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NATAL AND BREEDING DISPERSAL IN BARN OWLS

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ABSTRACT.—I studied dispersal of the Barn Owl (*Tyto alba*) in northern Utah from 1977–96. Based on 144 recoveries of 2085 banded nestlings, the average dispersal distance was 102.9 km (median = 60 km, range = 0–1267 km), occurred in most compass directions from natal sites, but was not random with mountains, deserts, and the Great Salt Lake altering dispersal routes. Dispersal distance was not correlated with severity of winter weather nor population density. Among owls banded as nestlings and recaptured as breeders, females ($N = 48$) moved significantly farther ($\bar{x} = 61.4$ km, median = 57.5 km, range = 0–160 km) than males ($N = 34$, $\bar{x} = 35.7$ km, median = 14.7 km, range = 0.8–120 km, $P = 0.015$). Turnover of breeders at nest sites resulted mostly from individuals dispersing into the study area. Only 19 (of at least 500) breeders moved from one breeding site to another. The mean distance moved between breeding sites of 2.3 km (median = 2.25 km) was not significantly different between males and females ($P = 0.9$), but more females (16) than males (3) made these moves. Eight of the adults that shifted breeding sites did so in the same year either after a failed first attempt (2) or to produce a second brood (6). The remainder changed nest sites in subsequent years.

KEY WORDS: *Barn Owl;* Tyto alba; *breeding dispersal; long-term study; natal dispersal; Utah.*

Dispersión natal y reproductiva de *Tyto alba*

RESUMEN.—Estudié la dispersión de *Tyto alba* en el norte de Utah desde 1977–96. Con base en 144 recapturas de 2085 pichones anillados, encontré que la distancia de dispersión fue de 102.9 km (media = 60 km, rango = 0–1267 km), ocurridas en todas las direcciones desde el sitio de nacimiento. Esta situación no ocurrió al azar en montañas, desiertos y el Great Salt Lake los cuales alteraron las rutas de dispersión. La distancia de dispersión no estuvo correlacionada con la severidad del clima invernal, ni con la densidad poblacional. Entre las lechuzas anilladas como pichones y recapturadas como reproductores, las hembras ($N = 48$) se movilizaron significativamente mas lejos ($\bar{x} = 61.4$ km, media = 57.5 km, rango = 0–160 km) que los machos ($N = 34$, $\bar{x} = 35.7$ km, media 14.7 km, rango = 0.8–120 km, $P = 0.015$). El regreso de los reproductores a los sitios de los nidos, fue el resultado de individuos dispersados dentro del área de estudio. Sólo 19 (de por lo menos 500) reproductores se movilizaron de un sitio de reproducción a otro. La distancia promedio recorrida entre los sitios de reproducción fué de 2.3 km (media = 2.25 km). Esta distancia no fue significativamente diferente entre machos y hembras ($P = 0.9$). Mas hembras (16) que machos (3) hicieron estos movimientos. Ocho de los adultos que cambiaron sus sitios de reproducción lo hicieron en el mismo año despues de fracasar en un primer intento (2) o para producir una segunda nidada (6). El resto cambió el sitio del nido en los años subsecuentes.

[Traducción de César Márquez]

The Barn Owl (*Tyto alba*) is among the most widespread of land birds, and although some aspects of its biology closely resemble other owls (e.g., trophic biology), other attributes are strikingly different. Among the important disparities are aspects of the Barn Owl's reproductive biology and life-history (Marti 1997). Here, I show that dis-

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persal in Barn Owls conforms with the species' r-selected life-history strategy (reproduction at an early age, short reproductive life, high reproductive output, and an ability to find new resources—sometimes at great distances—through natal dispersal), but also fits some patterns of dispersal that are widespread in other birds.

Dispersal is a very important but poorly understood element of population biology (Begon et al. 1990). Dispersal may be either natal—the one-way movement by an individual from its birthplace to a breeding (or potential breeding) site, or breeding—the movement by adults between breeding sites. Natal dispersal usually covers greater distances than breeding dispersal (Greenwood and Harvey 1982). Advantages attributed to natal dispersal include reducing the chance of inbreeding, reducing competition, and extending the range (Greenwood 1983, Swingland 1983). In many bird species, dispersal patterns differ between adults and juveniles and between males and females (Greenwood 1983, Greenwood and Harvey 1982).

Relatively few studies of dispersal have been conducted on raptors. See for example, Newton (1979) and references within, Newton (1986) and Ferrer (1993) for European diurnal raptors, and Korpimäki et al. (1987), Korpimäki (1988), Korpimäki and Lagerström (1988), and Coles and Petty (1997) for European owls. In North America, see Jacobs (1995), Woodbridge et al.(1995), Steenhof et al. 1984, and Miller and Smallwood (1997) for diurnal raptors, and VanCamp and Henny (1975), Adamcik and Keith (1978), Marks (1985), Bull et al. (1988), Belthoff and Ritchison (1989), Ganey et al. (1998), Gehlbach (1994), and Arsenault et al. (1997) for owls.

Dispersal in Barn Owls has been studied in North America (Stewart 1952), Europe (Frylestam 1972, Schönfeld 1974, Glutz von Blotzheim 1979, Bairlein 1985, Baudvin 1986, Chanson et al. 1988, Taylor 1994, Martínez and López 1995), and to a very minor extent in Australia (Purchase 1972). Only Taylor (1994) presented data on both the dispersal of nestlings to breeding sites and movements of adults between nest sites.

Previously, I documented the reproductive pattern (Marti 1994) and lifetime reproductive success (Marti 1997) in a Barn Owl population breeding close to the northern limit of its range. Here, I present dispersal patterns in the same population, test whether sex and age differences in dispersal occurred and look for support that dispersal reduces inbreeding.

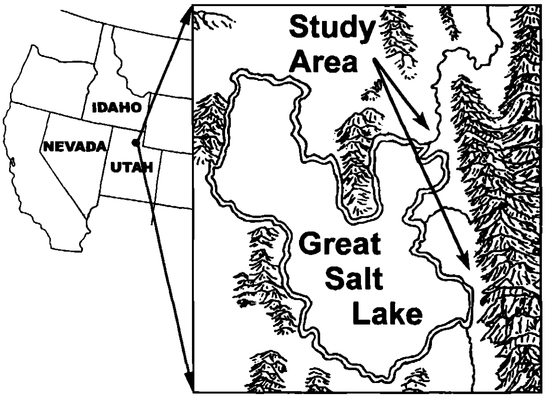

Figure 1. Location and topographic features of Barn Owl study area in northern Utah.

STUDY AREA AND METHODS

The study area was a narrow (12–25 km wide, 500 km^2) valley lying between the Wasatch Mountains and the Great Salt Lake in Box Elder, Weber, and Davis counties of northcentral Utah (Fig. 1) that is close to the Barn Owl's northern range limit in the Intermountain Region (Marti 1992). The area was shrubsteppe desert but that community has been entirely supplanted by irrigated agriculture and urban development. Hot dry summers and cold winters characterize the region; mean temperatures for July and January are 23.9°C and −3.5°C, respectively.

Barn Owl nesting habitat is limited and disjunct in this area; most Barn Owls nest in lower elevation valleys where irrigated agriculture occurs. Rugged mountains and high elevation valleys immediately east of the study area were unsuitable Barn Owl habitat, and, likewise, the Great Salt Lake and alkali deserts to the west of the study area offered little habitat for Barn Owls. See Marti (1994) for more details on the study area and owl nest sites.

Most of the Barn Owls on my study area nested in nest boxes (Marti et al. 1979). From 1977–96, I visited these nest boxes year-round at least once per month. I made additional visits as needed to band and color mark nestlings and adults with a standard USGS aluminum band and a combination of colored plastic bands unique to each bird (two bands per leg) permitting identification of individuals without having to recapture them. Few other suitable nest sites existed on the study area, but owls occasionally nested in buildings and hay stacks. These were often reported to me by farmers or by owners of buildings having various problems caused by the nesting owls. Thus, I was able to document nesting in these sites as well.

I attempted to capture all breeding owls each year to determine their identity, age, and movements. Most females and some males were caught by hand in nest boxes but, because males were less often found in nest boxes, I sometimes used nest-box traps to capture them (Sau-

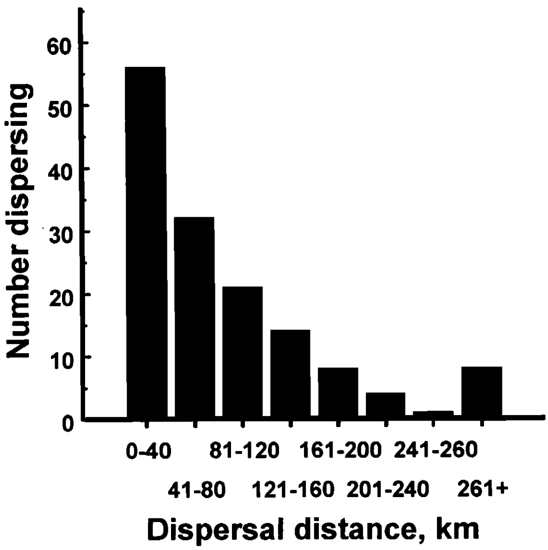

Figure 2. Dispersal distances in Barn Owls banded as nestlings in northern Utah.

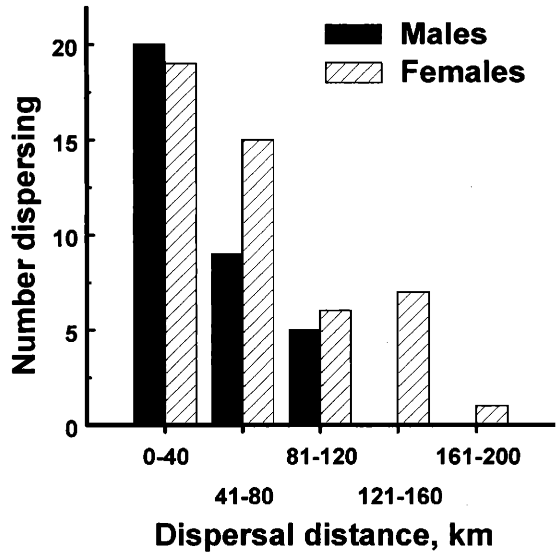

Figure 3. Comparison of dispersal distances between breeding male and female Barn Owls banded as nestlings in northern Utah.

rola 1987). For breeding owls not banded as nestlings, age was determined by wing-molt pattern. Barn Owls do not molt any primaries until 13 months of age (P. Bloom pers. comm., Lenton 1984, Taylor 1993). Thus, in the spring, breeding owls with one generation of primaries are in their first year of life, and those with two generations of primary feathers are at least 2-yr old. I also included data from some nestling owls that I banded on a site similar to my study area located in Cache County, Utah. Similarly, I used data from several Barn Owls banded as nestlings by the Utah Division of Wildlife Resources in Utah County, Utah and recaptured in my study area. Barn Owls were nonmigratory in northern Utah as they appear to be in most if not all other parts of the species' range (Schneider 1937, Cramp 1985, Taylor 1994).

Statistical analyses (t-tests and linear correlation) were performed using the Statistical Analysis System (SAS Inst. 1988). Rayleigh's test was used to check for uniformity in direction of owl dispersal after the data were transformed into unimodal data (Zar 1984). Alphas for all tests were 0.05 and all tests were two-tailed.

RESULTS

Natal Dispersal. I banded 2085 nestlings (locals in USGS Bird Banding Laboratory terminology), 384 breeding adults (adults) and 161 fledglings (hatch year) from 451 nesting attempts by at least individual Barn Owls. To exclude birds that may have died before completing their dispersal, only those that were recovered >6 mo after fledging or after they began breeding were included in the following analyses.

Of those banded as nestlings, 144 (6.9%) were recovered (either found dead or identified alive) at an average of 102.9 ± 162.03 (±SD) km from their natal sites (median = 60 km, range = 0–1267 km; Fig. 2). Among owls banded as nestlings and recaptured as breeders, females (N = 48) moved significantly farther ($\bar{x}$ = 61.4 ± 52.04 km, median = 57.5 km, range = 0–160 km) than males (N = 34, $\bar{x}$ = 35.7 ± 36.61 km, median = 14.7 km, range = 0.8–120 km; t = 2.48, df = 80, P = 0.015, power = 0.66; Fig. 3). One female nested in her natal site and two siblings that dispersed only 8 km from their natal site paired and raised young.

Sixty-two owls banded as nestlings were found dead off the study area at distances of 7–1267 km ($\bar{x}$ = 171.98 ± 223.63 km, median = 109 km) from their natal sites. Sex was determined for only 17 of these and dispersal distances were not significantly different between sexes in this small sample (female, N = 8, $\bar{x}$ = 93.5 ± 63.5 km, median = 110.3, range = 7–167 km; male, N = 9, $\bar{x}$ = 94.2 ± 90.44 km, median = 52, range = 7–221 km; t = 0.02, df = 15, P = 0.98, power = 0.98).

Owls dispersed in all compass directions from their natal sites (Fig. 4), but the pattern of dispersal direction was not random (Rayleigh's z = 38.43, P < 0.0005, N = 82). The local topography (Fig. 1) caused many owls to move either to the north, northwest or to the south, southeast. Those

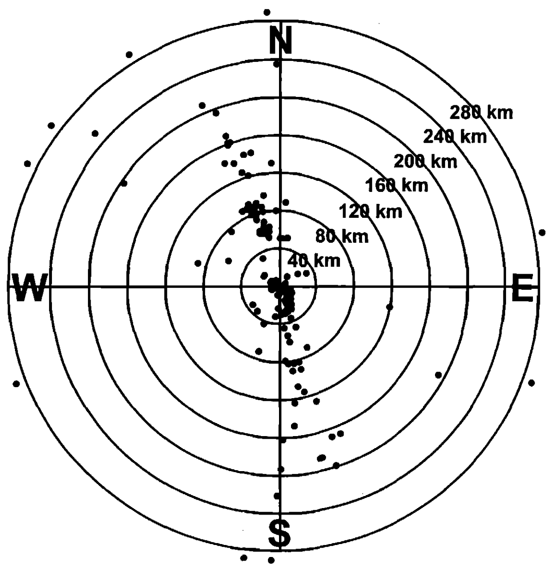

Figure 4. Direction and distance of natal dispersal in Barn Owls in northern Utah.

Figure 5. Long-distance natal dispersal by Barn Owls banded as nestlings in a northern Utah population.

that moved beyond the local topographic features dispersed in all directions (Fig. 5). No relationship was found between the year of fledging and the distance of dispersal (r = −0.08, P = 0.37, N = 135, power = 0.54). Likewise, the severity of a winter (based on ambient temperature and depth and persistence of snow cover) was not significantly correlated with dispersal distance (r = 0.07, P = 0.42, N = 137, power = 0.47). Population density on the study area did not appear to be a factor either; even though numbers of fledglings varied greatly among years (Marti 1994), the number fledged in a year was not correlated with the distance of dispersal (r = −0.01, P = 0.89, N = 18, power = 0.89). The distance moved from natal site to breeding site was not significantly correlated with lifetime breeding success in a 19-yr interval (success = number of young fledged in lifetimes [Marti 1997]; r = 0.11, P = 0.32, N = 82, power = 0.70).

Unbanded birds that became breeders on my study area provided a measure of dispersal into the area. On average, turnover of breeders at nest sites was 48.1% (range = 21.4–75.0%/yr), mostly individuals dispersing into the study area. Only 23.3% of first-time breeders had been banded as nestlings on the study area (range = 0–93.8%/yr). The remaining 76.7% (range = 6.2–100%/yr) were unbanded, apparently having been raised outside the study area (Fig. 6). The nearest known breeding populations were 100 km to the south and >100 km to the north and northwest.

Breeding Dispersal. Nineteen of at least 500 breeders dispersed from one breeding site to another. The mean distance moved between breeding sites, 2.28 ± 1.77 km (median = 2.25, range = 0.1–6.2 km), did not differ significantly between males and females, but >5 times as many females made those moves (female, N = 16, $\bar{x}$ = 2.3 ± 1.63 km, median = 2.3, range = 0.1–6.2 km; male, N = 3, $\bar{x}$ = 2.17 ± 2.87 km, median = 0.5, range = 0.5–5.5 km; t = 0.12, df = 17, P = 0.90). Eight of the adults shifted breeding sites in the same year either after a failed first attempt (N = 2) or to produce a second brood following a successful first one (N = 6). The others changed nest sites in subsequent years.

DISCUSSION

The natal dispersal that I observed followed a pattern similar to that seen in other Barn Owl populations (Taylor 1994) with young dispersing soon after fledging and making one-way movements in any direction from the natal site subject to geographic constraints. Distances were usually about 60 km but the longest exceeded 1000 km. Adults, in contrast, tended to be sedentary, rarely moving far from their breeding sites.

Stewart (1952) analyzed all banded Barn Owls recovered to 1950 in the U.S. Nestlings banded south of 35°N were all recovered within 144 km of the banding site. Those banded north of 35°N moved farther: 61% moved >80 km, 28% >320 km and 1% >1600 km. Dispersal, even in the north, was in all directions. Other Barn Owls have been

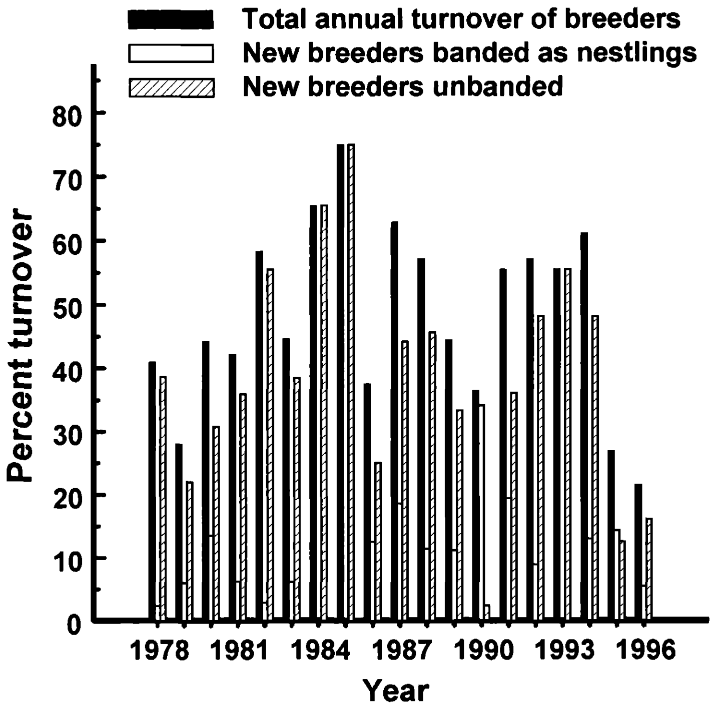

Figure 6. Annual turnover rates of breeding Barn Owls in northern Utah.

recovered in the U.S. after the 1950s over >1000 km from their banding sites (Broun 1954, Mueller and Berger 1959, Bolen 1978, Soucy 1985).

In the United Kingdom, natal dispersal was relatively short; only one individual banded as a nestling in Scotland moved >20 km to a breeding site (Taylor 1994) and the longest dispersals were <200 km (Bunn et al. 1982). In continental Europe, dispersals >1000 km were reported from Barn Owl populations in France (Baudvin 1986) and Switzerland (Glutz von Blotzheim 1979). Over 50% of nestlings banded in Germany bred at distances <50 km from their site of birth, but 24% were recovered at distances >100 km (Bairlein 1985); movements were shorter in high vole years than in low vole years (Schönfeld 1974). In Spain, natal dispersal covered significantly greater distances than did breeding dispersal (Martínez and López 1995). Natal dispersal occurred in all compass directions in Europe, even in Scandinavia (Frylestam 1972) which, like Utah, is at the northern edge of the Barn Owl's range. In Australia, two nestlings were recovered 250 and 840 km from their nests (Purchase 1972).

Dispersal studies of other raptors reveal many similarities. Newton (1979) noted that numerous diurnal raptors in Europe rarely dispersed >50 km and that females dispersed farther than males. The most comprehensive study of dispersal in a diurnal raptor was Newton's (1986) study on the Sparrowhawk (*Accipiter nisus*). Female Sparrowhawks dispersed significantly farther from their natal areas than did males and both sexes moved in all directions. Most of the natal dispersal occurred in late summer, and population density did not seem to affect dispersal. Dispersal distances were shorter than in Barn Owls (<1–265 km) and 75% settled within 20 km of their natal site. Newton did not record any inbreeding in Sparrowhawks. Breeding dispersal by Cooper's Hawks (*Accipiter cooperii*) also resembled the pattern I found in Barn Owls. Male Cooper's Hawks did not change breeding sites, but a few females moved short distances to new sites (Rosenfield and Bielefeldt 1996).

American kestrels (*Falco sparverius*) in Florida dispersed out of their natal territories but distances were short (71% were <8 km) and the sexes did not differ significantly in distance (Miller and Smallwood 1997). In Wisconsin, natal dispersal by kestrels was much greater and males dispersed farther than females (Jacobs 1995). Natal dispersal was not sex-biased in Lesser Kestrels (*Falco naumanni*) and 57% settled to breed in their natal colonies. Those that dispersed moved on average only 18.5 km (Negro et al. 1997). Swainson's Hawks (*Buteo swainsoni*) moved on average just 8.2 km (0–18.1 km) between natal and breeding sites and distances were not significant between the sexes (Woodbridge et al. 1995). Natal dispersal in a small sample of Ospreys (*Pandion haliaetus*) averaged 441 km (Johnson and Melquist 1991).

Dispersal in owls has not been well documented, but most other species appear to move shorter distances in natal dispersal than do Barn Owls. Median distance moved by radio-tagged Eastern Screech-Owls (*Otus asio*) from natal sites was only 4.4 km (0.4–16.9) (Belthoff and Ritchison 1989). Also in Eastern Screech-Owls, Gehlbach (1994) recorded a mean natal dispersal of 3.2 km, but VanCamp and Henny (1975) gave 32 km as the mean natal dispersal distance. However, about half of their birds dispersed <16 km. Mean dispersal by Great Gray Owls (*Strix nebulosa*) was 18.5 km (7.5–32; Bull et al. 1988), but Tengmalm's Owls (*Aegolius funereus*) in Finland dispersed on average 55–70 km (0–320 km) depending on the stage of the vole population cycle (Korpimäki and Lagerström 1988). Great Horned Owl (*Bubo virginianus*) fledglings from northern populations moved up to 1305 km from their nests but 53% were recovered within 25 km (Adamcik and Keith 1978). A few male Long-eared Owls (*Asio otus*) were known to nest within 2.0 km of their natal nest, but females apparently dispersed farther than males before nesting (Marks et al. 1994). Dispersal in Spotted Owls (*Strix occidentalis*), despite recent intense study of the species' biology, is poorly known. Arsenault et al. (1997) and Ganey et al. (1998) radiotracked fledgling Mexican Spotted Owls to distances of 2.1–73.5 km, but only one individual was tracked to a breeding territory at 5.8 km from its natal site. Dispersing juvenile Northern Spotted Owls were tracked from 20–98 km, but none were traced to a breeding territory (Gutiérrez et al. 1985).

Distance and direction of the natal dispersal I found in northern Utah were effective in reducing inbreeding. The only known inbreeding in my population occurred when dispersal distance was short and siblings from the same brood paired and raised young. Another female bred in her natal site but her mate was not identified. Shaw and Dowell (1989) found one instance of pairing between siblings that moved only 5.4 km from their natal site, and another between a mother and son. Incest and close inbreeding have been reported only rarely in other raptors (VanCamp and Henny 1975, Bowman et al. 1987, James et al. 1987, Postupalsky 1989, Millsap and Bear 1990, Rosenfield and Bielefeldt 1992, Taylor 1994, Gutiérrez et al. 1995, and Carlson et al. 1998). It is not clear whether this low level of reported inbreeding is due to the difficulty of detecting it or to a truly low level of occurrence.

Natal dispersal may aid in range expansion and repopulation of areas where extinction has occurred. The Barn Owls' ability for long-distance dispersal coupled with their versatility in nest-site and foraging habitat have permitted them to expand their range particularly in response to human-caused habitat changes (Brown 1971, Reese 1972, Stewart 1980, Lenton 1985, McLarty 1995). Barn Owls probably did not nest on my study area until humans provided nesting places (buildings) and increased food availability through irrigated agriculture.

Even though I document long-distance movements by Barn Owls out of my study area, I do not have any data on the reproductive success of those individuals. However, several individuals that were banded as nestlings made long-distance movements out of my study area and were recovered several years later (one 12-yr old), making it likely that they did reproduce. Martínez and López (1995) considered long-distance dispersal by Barn Owls in Spain to be a disadvantage, and Newton and Marquiss (1983) showed that reproductive success for Sparrowhawks that dispersed furthest was less than those that moved shorter distances. I have considerable data on reproduction by individuals dispersing into my area, but no knowledge of the origin of most of them.

Dispersal may also speed the flow of genes among breeding populations, but almost nothing is known about this in Barn Owls or other raptor species. McLarty (1995) compared genetic similarity among three Barn Owl populations in British Columbia, northern Utah and southern California, and found sufficient genetic differences to suggest that little gene flow occurs between these populations. Utah and California populations were more similar to each other than the British Columbia population was to either suggesting more east-west than south-north movement by dispersing owls. The British Columbia population is at the northern limit of the species' range and is of relatively recent origin.

My results offer little evidence that natal dispersal relieves competition because I have reproductive data only on birds that moved relatively short (for Barn Owls) distances between natal and breeding sites. I was able to show that lifetime reproductive success was not related to distance of dispersal up to the dispersal distances I was able to track, and that dispersal distance was not related to population density.

Dispersal in Barn Owls in northern Utah conformed to the patterns seen in many birds with natal dispersal covering much greater distances than breeding dispersal, and females dispersing farther than males. Natal dispersal apparently was effective in reducing inbreeding, because the distance and randomness of the direction of natal dispersal made pairings by close relatives unlikely.

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LITERATURE CITED

ADAMCIK, R.S. AND L.B. KEITH. 1978. Regional movement and mortality of Great Horned Owls in relation to snowshoe hare fluctuations. *Can. Field-Nat.* 92:228–234.

ARSENAULT, D.P., A. HODGSON AND P.B. STACEY. 1997. Dispersal movements of juvenile Mexican Spotted Owls (*Strix occidentalis lucida*) in New Mexico. Pages 47–57 *in* J.R. Duncan, D.H. Johnson and T.H. Nicholls [EDS.], Biology and conservation of owls on the northern hemisphere. USDA For. Serv. Gen. Tech. Rep. NC-190, St. Paul, MN U.S.A.

BAIRLEIN, F. 1985. Dismigration und Sterblichkeit in Süddeutschland beringter Schleiereulen (*Tyto alba*). *Vogelwarte* 33:81–108.

BAUDVIN, H. 1986. La reproduction de la Chouette effraie (*Tyto alba*). *Le Jean-le-Blanc* 25:1–125.

BEGON, M., J.L. HARPER AND C.R. TOWSEND. 1990. Ecology, individuals, populations, and communities. Blackwell Sci. Publ., Boston, MA U.S.A.

BELTHOFF, J.R. AND G. RITCHISON. 1989. Natal dispersal of Eastern Screech-Owls. *Condor* 91:254–265.

BOLEN, E.C. 1978. Long-distance displacement of two southern Barn Owls. *Bird-Banding* 49:78–79.

BOWMAN, R., J.R. DUNCAN AND D.M. BIRD. 1987. Dispersal and inbreeding avoidance in the American Kestrel: are they related? Pages 145–150 *in* D.M Bird and R. Bowman [EDS.], The ancestral kestrel. Raptor Res. Rep. No. 6, Raptor Research Foundation, Hastings, MN U.S.A.

BROUN, M. 1954. Long-distance recovery of Barn Owl. *Bird-Banding* 25:149.

BROWN, L. 1971. African birds of prey. Houghton Mifflin, Boston, MA U.S.A.

BULL, E.L., M.G. HENJUM AND R.S. ROHWEDER. 1988. Home range and dispersal of Great Gray Owls in northeastern Oregon. *J. Raptor Res.* 22:101–106.

BUNN, D.S., A.B. WARBURTON AND R.D.S. WILSON. 1982 The Barn Owl. T. & A.D. Poyser, Calton, U.K.

CARLSON, P.D., W.S. LAHAYE AND A.B. FRANKLIN. 1998. Incestuous behavior in Spotted Owls. *Wilson Bull.* 110: 562–564.

CHANSON, J.M., P. COURBET, P. GIRAUDOUX, G. MICHAUD AND D. MICHELAT. 1988. Étude sur la reproduction et les déplacements de la Chouette effraie (*Tyto alba*) en Franche-Comté: réflexions méthodologiques. *Alauda* 56:197–225.

COLES, C.F. AND S.J. PETTY. 1997. Dispersal behavior and survival of juvenile Tawny Owls (*Strix aluco*) during the low point in a vole cycle. Pages 111–118 *in* J.R. Duncan, D.H. Johnson and T.H. Nicholls [EDS.], Biology and conservation of owls on the northern hemisphere. USDA For. Serv. Gen. Tech. Rep. NC-190, St. Paul, MN U.S.A.

CRAMP, S. [ED.]. 1985. Handbook of the birds of Europe, the Middle East and North Africa, Vol. 4. Oxford Univ. Press, Oxford, U.K.

FERRER, M. 1993. Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* 135:132–138.

FRYLESTAM, B. 1972. Über Wanderungen und Sterblichkeit beringter skandinavischer Schleiereulen *Tyto alba*. *Ornis Scand.* 3:45–54.

GANEY, J.L., W.M. BLOCK, J.K. DWYER, B.E. STROHMEYER AND J.S. JENNESS. 1998. Dispersal movements and survival rates of juvenile Mexican Spotted Owls in northern Arizona. *Wilson Bull.* 110:206–217.

GEHLBACH, F.R. 1994. Eastern Screech-Owl *Otus asio*: life history, ecology and behavior in suburbia and the countryside. Texas A&M Univ. Press, College Station, TX U.S.A.

GLUTZ VON BLOTZHEIM, U.N. 1979. Zur Dismigration junger Schleiereulen *Tyto alba*. *Ornithol. Beob.* 76:1–7.

GREENWOOD, P.J. 1983. Mating systems and the evolutionary consequences of dispersal. Pages 116–131 *in* I.R. Swingland and P.J. Greenwood [EDS.], The ecology of animal movement. Clarendon Press, Oxford, U.K.

——— AND P.H. HARVEY. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* 13:1–21.

GUTIÉRREZ, R.J., A.B. FRANKLIN AND W. LAHAYE. 1995. Spotted Owl (*Strix occidentalis*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 17. Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.

———, ———, ———, V.J. MERETSKY AND J.P. WARD. 1985. Juvenile Spotted Owl dispersal in northwestern California: preliminary results. Pages 60–65 *in* R.J. Gutiérrez and A.B. Carey [TECH. EDS.], Ecology and management of the Spotted Owl in the Pacific Northwest. USDA For. Serv. Gen. Tech. Rep. PNW-185, Portland, OR U.S.A.

JACOBS, E.A. 1995. American Kestrel reproduction and dispersal in central Wisconsin. *J. Raptor Res.* 29:135–137.

JAMES, P.C., L.W. OLIPHANT AND I.G. WARKENTIN. 1987. Close inbreeding in the Merlin (*Falco columbarius*). *Wilson Bull.* 99:718–719.

JOHNSON, D.R. AND W.E. MELQUIST. 1991. Wintering distribution and dispersal of northern Idaho and eastern Washington Ospreys. *J. Field Ornithol.* 62:517–520.

KORPIMÄKI, E. 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's Owl. *J. Anim. Ecol.* 57:97–108.

——— AND M. LAGERSTRÖM. 1988. Survival and natal dispersal of fledglings of Tengmalm's Owl in relation to fluctuating food conditions and hatching date. *J. Anim. Ecol.* 57:433–441.

———, ——— AND P. SAUROLA. 1987. Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. *Ornis Scand.* 18:1–4.

LENTON, G.M. 1984. The feeding and breeding ecology of Barn Owls *Tyto alba* in peninsular Malaysia. *Ibis* 126: 551–575.

———. 1985. History, distribution and origin of Barn Owls *Tyto alba* in the Malay peninsula. *Bull. Br. Ornithol. Club* 105:54–58.

MARKS, J.S. 1985. Yearling male Long-eared Owls breed near natal nest. *J. Field Ornithol.* 56:181–182.

———, D.L. EVANS AND D.W. HOLT. 1994. Long-eared Owl (*Asio otus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 133. Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.

MARTI, C.D. 1992. Barn Owl (*Tyto alba*). *In* A. Poole, P. Stettenheim and F. Gill [EDS.], The birds of North America, No. 1. Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.

———. 1994. Barn Owl reproduction: patterns and variation near the limit of the species' distribution. *Condor* 96:468–484.

———. 1997. Lifetime reproductive success in Barn Owls near the limit of the species' range. *Auk* 114:581–592.

———, P.W. WAGNER AND K.W. DENNE. 1979. Nest boxes for the management of Barn Owls. *Wildl. Soc. Bull.* 7: 145–148.

MARTÍNEZ, J.A. AND G. LÓPEZ. 1995. Dispersal and causes of mortality of the Barn Owl (*Tyto alba*) in Spain. *Ardeola* 42:29–37.

MCLARTY, J.R. 1995. Genetic variation in three North American Barn Owl (*Tyto alba*) populations using DNA fingerprinting. M.S. thesis, Univ. British Columbia, Vancouver, B.C. Canada.

MILLER, K.E. AND J.A. SMALLWOOD. 1997. Natal dispersal and philopatry of southeastern American Kestrels in Florida. *Wilson Bull.* 109:226–232.

MILLSAP, B.A. AND C. BEAR. 1990. Double-brooding by Florida Burrowing Owls. *Wilson Bull.* 102:313–317.

MUELLER, H.C. AND D.D. BERGER. 1959. Some long distance Barn Owl recoveries. *Bird-Banding* 30:182.

NEGRO, J.J., F. HIRALDO AND J.A. DONAZAR. 1997. Causes of natal dispersal in the Lesser Kestrel: inbreeding avoidance or resource competition? *J. Anim. Ecol.* 53: 901–912.

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

———. 1986. The Sparrowhawk. T. & A.D. Poyser, Calton, U.K.

——— AND M. MARQUISS. 1983. Dispersal of Sparrowhawks between birthplace and breeding place. *J. Anim. Ecol.* 52:463–477.

POSTUPALSKY, S. 1989. Inbreeding in Ospreys. *Wilson Bull.* 101:124–126.

PURCHASE, D. 1972. A report on the banding of Barn Owls. *Aust. Bird Bander* 10:74–75.

REESE, J.G. 1972. A Chesapeake Barn Owl population. *Auk* 89:106–114.

ROSENFIELD, R.N. AND J. BIELEFELDT. 1992. Natal dispersal and inbreeding in the Cooper's Hawk. *Wilson Bull.* 104:182–184.

——— AND ———. 1996. Lifetime nesting area fidelity in male Cooper's Hawks in Wisconsin. *Condor* 98:165–167.

SAS INSTITUTE, INC. 1988. SAS/STAT user's guide: statistics. SAS Institute, Inc., Cary, NC U.S.A.

SAUROLA, P. 1987. Mate and nest-site fidelity in Ural and Tawny Owls. Pages 81–86 *in* R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.

SCHNEIDER, W. 1937. Berigungs-Ergebnisse an der Mitteleurpäischen Schleiereulen (*Tyto alba guttata* Brehm). *Vogelzug* 8:159–170.

SCHÖNFELD, M. 1974. Ringfundauswertung der 1964–1972 in der DDR beringten Schleiereulen (*Tyto alba guttata* Brehm). *Jahrb. Vogelwarte Hiddensee* 4:90–122.

SHAW, G. AND A. DOWELL. 1989. Breeding by closely related Barn Owls. *Ringing & Migr.* 10:98.

SOUCY, L.J. 1985. Bermuda recovery of a Common Barn-Owl banded in New Jersey. *J. Field Ornithol.* 56:274.

STEENHOF, K., M.N. KOCHERT AND M.Q. MORITSCH. 1984. Dispersal and migration of southwestern Idaho raptors. *J. Field Ornithol.* 55:357–368.

STEWART, P.A. 1952. Dispersal, breeding behavior and longevity of banded Barn Owls in North America. *Auk* 69:227–245.

———. 1980. Population trends of Barn Owls in North America. *Am. Birds* 34:698–700.

SWINGLAND, I.R. 1983. Intraspecific differences in movement. Pages 102–115 *in* I.R. Swingland and P.J. Greenwood [EDS.], The ecology of animal movement. Clarendon Press, Oxford, U.K.

TAYLOR, I. 1993. Age and sex determination of Barn Owls *Tyto alba alba*. *Ringing & Migr.* 14:94–102.

———. 1994. Barn Owls: predator-prey relationships and conservation. Cambridge Univ. Press, Cambridge, U.K.

VANCAMP, L.F. AND C.J. HENNY. 1975. The Screech Owl: its life history and population ecology in northern Ohio. *N. Am. Fauna* 71:1–65.

WOODBRIDGE, B., K.K. FINLEY AND P.H. BLOOM. 1995. Reproductive performance, age structure, and natal dispersal of Swainson's Hawks in the Butte Valley, California. *J. Raptor Res.* 29:187–192.

ZAR, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ U.S.A.

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