate fit to the data ($P = 0.26$). Age was the strongest predictor of both apparent annual survival and recapture probability; models without an age effect, especially for the survival parameter, performed

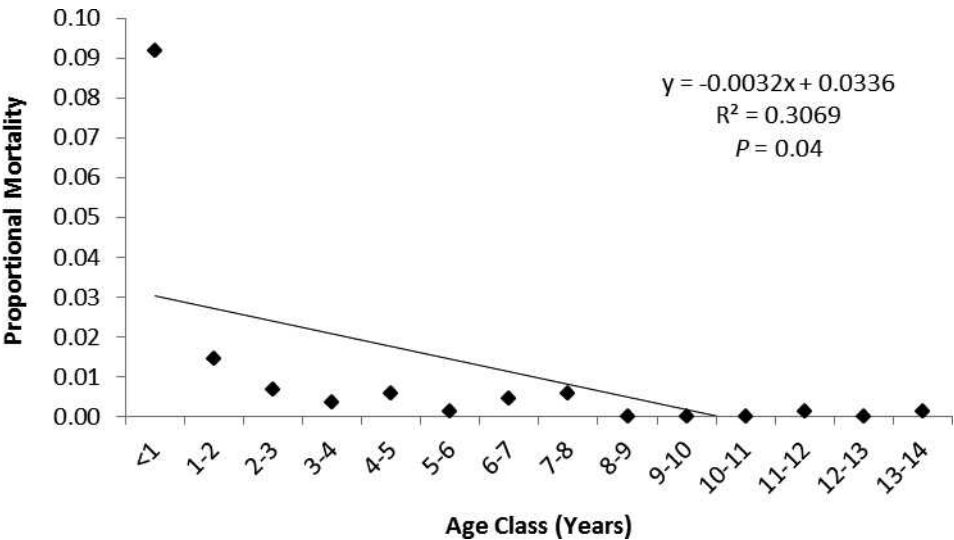


Figure 4. Proportional mortality (number recovered dead/number not recovered) by age class of Peregrine Falcons banded as nestlings in New England from 1990–2009. Mortality was significantly greater for birds <1 yr old than for all other age classes.

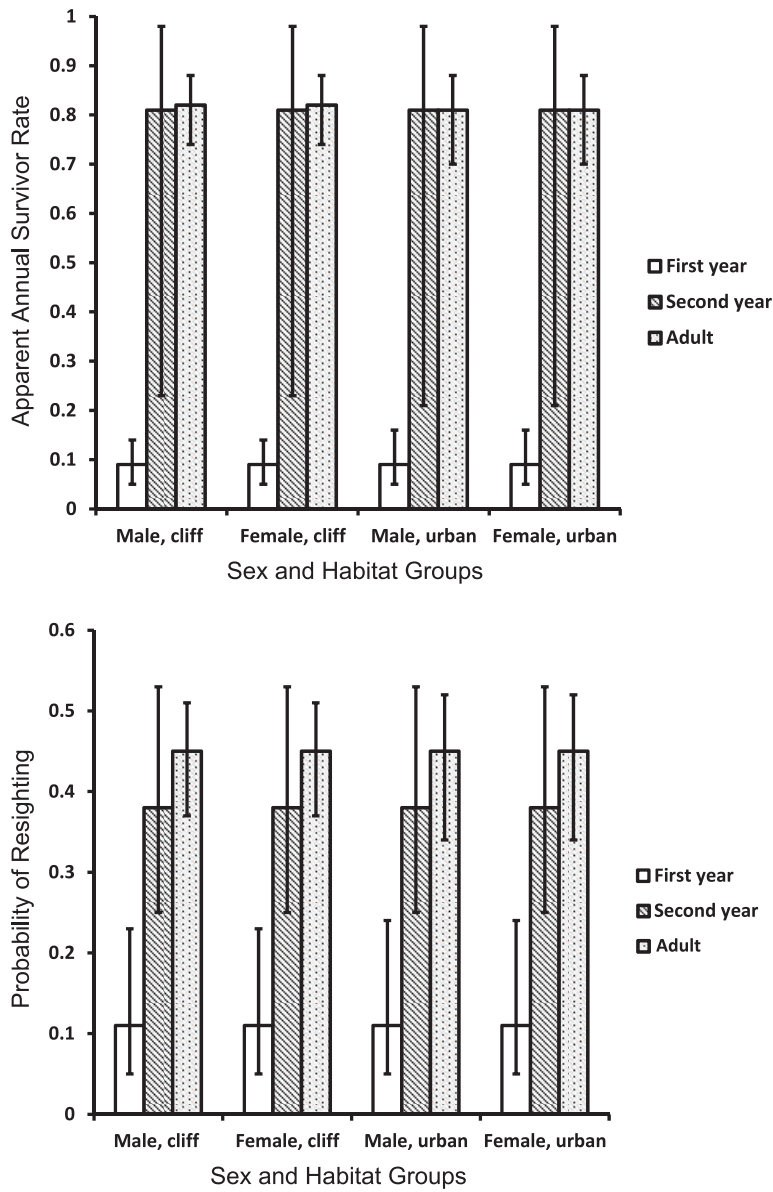


Figure 5. Apparent annual survival rate (upper panel) and probability of resighting (lower panel), grouped by sex and natal-eyrie habitat type, for three age classes of Peregrine Falcons banded in New England from 1990–2009.

poorly (Table 7). Based on model-averaged estimates (Fig. 5), only age was an important predictor of variation in apparent survival. The apparent survival rate for first-year birds (0.09, 95% CI = 0.05–0.14) was significantly lower than that for second-year birds (0.81, 95% CI = 0.25–0.98) and for adults (0.81, 95% CI = 0.74–0.87), with no difference indicated for the two older age classes (Fig. 5). Recap-

ture probability also was substantially lower for first-year birds (Fig. 5).

DISCUSSION

Movement Patterns and Natal Dispersal. Despite wide variation among individuals of both sexes, we found that female Peregrine Falcons tended to travel farther from their natal nesting sites than did males.

Table 7. Relative degree of support (ΔQAIC_c and model weight) and quality of fit (deviance) for models calculated using Program MARK to estimate apparent annual survival and recapture probability of Peregrine Falcons banded as nestlings in New England from 1990–2009.

MODEL	ΔQAIC_c^a	MODEL WEIGHT	DEVIANCE
$\Psi_{age} + \rho_{age}$	0	0.75	542.9
$\Psi_{age*habitat} + \rho_{age}$	3.8	0.14	540.3
$\Psi_{age} + \rho_{age*sex}$	5.4	0.05	542.1
$\Psi_{age} + \rho_{age*habitat}$	5.4	0.05	542.2
$\Psi_{age*habitat*sex} + \rho_{age}$	13.7	0	537.7
$\Psi_{age} + \rho_{age*habitat*sex}$	15.0	0	539.2
$\Psi_{age} + \rho$	18.3	0	568.7
$\Psi_{age*habitat*sex} + \rho_{age*habitat*sex}$	29.1	0	534.0
$\Psi + \rho_{age}$	97.2	0	659.3
$\Psi_{habitat} + \rho_{age}$	99.2	0	659.3
$\Psi_{sex} + \rho_{age}$	99.2	0	659.3
$\Psi + \rho$	236.1	0	823.8

^a Lowest $\text{QAIC}_c = 880.0$.

Such female-biased dispersal is common among bird species (Greenwood 1980) and has been reported in studies of Peregrine Falcons from other regions, including the midwestern U.S.A. (Tordoff and Redig 1997), Pennsylvania (Katzner et al. 2012), Alaska (Ambrose and Riddle 1988), and Scotland (Mearns and Newton 1984). We observed a tendency for more females to disperse out of the study area to breed than would be expected based on the nestling sex ratio, although our sample size was small; however, we did not observe a sex bias among recruits. In Greenland, where there was a significantly higher proportion of male than female recruits, more female Peregrine Falcons dispersed out of the study area (Restani and Mattox 2000).

In addition to sex-biased dispersal, juveniles of many raptor species tend to migrate farther than adults (Newton 1979). Among Peregrine Falcons banded as nestlings in the northeastern United States, Barclay (1995) found that first-year birds were encountered at greater distances from their natal site than were adults. Our results followed this pattern, showing that most long-distance movements involved first-year birds. In part, this may help explain why young peregrines in our study had a higher mortality rate than all other age classes. Seven birds (four males, three females), six of which were first-year birds and one a second-year bird, were encountered at much greater distances compared to the rest of our banded population. Five of these long-distance encounters involved birds recovered dead during winter, including a second-year male that struck a chain-link fence while chasing

prey in San Jacinto, Nicaragua (3710 km from its natal site in Vermont), and a first-year male shot in Camaguey, Cuba (2696 km from its natal site in Maine). The other two long-distance encounters involved first-year males captured and released by banders in south Florida, one during autumn migration and the other in early January.

New England Peregrine Falcons showed a strong preference to settle at nest sites similar to those from which they fledged. We also documented movement between habitats, however, with similar proportions of birds moving from urban natal sites to rural breeding sites (18%) as moved from rural natal sites to urban breeding sites (19%; Table 4). This contrasted with the findings of Kauffman et al. (2003), who documented habitat switching in California by a small number of cliff-fledged peregrines that were later confirmed breeding at urban sites, but found no urban-fledged falcons breeding on cliffs. They attributed this unequal dispersal to California’s relatively small population of urban peregrines, higher prey abundance in urban areas, and a general tendency for California’s peregrines to disperse from inland rural sites to coastal urban areas. They also speculated that, as densities of urban-breeding peregrines increase, dispersal out of urban habitats may become more common. Indeed, that appears to be the pattern in New England, where movement out of urban areas has become more common since the late 1990s as the region’s population density has increased. There may also be some observer bias that favors confirming movement from rural to urban sites, because urban birds

are observed or recovered more often than those breeding at more remote cliffs (Kauffman et al. 2003).

The tendency for natal dispersers to move in a southwesterly direction from New England hatch sites was similar to results reported by Barclay (1995). Such directionality was expected, given the proximity of the Atlantic Ocean limiting easterly and southeasterly dispersal.

Causes of Mortality. The causes and rates of mortality in this banded population were similar to those reported from other studies of reintroduced peregrines. Among mortalities with known causes, Barclay (1995) and Katzner et al. (2012) also reported a relatively high proportion of aircraft strikes and collisions with stationary objects. Our data confirmed death due to poisoning for only one bird, but a general lack of toxicological screening precluded an effective evaluation of the prevalence of this cause of mortality. The single bird died as a result of secondary-poisoning after consuming a European Starling (*Sturnus vulgaris*) that had been poisoned with fenthion (an organophosphate pesticide). Highly toxic to birds, fenthion was formerly used to control pest bird species, including starlings and Rock Pigeons (*Columba livia*), often at roosts on farms, airports, and public buildings (Van Driesche 1985). Although its use as an avicide was banned in 1998, fenthion is still used to control adult mosquitoes in Florida (U.S. Environmental Protection Agency 2001). The poisoned bird was found dead in January 2001 in New York's Adirondack Mountains, suggesting that fenthion use to control birds may continue illegally in some areas.

Survivorship. Our survival estimates appear to be the first reported for first-year, second-year, and adult Peregrine Falcons in the eastern United States. Our estimates of 81% survival for both second-year and adult birds were consistent with those reported in Kauffman et al. (2003: Table 4); however, we believe our first-year survival estimate of 9% significantly underestimates the actual survival rate, most likely due to the transient nature of young peregrines, combined with the nonrandom sampling protocol of the original monitoring program. Kauffman et al. (2003) estimated survival of first-year peregrines in California at 38%, but found that first-year birds fledged from rural habitats had much lower survival (28%) than those from urban habitats (65%). Tordoff and Redig (1997) used resightings of banded peregrines in the Midwest to estimate a minimum first-year survival of 23%, al-

though they stressed that actual survival probably exceeded 30% because of birds that survived but were not resighted. Because young peregrines tend to wander widely during their first year and rarely occupy a breeding territory (Newton and Mearns 1988), the chances of resightings are greatly diminished, as borne out by our low probability of recapture estimate. Moreover, we used data from a monitoring program that was not designed as a mark-recapture study, but rather to monitor nesting activity and breeding success of a reintroduced population. This resulted in a relatively small sample of birds ($n = 61$) resighted during the breeding season and included in the survivorship models.

We found no effect of natal habitat on peregrine survival, contrary to the findings of Kauffman et al. (2003), who reported that first-year survival was much greater for urban-hatched birds than for rural-hatched birds. However, because our estimates of first-year survival were unreliable as explained above, we may have been unable to detect an actual habitat effect on that age class. We did find that first-year falcons had a significantly higher proportional mortality rate than any other age class, but we did not calculate that metric separately for each habitat.

MANAGEMENT IMPLICATIONS

Peregrine Falcon dispersal ability, combined with adequate survivorship, has resulted in the successful reestablishment and recovery of this species in New England. Following its reintroduction at 17 discrete hack sites across the region during the 1970s and 1980s, the species has reoccupied the majority of its historic breeding sites and colonized sites that were not used prior to reintroduction, including a variety of urban structures and human-created "cliffs." It is difficult to predict the region's current carrying capacity, due to the widespread use of human-created habitats for nesting. Compared to natural cliff sites, many of these structures require management or maintenance to ensure that they remain suitable and accessible for nesting, as well as to minimize human disturbance. Similarly, cliff sites that receive regular use by rock climbers also require management to educate users and limit human disturbance during the breeding period. If management and maintenance at these sites declines or ceases altogether, it could negatively affect productivity, survival, and other demographic parameters at a time when monitoring programs are being scaled back or phased out. This would greatly impair our ability to detect Peregrine Falcon population changes,

identify causative factors, and take needed actions to address problems.

ACKNOWLEDGMENTS

The recovery of the Peregrine Falcon in New England has involved the cooperation of hundreds of individuals and dozens of organizations over the last 20-plus years. The following individuals deserve special recognition for their commitment and dedication to the management, recovery, and conservation of peregrines in the region; Bruce Connery, Doug Blodgett, Margaret Fowle, Moe Parienteau, Steve Parren, Paul Nickerson, Norm Smith, Charlie Todd, Julie Victoria, Robert Vallieres, Kathy Wohlfort, and Joe Zybrowski. In addition, we recognize and thank the many technical climbers who provided assistance in accessing nest ledges for banding, especially Paul Cormier, Nancy Koenig, Mike Pelchat, Todd Hindinger, Al Hospers, Travis Peckham, Alden Pellett, Jim Shimerberg, and Matt Stevens. We extend our thanks to Amber Boland and James Gorham for providing assistance verifying band-encounter locations and coordinates, error-checking data, and conducting literature searches. The authors are also grateful to Don Cowen for his willingness to search his color-band records and identify potential banders of resighted peregrines. This manuscript benefited from helpful reviews by P.D. Hunt, C.C. Rimmer, D.E. Varland, T.L. Maechtle, and one anonymous reviewer.

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Received 12 March 2012; accepted 6 April 2013
Associate Editor: Jeff P. Smith

Appendix 1. Breeding locations of adult Peregrine Falcons banded as nestlings in New England, 1990–2009.

SEX	BANDING LOCATION	YEAR OF BANDING	BREEDING LOCATION	YEAR OF FIRST KNOWN BREEDING	MOVEMENT FROM NATAL NEST	
					DISTANCE (km)	DIRECTION (°)
Female	Boarstone Mtn, ME ^a	1991	Customs House Tower, MA	1994	360.59	208.71
	Square Mtn, NH	1993	Holts Ledge, NH	1995	105.70	224.28
	Customs House Tower, MA	1993	Passaic River Bridge, NJ	1994	315.21	242.54
	Precipice Cliff, ME	1994	Christian Science Building, MA	1996	323.65	235.26
	Precipice Cliff, ME	1994	Devils Slide, NH	1997	257.90	274.51
	Frankenstein Cliff, NH	1995	Bald Mt, VT	1998	175.25	254.47
	Customs House Tower, MA	1995	Newport Bridge, RI	2002	97.96	210.70
	Fairlee Cliff, VT	1997	Cross-Valley Expressway Bridge, PA	1998	426.45	234.52
	McCormack PO, MA	1997	Braga Bridge, MA	1999	72.64	189.98
	Traveler's Tower, CT	1997	Rattlesnake Cliff, NH	2001	256.02	22.61
	Fairlee Cliff, VT	1999	Deer Leap, VT	2002	77.19	283.67
	Devils Slide, NH	1999	Holts Ledge, NH	2000	107.13	219.81
	Painted Walls, NH	1999	Nichols Ledge, VT	2001	98.70	291.85
	Abeniki Mtn, NH	1999	Ryegate Quarry, VT	2001	92.30	218.37
	Jordan Cliff, ME	2000	Nichols Ledge, VT	2005	324.50	271.76
	Christian Science Building, MA	2000	Mid-Hudson Bridge, NY	2003	247.35	257.36
	Painted Walls, NH	2000	Ryegate Quarry, VT ^b	2004	70.17	297.31
	Devils Slide, NH	2001	Frankenstein Cliff, NH ^c	2002	101.92	113.75
	Cathedral Ledge, NH	2001	Sawyer Mtn, VT ^d	2004	77.80	263.01
	Christian Science Building, MA	2001	Girard Point Bridge, PA	2006	439.25	233.17
	Springfield, MA	2001	West Rock Ridge State Park, CT	2002	91.01	205.76
	Abeniki Mtn, NH	2002	Square Ledge, NH	2004	102.47	183.15
	Cathedral Ledge, NH	2002	Dept of Justice Building, VA	2004	763.25	228.77
	Deer Leap, VT	2003	Berkley Bridge, VA	2004	853.49	203.85
	Federal Reserve Bank, MA	2004	Springfield, MA	2006	129.85	258.23
	Fallon Health Building, MA	2006	8th Street Bridge, PA ^e	2007	361.65	240.68
	Nichol's Ledge, VT	2006	Quarry, Quebec, Canada	2008	128.63	326.11
	West Rock Ridge, CT	2007	Campbell's Ledge, PA	2009	236.48	271.54
Male	Portland, ME ^f	1986	Customs House Tower, MA	1994	158.97	210.47
	Deer Leap, VT	1992	Bird Mt, VT	1997	61.32	185.70
	Fairlee Cliff, VT	1994	Holts Ledge, NH	1996	14.71	165.09
	Eaglet Spire, NH	1995	Deer Leap, VT	1998	110.67	268.56
	Abeniki Mtn, NH	1995	Eaglet Spire, NH	2008	83.36	200.00
	Devils Slide, NH	1996	Barnet Roadcut, VT ^g	1998	73.53	224.59
	McCormack PO, MA	1997	Fleet Bank Building, RI	1998	196.84	213.76
	Precipice Cliff, ME	1997	Cobb Island Tower, VA	2004	1009.72	227.10
	Devils Slide, NH	1997	Sawyer Mtn, VT	1998	92.53	226.91
	Devils Slide, NH	1999	Cathedral Ledge, NH	2002	63.56	155.34
	Painted Walls, NH	1999	Skitchewaug Mtn, VT	2005	125.19	237.36
	Fleet Bank Building, RI	2000	Newport Bridge, RI	2002	36.08	167.96
	Cathedral Ledge, NH	2000	Brady Sullivan Tower, NH	2001	121.36	195.59
	Fleet Bank Building, RI	2001	Fleet Bank Building, RI ^h	2002	0.00	0.00
	Customs House Tower, MA	2001	Goliath Crane, Quincy Shipyard, MA	2004	14.91	143.77
	NH Tower Building, NH	2001	Mill Building, MA	2003	41.35	134.22
	NRG Energy Plant, Devon, CT	2003	Holts Ledge, NH	2006	293.99	20.45
	Rattlesnake Cliff, NH	2003	West Rock Ridge State Park, CT	2005	289.52	204.49
	Federal Reserve Bank, MA	2004	62nd St Bridge, PA	2008	768.19	256.81

Appendix 1. Continued.

SEX	BANDING LOCATION	YEAR OF BANDING	BREEDING LOCATION	YEAR OF FIRST KNOWN BREEDING	MOVEMENT FROM NATAL NEST	
					DISTANCE (km)	DIRECTION (°)
	Brady-Sullivan Tower, NH	2004	Goliath Crane, Quincy Shipyard, MA	2006	93.96	146.89
	Rattlesnake Cliff, NH	2004	Owl's Head Cliff, NH	2008	23.24	346.08
	Holts Ledge, NH	2007	Fairlee Palisades, VT	2009	14.71	347.67

^a Natural cliff hack-site; killed and replaced resident nesting female at Customs House.

^b Breeding female at Ryegate Quarry 2004–05, and Barnet Roadcut (7 km south) 2007–08; held territory at Barnet Roadcut 2002, but did not nest.

^c First found breeding at Frankenstein Cliff for 1 yr before moving 63 km to nest on a building in Lewiston, ME for 2 yr.

^d Breeding female at Sawyer Mountain 2004–05, before moving 2 km and replacing unbanded female at Fairlee Cliff 2008–09; was found in February 2005 with a mild head injury in Boston, MA, treated, and released.

^e First found breeding on building for 2 yr, then moved to nearby, unoccupied bridge.

^f Urban hack-site.

^g Breeding male at Barnet Roadcut 1998–2000 and 2002, and at Ryegate Quarry 2001–06; maintained two territories with separate females in 2002.

^h Found breeding at natal hatch site at 1 yr of age.