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Authors: Dennhardt, Andrew J., and Wakamiya, Sarah M.

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EFFECTIVE DISPERSAL OF PEREGRINE FALCONS (*FALCO PEREGRINUS*) IN THE MIDWEST, U.S.A.

Andrew J. Dennhardt[1] and Sarah M. Wakamiya[2]
Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, IL 62901 U.S.A.

Abstract.—Dispersal is a significant life-history trait of vagile species that affects the distribution and genetic structure of populations. Natal dispersal in birds is the movement of an individual from its hatch site to a new location where its first reproductive effort occurs. To examine the ongoing recovery of the Peregrine Falcon (*Falco peregrinus*) in the upper Midwest, U.S.A., we assessed the influence of sex, hack-status (hacked or wild-fledged), and hatch site (cliff or human-made) on natal dispersal distance, and we evaluated directional trends of dispersal in the midwestern Peregrine Falcon subpopulation. We found that mean dispersal distance of female peregrines was >2 times farther than that of males. Dispersal distance did not differ between hacked females and wild-fledged females; however, hacked males dispersed significantly farther than wild-fledged males. Dispersal distance among urban-hatched females and cliff-hatched females did not differ, nor did dispersal distance of urban-hatched males and cliff-hatched males, probably because the sample size for cliff-hatched birds was small. As a whole, the direction of dispersal in midwestern peregrines was nonuniformly distributed and skewed to the northwest and southeast. This report may benefit future studies of peregrine demographics and population viability analyses by providing wildlife managers with information about the patterns and natal movements of Peregrine Falcons in the midwestern U.S.

Key Words: *Peregrine Falcon*; Falco peregrinus; *dispersal*; *hacking*; *natal dispersal*; raptors.

DISPERSIÓN EFECTIVA DE *FALCO PEREGRINUS* EN EL MEDIO OESTE, ESTADOS UNIDOS.

Resumen.—La dispersión es un atributo en la historia de vida de las especies vágiles que afecta la distribución y la estructura genética de las poblaciones. En las aves, la dispersión natal es el movimiento de un individuo desde su sitio de nacimiento hacia una nueva ubicación donde ocurre su primer esfuerzo reproductivo. Para examinar la actual recuperación de *Falco peregrinus* en el Medio Oeste superior, Estados Unidos, evaluamos la influencia del sexo, del modo de cría (cría asistida o silvestre), y del sitio de eclosión (acantilado o artificial) sobre la distancia de dispersión natal, y evaluamos las tendencias en la dirección de dispersión en la subpoblación de *F. peregrinus* del Medio Oeste. Encontramos que la distancia media de dispersión de las hembras fue >2 más lejana que la de los machos. La distancia de dispersión no difirió entre las hembras criadas de modo asistido y de forma silvestre; sin embargo, los machos criados con asistencia se dispersaron significativamente más lejos que los machos criados de forma silvestre. Las distancias de dispersión entre las hembras que eclosionaron en sitios urbanos y las que lo hicieron en acantilados no difirió; lo mismo ocurrió con la distancia de dispersión de los machos que eclosionaron en sitios urbanos y los machos que eclosionaron en acantilados, probablemente debido a que el tamaño de la muestra de las aves que nacieron en los acantilados fue pequeño. En general, la dirección de la dispersión de los individuos de *F. peregrinus* del Medio Oeste no estuvo distribuida de manera uniforme y estuvo sesgada hacia el noroeste y el sudeste. Este informe puede ayudar a futuros estudios demográficos y de análisis de viabilidad poblacional de esta especie, al proveer a los encargados del manejo de vida silvestre información de los patrones de movimiento natal de los individuos de *F. peregrinus* en el Medio Oeste de Estados Unidos.

[Traducción del equipo editorial]

Dispersal is a significant life-history trait of vagile species that affects the distribution and genetic structure of populations (Greenwood 1980, Greenwood and Harvey 1982, Sternalski et al. 2007, Calabuig et al. 2008, Jacobsen et al. 2008, Ortego et al. 2008). Natal dispersal is the movement of an individual from its birth site to a new location where its

[1] Present address: Division of Forestry and Natural Resources, P.O. Box 6125, Morgantown, WV 26506 U.S.A.; email address: ajdennhardt@gmail.com
[2] Present address: National Park Service, Mid-Atlantic Network, 120 Chatham Lane, Fredericksburg, VA 22405 U.S.A.

first reproductive effort occurs (Greenwood 1980, Greenwood and Harvey 1982). If a breeding pair is successful in producing offspring, then those breeders are defined as effective dispersers (Greenwood and Harvey 1982). Breeding dispersal occurs when an individual moves subsequently between established breeding sites and territories (Clobert et al. 2001). The characteristics of natal dispersal significantly influence population dynamics.

Natal dispersal behavior can vary in terms of distance and frequency, according to the sex of the disperser. The phenomenon of sex-biased natal dispersal in mammal (Bradshaw et al. 2003, Höner et al. 2007, Paplinska et al. 2009) and bird (Restani and Mattox 2000, Dale 2001, Dallimer et al. 2002, Sternalski et al. 2007) populations has been well studied. Sex-biased natal dispersal may occur to avoid mate competition, to avoid inbreeding, or to reduce territorial competition for resources (Restani and Mattox 2000, Höner et al. 2007, Sternalski et al. 2007). In populations of social mammals, greater distance and frequency of natal dispersal by males may be influenced by female mate-choice (Höner et al. 2007). In contrast, most avian species exhibit female-biased natal dispersal behavior, which is thought to be influenced by resource competition among females (Greenwood 1980, Greenwood and Harvey 1982, Restani and Mattox 2000, Sternalski et al. 2007). Because Peregrine Falcons have a resource-based breeding system, whereby males acquire and defend territories, female movements should be influenced by assessments of the quality of potential breeding opportunities (Greenwood 1980, Newton and Mearns 1988, Restani and Mattox 2000, Wightman and Fuller 2006).

The Midwest Peregrine Society (MPS) was established in 1982 to facilitate regional Peregrine Falcon restoration and monitoring projects following population declines in the 1950s caused by widespread agricultural use of dichloro-diphenyl-trichloroethane (DDT; Temple 1988, Septon et al. 1995, Tordoff and Redig 1997, Brown et al. 2007, Clark et al. 2009). Using captive-bred (hereafter, hacked) stocks of nonindigenous subspecies (*F. p. tundrius, F. p. brookei, F. p. pealei, F. p. cassini*, and others) and annual monitoring (e.g., resighting and mark-recapture data), the MPS has hacked nestlings in various parts of the species' pre-DDT range (Barclay and Cade 1983, Tordoff and Redig 1997, Dzialak et al. 2005, Dzialak et al. 2006). Because hacking efforts have decreased in frequency, this midwestern population has shifted from primarily hacked to primarily wild-fledged (Redig et al. 2008). Despite information about its composition, research on the characteristics of natal dispersal in the population has been limited in recent years, particularly in regard to the influences of sex, hack-status (i.e, hacked or wild-fledged), hatch site (i.e., cliff or human-made structure), and directional movements on effective natal dispersal (hereafter, effective dispersal; Greenwood 1980). To our knowledge, an analysis by Tordoff and Redig (1997), using MPS resighting data, was the only study in which midwestern Peregrine Falcon natal dispersal was assessed in some detail. Nevertheless, their research lacked information on the breeding success of the individuals sampled. We were particularly interested in effective dispersers because such information was needed to model population growth and demography for evaluating the efficacy of further falcon reintroductions in the region (Wakamiya and Roy 2009).

Our study builds on previous research on natal dispersal by including comprehensive breeding information with dispersal records drawn from available resighting data. We were especially interested in the factors associated with natal dispersal in this recovering population. As part of a larger population viability analysis investigating the potential for Peregrine Falcon reintroductions in Illinois (Wakamiya and Roy 2009), we assessed the influence of sex, hack-status, and hatch site on natal dispersal distance and examined the directional trends of dispersal. We examined sexual differences in natal dispersal distance in order to provide new information on the dispersal characteristics of both sexes in the study region, and in addition to that, we wanted to analyze differences in natal dispersal distance as they related to both sex and hatch status. We also considered the potential influence of both an individual's sex and hatch site on its natal dispersal distance. Finally, our last objective was to evaluate any existing directional trends in the overall natal dispersal of the successful breeders in order to provide new information on patterns that could be used in future work for assessing limits on natal dispersal associated with movement direction and other factors.

METHODS

Data, Study Area, and Classification. We used resighting data (described by state, county, and general location) provided by the MPS from 1983–2006 to identify Peregrine Falcons that had dispersed and bred successfully. The MPS dataset we analyzed included information from the following states and regions: Minnesota, Wisconsin, Michigan, South Dakota, Nebraska, Iowa, Illinois, Indiana, Ohio, Kansas, Missouri, Kentucky, the Lake Superior basin of Ontario, and southeastern Manitoba (Tordoff and Redig 2001). Each bird was identified by its U.S. Fish and Wildlife Service band number, affixed during its hatch year. For the purposes of this project, we used data from 191 falcons sampled from a larger database of 492 individuals reared <250 km from the Mississippi River, which contained urban centers with >1 nesting pairs (Wakamiya and Roy 2009). Only dispersals that resulted in a successful breeding effort (fledged young in this case) were included in this analysis. This allowed us to focus exclusively on effective dispersals (Greenwood 1980), which can provide valuable insights into other factors that may be limiting effective dispersal distance (e.g., differences in habitat quality). By focusing on effective dispersers, we can identify areas that require monitoring, management, reintroduction and/or restoration efforts (e.g., midwestern cliff sites) leading to increased recovery of the population, which is essential to the conservation of the species (Kauffman et al. 2004, Wakamiya and Roy 2009). Hatch sites, sites of first breeding attempts, and reproductive outcomes (i.e., successful and unsuccessful) were available in the database, allowing us to distinguish birds that had dispersed effectively from those that had not. Individuals with unclear descriptions of natal movement (i.e., records lacking location/breeding information) and unknown reproductive outcomes were excluded from the analysis. Moreover, we did not include birds that bred at their hatch sites.

Mapping Sites and Effective Dispersal Characteristics. After identifying effective dispersers, we described hatch site and first nesting sites for each individual by the year, hack-status (hacked or wild-fledged), type of hatch site (cliff or human-made structure), county, state, and site location. Using www.topozone.com (TopoZone 1999), we estimated geographic coordinates (Universal Transverse Mercator, North American Datum-83) of the hatch site and first nesting site based on location descriptions. We then imported and mapped all locations into ArcGIS 9.3 (ESRI, Redlands, California, U.S.A.). We determined effective dispersal distance between natal and first breeding sites using the Animal Movements package in Hawth's Analysis Tools for ArcGIS 9.3 (Beyer 2004). Dispersal directions were determined using ArcGIS 9.3 software and the Azimuth between Two Points tool, provided on the Environmental Systems Research Institute (ESRI) ArcScripts website (Kimball 2004).

Data Analysis. Statistical procedures were completed with Statistical Analysis Software v. 9.2 (SAS 2011). Distributions of Peregrine Falcon dispersal data were not normal. Therefore, we compared effective dispersal distance by sex, hack-status, and type of hatch site using nonparametric Wilcoxon two-sample tests (PROC NPAR1WAY; SAS 2011). Directions of effective dispersal paths were analyzed using a Chi-square test of independence for circular distributions (Zar 2010), grouping paths into 30° bins starting with 0–30°. A rosette diagram was produced for the azimuth angles of dispersal direction and their frequencies, using Rozeta 2.0 software (Pazera 2003).

RESULTS

Sex, Hack-status, and Hatch Site. We collected natal dispersal data from 90 male and 101 female effective dispersers. Mean (±SE) distance of effective dispersal from the natal site was 170 ± 10.77 km. Minimum distance dispersed was 0.19 km (male) and maximum distance was 876.08 km (female). Of the 17 peregrines that had dispersed to cliff habitats, 13 (76%) were urban-hatched and 4 (24%) were cliff-hatched; of the 174 peregrines that dispersed to urban habitats, 5 (3%) were cliff-hatched and 169 (97%) were urban-hatched. Overall, variance in dispersal distance was higher for females (SD = 168 km, n = 101) than males (SD = 90; n = 90, $F_{100,89} = 3.49$, $P < 0.001$).

Mean dispersal distance for females (226 ± 16.70 km) was >2 times farther than that for males (108 ± 9.47 km; $P < 0.0001$). Mean distance for hacked females (283 ± 43.41 km, n = 22) did not differ from those of wild-fledged females (211 ± 17.36 km, n = 79), but suggested that hacked females may travel farther (P = 0.09). Hacked males (140 ± 19.74 km, n = 29) dispersed farther than wild-fledged males (92 ± 9.90 km, n = 61; P = 0.05). In contrast, dispersal distance among urban-hatched females (229 ± 17.28 km, n = 97) and cliff-hatched females (170 ± 45.16 km, n = 4) did not differ (P = 0.60), nor did dispersal distance of urban-hatched males (106 ± 9.95 km, n = 85) and cliff-hatched males (133 ± 19.73 km, n = 5; P = 0.26); however, sample sizes for cliff-hatched birds (by sex) were very low.

Directional Trends. As a whole, the direction of effective dispersal was nonuniformly distributed. Dispersal directions (n = 191) differed about a circular distribution ($\chi^2 = 113.12$, df = 11; $P < 0.001$),

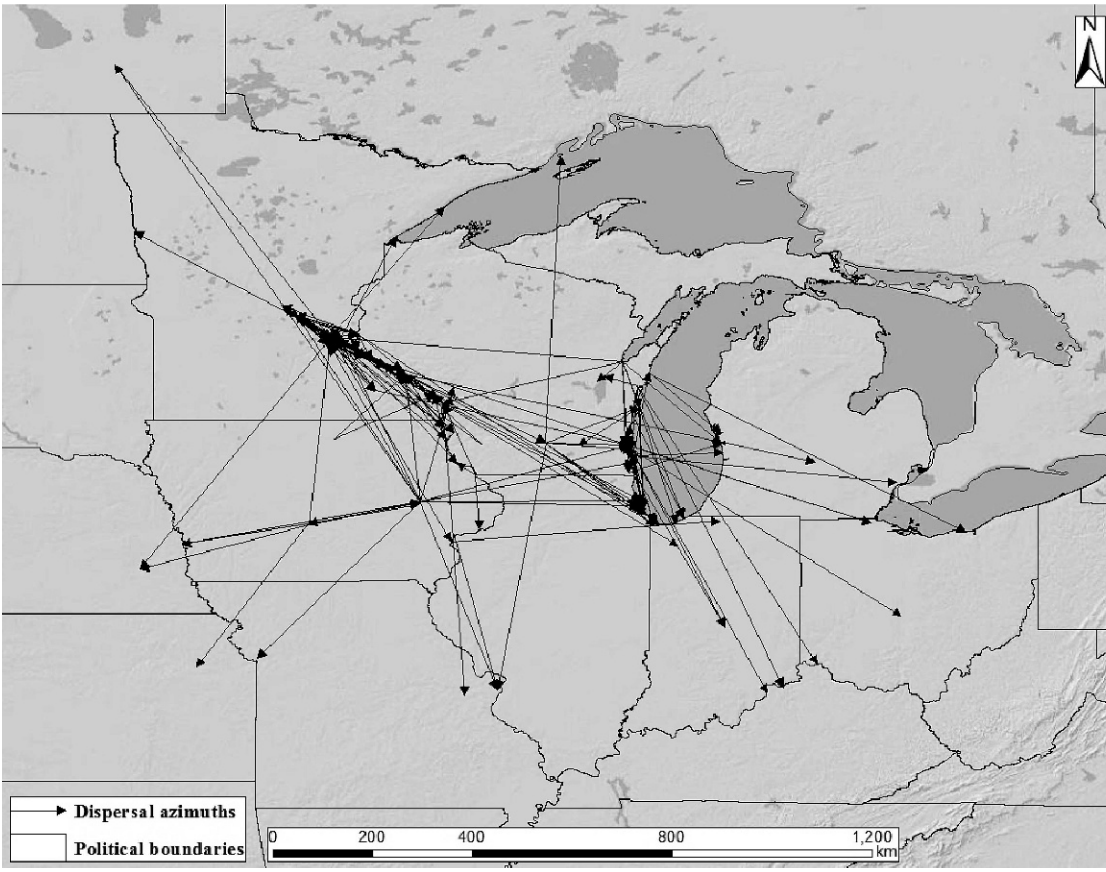

Figure 1. Dispersal directions (n = 191) of Peregrine Falcons in the midwestern United States from 1983–2006. The study was limited to falcons reared within 250 km of the Mississippi River, and only dispersals that resulted in a successful breeding effort (effective natal dispersal) were included in this analysis. Sites were plotted by UTM zone, using ArcGIS 9.3 software.

with the majority of dispersal paths directed to the northwest (270–360°) and the southeast (90–180°; Figs. 1–3). These northwesterly and southeasterly movements in dispersing peregrines appeared to be fixed toward the major urban centers of the region, along with areas near large bodies of water.

Discussion

Sex and Hack-status. Our results corroborated those of previous studies of Peregrine Falcons (Newton and Mearns 1988, Ambrose and Riddle 1988, Tordoff and Redig 1997), namely that females tended to disperse approximately two times farther than males (Table 1; Greenwood 1980, Greenwood and Harvey 1982, Restani and Mattox 2000). We also found that effective dispersal distance of hacked and wild-fledged birds differed between the sexes. We did not find significant evidence of hacked females dispersing farther than wild-fledged females; however, the result of this specific test suggested that hacked females may, in fact, travel farther than wild-females. Hacked males dispersed significantly farther than wild-fledged males, and overall variance in male dispersal distance was nearly 2 times less than that of females. This finding suggests a potential trend in male dispersal that may be related to an effective minimum distance, whereby the relative number of males with secured territories, the availability of nest sites in different habitats, and the proximity of sites to one another might be limiting the dispersal distance of male peregrines. More information on dispersal distance is still needed for identifying any differences among cliff-hatched, cliff-nesting, and urban peregrines with respect to

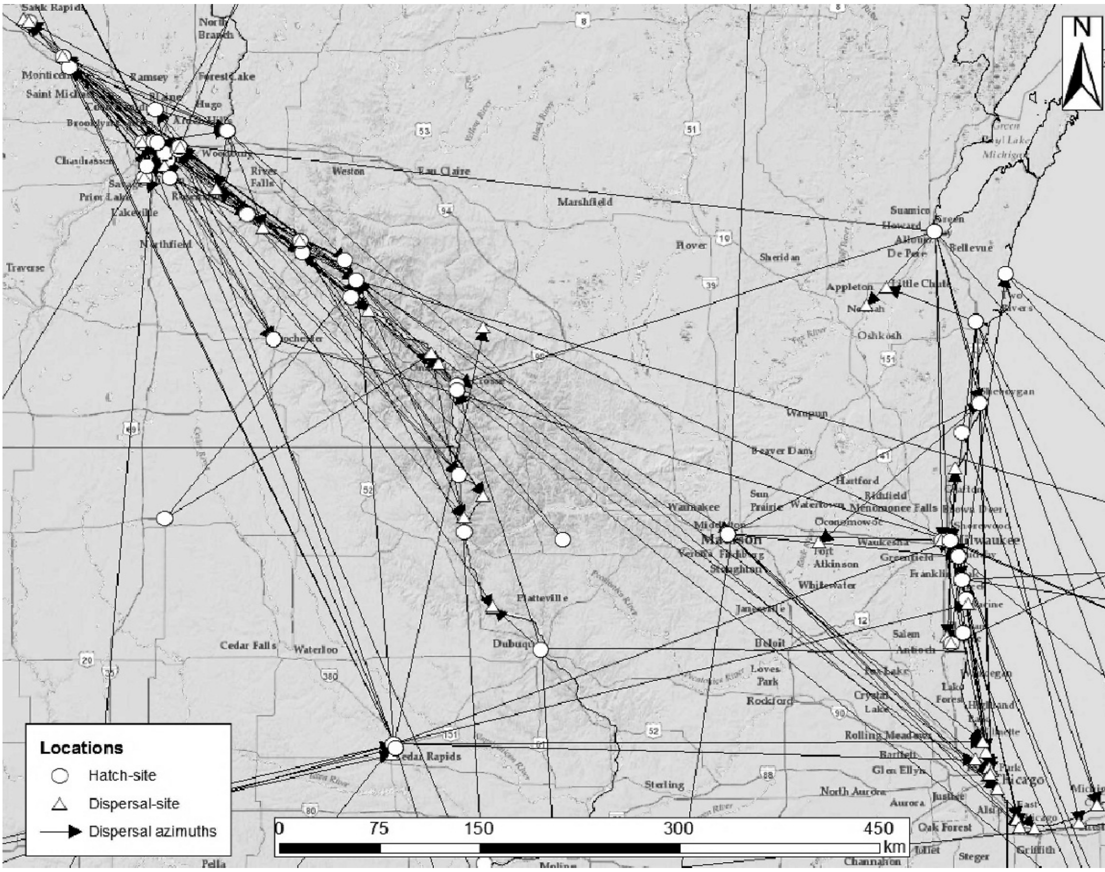

Figure 2. Enlarged view of Peregrine Falcon movements from hatch sites to effective natal dispersal sites near midwestern urban centers: Minneapolis-St. Paul (MN), Milwaukee (WI), and Chicago (IL). The study was limited to falcons reared within 250 km of the Mississippi River.

both sex and hack-status in the Midwest (Wakamiya and Roy 2009).

Hatch Site. Our analysis for site-type differences did not yield results lending support to the idea of an effect of hatch site on dispersal, and this may be attributable to small sample sizes. Therefore, the *P*-values reported for cliff-hatched birds (by sex) are of limited value for inference likely due to the fact that these particular tests had low statistical power as a result of small sample sizes (Zar 2010). Despite this fact, we did not conduct a retrospective power analysis because of fundamental flaws with the approach discussed in previous work (Hoenig and Heisey 2001). In addition, it is possible that this result may be a product of a bias in the resighting data, whereby urban birds are more likely to be seen and reported than cliff-dwelling birds. For results based on the dataset we analyzed, we do not believe that this bias is present because those individuals contributing data on both urban and rural birds are mainly regional biologists/naturalists who have detailed information on historical nest sites and who survey for new sites annually (MPS 2006). Rather, we believe that the low number of effective-dispersing, cliff-hatched birds may have much more to do with both the availability and quality of actual cliff sites in the region, although such assessments are purely qualitative at this point.

Despite the nonsignificant results of our analysis for hatch site differences, prior research suggests that hacked Peregrine Falcons may imprint to urban habitat types rather than dispersing to historical cliff habitats (Cade 1980). In fact, 92% of pairs outside the Midwestern/Northeastern region nest on natural substrates (e.g., cliff ledges, tree nests, etc.), compared to only 32% of pairs within the

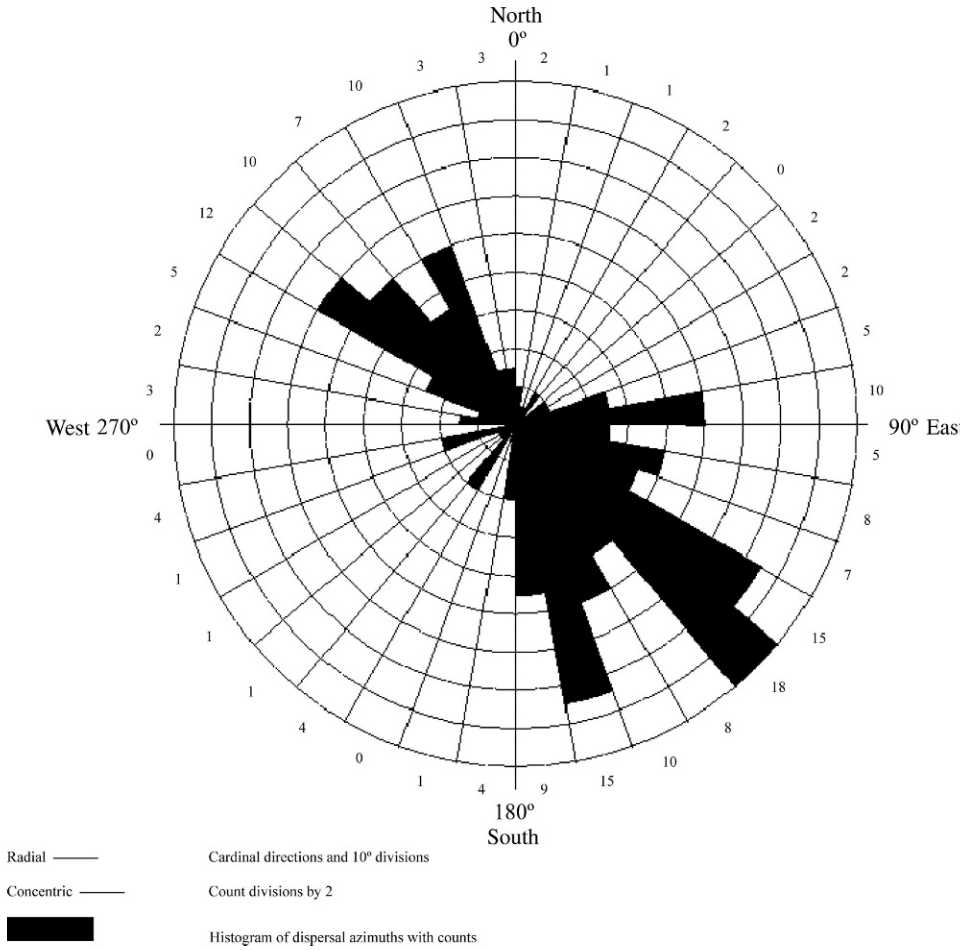

Figure 3. Rosette diagram of the frequency distribution of dispersal azimuths by Peregrine Falcons in the midwestern United States from 1983–2006. The direction of dispersal is nonuniformly distributed ($\chi^2 = 113.12$; $P < 0.0001$).

same region (McKay 2006). It has also been shown that natal dispersal distance affects the median time until occupation of new nesting habitats, including cliff sites in rural areas (Wakamiya and Roy 2009). The large number of peregrines raised in urban settings may explain why peregrines have not yet returned to many historical cliff nesting sites in the Midwest, and an analysis of site choice post-dispersal may help explain patterns of effective dispersal to different habitat types. We were unable to test differences in site choice post-dispersal between urban-hatched and cliff-hatched peregrines because we did not estimate resight probabilities, and we recognize that conducting an analysis of site choice without knowledge of such probabilities would produce unreliable results. In addition, information on the actual availability of urban and rural nesting sites would also be valuable for an analysis of site choice post-dispersal.

Dispersal Distance. Overall, the mean effective dispersal distances we report were shorter than the natal dispersal distances reported previously (Table 1; Tordoff and Redig 1997). We believe that the difference in mean dispersal distance (i.e., between both studies) could have occurred because of several different influences. First, conspecific attraction may have contributed to the difference, prompting individuals to congregate in similar areas such as urban centers. Specifically, conspecific attraction may influence dispersal distance via nonbreeding behaviors in which individuals congregate in areas with a greater abundance of food, which

Table 1. Peregrine Falcon natal dispersal distances published in previous research (1988–2000). General geographic locations are listed below each study.

STUDIES	SAMPLE SIZE (n)	DISPERSAL DISTANCE (km)	STATISTICAL RESULTS ($\alpha = 0.05$)
Ambrose and Riddle (1988) Alaska, USA	26	mean: 121 km (♀), 69 km (♂)	
Newton and Mearns (1988) Scotland	39	median: 68 km (recaptured ♀) 20 km (recaptured ♂) 83 km (resighted ♀) 58 km (resighted ♂)	$\chi^2 = 10.1, P < 0.01$ (mark-recapture falcons)
Tordoff and Redig (1997) Midwest, USA	140	mean: 354 km (♀) 174 km (♂)	$\chi^2 = 79.1, P < 0.001$ (resighted falcons)
Restani and Mattox (2000) Greenland	27	mean: 27.1 ± 4.4 km (♀) 28.1 ± 4.4 km (♂)	

(without a proper assessment of food availability differences among sites) we presume to be those urban areas with numerous, suitable nest sites (Cade 1980). It is possible that more peregrines are congregating in urban areas than they were at the time of Tordoff and Redig's (1997) study, as a result of an influence from conspecific attraction. If individuals find abundant food and nest sites in an urban area, and other birds take notice, then it would be reasonable to expect more birds to inhabit these areas in greater frequency, given enough resources and space for all. This could certainly affect mean dispersal distances, especially if individual peregrines disperse shorter distances away from natal sites in sprawling urban/suburban areas containing abundant resources and evidence of other successful breeding pairs (Cade 1980). Second, differences in reproductive rate and survivorship between urban and rural areas could through density-dependent processes, influence dispersal distances as occurs in other regions (Kauffman et al. 2003).

On its own, an increase in the number of urban sites in the Midwest relative to the number of rural sites available to peregrines could be another explanation for the difference found in mean dispersal distance. Increasing urbanization may provide additional urban nest sites, subsequently regulating dispersal distance of the birds—depending on the proximity of suitable urban habitats to one another. Similarly, Tordoff and Redig (1997) suggested that, based on the results of Ambrose and Riddle (1988), midwestern peregrines had dispersed farther than Alaskan conspecifics, because cliff habitats are more readily found in Alaska than in the midwestern U.S. However, this difference could be attributed to the migratory behavior of several Alaskan subpopulations or other factors; whereas, midwestern peregrines are mainly nonmigratory (Alderfer 2005). Finally, the mean effective dispersal distance of peregrines may be different now due to the increased number of wild-fledged vs. hacked birds, especially considering that we found that hacked birds tended to disperse farther than wild-fledged birds (within the sexes).

Directional Trends. Habitat availability and quality may influence natal dispersal corridors, as indicated by preference for northwesterly and southeasterly movements in dispersing peregrines. Directional trends could also be explained by geographic landmarks, most notably by metropolitan areas such as the Minneapolis-St. Paul region (Fig. 1). Peregrines in this urban area appear to have dispersed along the Mississippi River corridor, which runs from the northwest to the southeast in the region. West of the Mississippi River, peregrines dispersed to the northwest and southeast, perhaps toward urban habitats around Chicago, Illinois or Milwaukee, Wisconsin (Fig. 2). These findings corroborated a well-known preference for peregrines to nest near bodies of water, such as on Lake Michigan near Chicago and Milwaukee (Mearns and Newton 1984, Restani and Mattox 2000, Powell et al. 2002, Wightman and Fuller 2006). The spatial distribution of urban habitats in the midwest may also influence the directions of dispersing peregrines, considering the locations of urban centers such as Chicago, Illinois; Minneapolis-St. Paul, Minnesota; St. Louis, Missouri; Milwaukee, Wisconsin, and others. At least in one example, Minneapolis-St. Paul and Chicago are relatively northwest and southeast of each other, respectively. In addition, previous research suggests that the advantageous qualities (e.g., abundant prey, few predators, protective shelter, etc.) of urban habitats would cause a subsequent decrease in the percentage of rural occupants in regional subpopulations (Cade 1980).

Summary. The Peregrine Falcon population in the Midwest is gradually recovering throughout its historical range. Natal dispersal in this subpopulation is influenced by sex and hack-status, and the directions of dispersal movements are directed northwest and southeast on average, often toward urban centers and areas with large bodies of water. Recolonization to rural cliff habitats is low; however, this might be attributable to lower resighting rates or effects of low habitat quality. Moreover, our work demonstrates the value of gathering post-monitoring (e.g., resighting) data in the management, study, and recovery of animal species, especially raptors (Jenny et al. 2004, Steenhof et al. 2005, Brown et al. 2006, Wakamiya and Roy 2009). Detailed resighting data can be used to identify effective natal dispersal in peregrines, providing opportunities for identifying important local areas from success rates and assessing other population-level demographic parameters. We recommend additional research assessing available urban and rural nest sites, site choices post-dispersal, and real differences in habitat quality and how these affect natal dispersal patterns. Such research will benefit future analyses of peregrine demographics and help further the recovery of the species throughout its range.

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