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FIRST-YEAR MOVEMENTS BY JUVENILE MEXICAN SPOTTED OWLS IN THE CANYONLANDS OF UTAH

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ABSTRACT.—We studied first-year movements of Mexican Spotted Owls (*Strix occidentalis lucida*) during natal dispersal in canyonlands of southern Utah. Thirty-one juvenile Mexican Spotted Owls were captured and radiotracked during 1992–95 to examine behavior and conduct experiments related to the onset of natal dispersal. Juvenile Spotted Owls dispersed from their nest areas during September to October each year, with 85% leaving in September. The onset of movements was sudden and juveniles dispersed in varied directions. The median distance from nest area to last observed location was 25.7 km (range = 1.7–92.3 km). Three of 26 juveniles tracked (11%) were alive after one year, although none were observed with mates. We conducted a feeding experiment, using Mongolian gerbils (*Meriones unguicuculatus*), to test the influence of increased food supply on dispersal onset. The mean dispersal date of five owls that received supplemental food (Julian day no. 255 ± 2.6 SD) was significantly different than a control group (day no. 273 ± 12.3).

KEY WORDS: *Mexican Spotted Owl;* Strix occidentalis lucida; *natal dispersal; telemetry; dispersal timing; canyonlands.*

Movimientos del primer año de juveniles de *Strix occidentalis lucida* durante la dispersión en tierras del Cañon al sur de Utah

RESUMEN.—Estudiamos los movimientos del primer año de *Strix occidentalis lucida* durante la dispersión natal en tierras del Cañon al sur de Utah. Treinta y un buhos juveniles fueron capturados y dotados de radiotransmisores durante 1992–95 con el fin de examinar su comportamiento y conducir experimentos relacionados con la iniciación de la dispersión natal. Los buhos juveniles se dispersaron de sus áreas de anidación durante Septiembre a Octubre de cada año, con un 85% partiendo en Septiembre. La iniciación de los movimientos fué repentina y los juveniles se dispersaron en varias direcciones. La distancia media del área del nido a la última localización observada fue de 25.7 (rango = 1.7–92.3 km). Tres de los 26 juveniles monitoreados (11%) estaban vivos después de un año, aunque ninguno fue observado con compañero. Conducimos un experimento de alimentación utilizando *Meriones unguicuculatus*, para probar la influencia del incremento en comida con relación a la dispersión. La fecha de dispersión media de cinco buhos que recibieron suplemento alimenticio (día no. 255 ± 2.6 SD) fue significativamente diferente que el grupo de control (día no. 273 ± 12.3).

[Traducción de César Márquez]

Study of the dispersal movements by raptors using radiotelemetry allows researchers to track individuals over prolonged time periods (e.g., Kenward et al. 1993). Using telemetry in Arizona, Ganey et al. (1998) showed that juvenile Mexican Spotted Owls (*Strix occidentalis lucida*) began dispersal each year during September, and that early movements were abrupt and in random directions

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from natal areas. In the Pacific Northwest, Spotted Owls (*S. o. caurina and occidentalis*) showed similar first-year movement patterns (Gutiérrez et al. 1995).

Although numerous studies of Spotted Owls have reported on early dispersal movements (Gutiérrez et al. 1995), few individuals have been observed to settle and find mates. This is likely due to the expense and difficulty of tracking birds over long distances and time periods, and due to high mortality rates. Because natal dispersal is defined as the movement of an individual from its birth site to the place where it reproduces (Howard 1960), few studies have examined true dispersal in raptors (Koenig et al. 1996). Only studies of Eastern Screech-Owls (*Otus asio*) and Burrowing Owls (*Athene cunicularia*) have used an experimental approach to assess proximate factors responsible for the onset of dispersal (Ritchison et al. 1992, Belthoff and Dufty 1998, King 1996).

In southern Utah, Mexican Spotted Owls occupy arid rocky canyon habitat within a matrix of desertscrub vegetation communities (Brown 1982, Willey 1995). Our goal was to examine aspects of Mexican Spotted Owl natal dispersal timing and preliminary movements in Utah, and attempt to track the owls using radiotelemetry from aircraft as long as possible. Our objectives were to describe first-year movement patterns by juvenile Spotted Owls and conduct field experiments to examine proximate mechanisms that influence the timing of natal dispersal by owls.

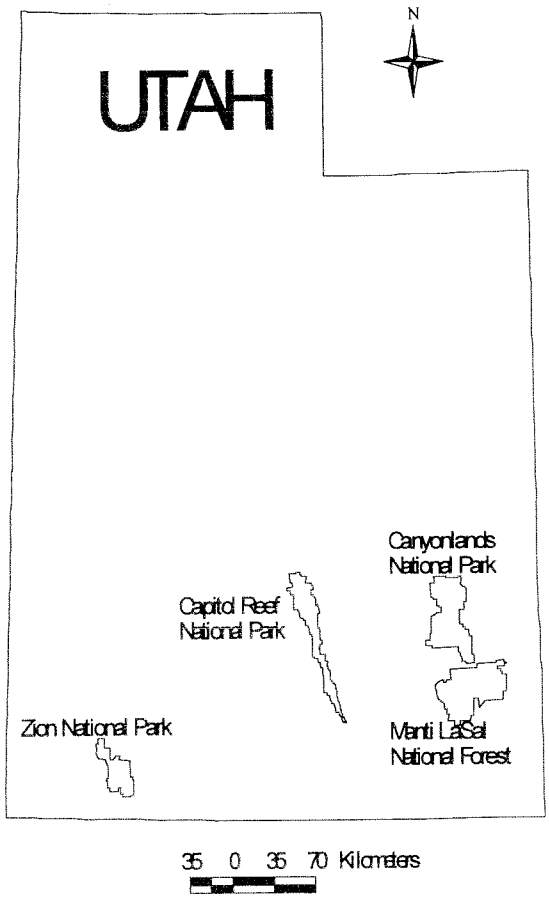

Figure 1. Location of four primary study areas where Mexican Spotted Owl natal dispersal was investigated in Utah during 1992–95.

STUDY AREA AND METHODS

Field work was conducted at four study areas in southern Utah: Zion, Capitol Reef and Canyonlands National Parks, and on the Manti LaSal National Forest (Fig. 1). The Zion National Park study area was located 1 km north of Springdale, in southwestern Utah. Capitol Reef was located 25 km northeast of Torrey in southcentral Utah. Canyonlands National Park was located 45 km southwest of Moab, Utah and the Manti LaSal was located on Elk Ridge 35 km east of Blanding in southeastern Utah. All areas were characterized by steep sandstone canyons isolated among alluvial valleys and uplifted plateaus (Thornbury 1965). Elevations ranged from 1109–3960 m. Total annual precipitation averaged 17 cm per yr and temperatures ranged seasonally from <0–>40°C (U.S. Weather Bureau, Climate and Precipitation Summaries, Utah). Pinyon-juniper (*Pinus edulis-Juniperus utahensis*) woodland and desertscrub vegetation dominated the landscape matrix (Brown 1982). Canyon vegetation included small patches of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), pinyon pine (*Pinus monticula*) and Utah juniper (*Juniperus osteosperma*). Box elder (*Acer negundo*), bigtooth maple (*A. grandidentatum*), Frémont cottonwood (*Populus fremontii*) and willows (*Salix* spp.) were present along mesic canyon bottoms and cliff seeps.

Juvenile Spotted Owls were trapped during 1–15 August each year of the study using Bal-Chatri traps or noose poles (Forsman 1983). Radiotransmitters (model RI-2C, Holohil Inc., Ontario, Canada), weighing 5.5–6.0 g with signal life ranging from 12–24 mo, were attached to the two central rectrices using quick-set epoxy and unwaxed dental floss (Reid et al. 1996).

We received radio signals using TR-4 and TR-2 receivers with handheld or airplane mounted H-antennas (Telonics Inc., Mesa, Arizona). Locations were based on aerial fixes or visual observation of roosting owls. We recorded the Julian date, time and Universal Trans Mercator coordinates for each owl location. From early August until the owls dispersed, we attempted to relocate owls every day. Once the owls began large movements outside of the natal area, we relocated them every 3–7 d. When owls could not be located by ground tracking, we

searched out 100 km in all directions from the last known location with fixed-wing aircraft.

We defined the beginning of Spotted Owl natal dispersal as the time when an individual initiated movement that led away from the nest site a distance equal to 1.68 km, the radius of a circle equal to an average adult home range (Willey 1998). We assigned the dispersal day to the Julian date halfway between the last known day in the natal area and the first day confirmed outside of the natal area. We assumed that dispersal movements ended when a juvenile settled on a home range and found a mate.

Total distance moved was defined as the sum of distances moved between successive relocations from the time a juvenile began dispersal to the last known location. Final distance was defined as the straight-line distance between the nest location and last known location. Movement rate (m/d) was defined as the distance between successive locations divided by the time interval. We determined azimuth from the nest site to final location for each individual and then estimated the dispersal direction and the angular dispersion around the mean direction (Batschelet 1981) for all individuals and each cohort (i.e., each year's group of juveniles). Rayleigh's test (Zar 1974) was used to determine if movements were random with respect to direction for individuals, among and within cohorts.

We conducted field experiments to examine hypotheses about proximate factors that influence the onset of natal dispersal. Our first hypothesis was that juveniles dispersed from the parental home range to search for food, an "Economic Hypothesis." The null hypothesis was that there would be no difference in the timing of dispersal between juvenile Spotted Owls that were given supplemental food and juvenile Spotted Owls that were not supplemented. An alternative hypothesis was that owls with food supplements would show a later dispersal date than owls not fed that leave to search for food outside the natal area (H_{a1}: $\upsilon_1 > \upsilon_2$). If dispersal onset was controlled by body condition rather than food availability, we postulated that the additional food would cause the treatment owls to leave sooner than controls (H_{a2}: $\upsilon_1 < \upsilon_2$).

An alternate mechanism was that juveniles were driven from the parental home range by adults (Howard 1960). Therefore, a second null hypothesis was that there is no difference in adult aggressive behavior in the vicinity of juveniles during the week preceding and the week following dispersal. We assumed that if adults drove young from the area, then the number of aggressive calls by adults would be greater in pre- versus post-dispersal observation periods (H_a: $\upsilon_1 > \upsilon_2$).

For the experiments, we located 10 juvenile Spotted Owls in August 1994 and attached radiotransmitters to their tail feathers. We were not able to determine the sex of the juvenile owls in the field; however, the age (Forsman 1983, Moen et al. 1991) and initial condition (sternal palpation) of the 10 juveniles were estimated at the time of capture and determined to be quite similar among the owlets. Therefore, five owls were randomly selected for the treatment group and five for the control group. The random allocation of owls to experimental groups resulted in two sibling pairs selected for the fed group. The treatment diet was two Mongolian gerbils per d (*Meriones unguicuculatus*, 350–500 g/d) fed to each treatment owl starting on 20 August at the start of the predispersal period. Juveniles were fed two gerbils each day (one each morning and evening). Juveniles were relocated each day and fed at the location where they were found by placing the gerbils on the ground within 5 m of the juveniles. The owls were fed each day until dispersal began and we conducted direct observation to confirm each feeding. Members of the control group had no food supplement. We used a two-sample *t*-test to compare the mean dispersal dates between treatment and control groups (Wilkinson 1990). Because the potential correlation in dispersal timing by siblings could bias our results, we repeated our analysis using only independent owls in the control group (i.e., we selected the juvenile that left first in two sibling pairs). Significance for the tests was set at $\alpha = 0.10$ (Steidl et al. 1997).

In testing Howard's (1960) "social hypothesis," we considered calls an index to adult agonistic behavior. Based on our interpretation of vocalization studies by Forsman et al. (1984) and Ganey (1990), we classified following "agitation" calls as agonistic: the bark call, screeches and sharp whistles and the agitated series call. These calls are only produced by subadults and adults, and not by juveniles. For the field test, the treatment group remained the same as the previous experiment. We selected this group because they were relatively more accessible in the rugged terrain; however, selection of this group may have biased our results because we did not know the influence of supplemental feeding on adult calls (i.e., we did not monitor calls of adults where juveniles were not fed gerbils).

We assumed that if adults chased juveniles from their natal areas we would observe aggressive vocalizations during crepuscular and nocturnal time periods when vocalizations appeared to be most common (Ganey 1990). Therefore, from mid-August–mid-September, when juveniles typically began dispersal, observers were positioned within 100 m of the juveniles and recorded calls of adults during 2-hr observation periods spaced throughout the night beginning 30 min before sunset and ending 30 min after sunrise. We sampled evenly across the night in both pre- and post-dispersal periods to account for nighttime variation in call rates (Ganey 1990). We contrasted the number of agonistic calls per hr by adults recorded each night during 1 wk pre-dispersal–1 wk post-dispersal. We tested the null hypothesis using a one-tailed paired *t*-test. Significance for this test was set at $\alpha = 0.10$.

RESULTS

Thirty-one juveniles were captured and radiotracked during 1992–95 in southern Utah (Table 1). Juveniles remained relatively close to their hatching sites until the onset of dispersal (range of locations from nest site = 67–520 m). Five owlets died prior to dispersal and were removed from the sample, leaving 26 that successfully dispersed from their natal areas. Mortality after initial dispersal was high for the 26 juveniles and only three (11.5%) were alive after 1 yr. The three owls that survived their first year appeared to settle in specific loca-

Table 1. Dispersal date, distance (km) and fate of radio-tagged juvenile Mexican Spotted Owls. Owls with no dispersal date, or distance, died in the vicinity of the nest.

OWL CODE	DISPERSAL DATE	LAST LIVE LOCATION	FATE[a]	FINAL DISTANCE[b]	TOTAL DISTANCE[c]
Ech474	1 Sep 92	15 Apr 93	Predation	21.2	189.9
Twi873	5 Oct 92	5 Feb 93	Predation	10.6	39.7
Cam784	19 Sep 92	21 Nov 93	Signal lost	26.5	187.8
Cam824	15 Sep 92	6 Feb 93	Exposure	43.6	97.1
Pea514		29 May 93	Exposure		
Ele915	26 Sep 92	24 Aug 93	Signal lost	8.01	112.1
Ele574	5 Sep 92	29 Jun 93	Signal lost	1.68	136.6
Twi374	20 Sep 93	3 Mar 94	Exposure	15.1	40.9
Twi354		21 Nov 93	Exposure		
Spr034	11 Sep 93	4 Mar 94	Exposure	21.2	27.9
Spr123		15 Sep 93	Exposure		
Ech414	11 Sep 93	3 Mar 94	Predation	28.8	58.0
Ech683	11 Sep 93	15 Dec 93	Exposure	24.3	25.3
Ham623	10 Sep 93	8 Nov 93	Predation	47.3	54.9
Ham262	10 Sep 93	6 Feb 94	Predation	90.0	106.1
Pea175	10 Sep 93	6 Nov 93	Exposure	36.6	68.6
Bcd824	11 Sep 94	3 Nov 94	Radio molt	26.8	52.0
Bcd873	15 Sep 94	15 Nov 94	Exposure	24.8	32.2
Cam944	14 Sep 94	25 Feb 95	Predation	43.0	92.1
Fiv803	21 Sep 94	3 Nov 94	Predation	5.1	12.1
Usp983		14 Oct 94	Predation		
Dar903	21 Sep 94	1 Oct 94	Signal lost	27.7	53.3
Bsp924	15 Oct 94	21 Oct 94	Radio molt	8.9	20.2
Sco783	14 Sep 94	5 Oct 94	Signal lost	17.1	31.3
Sco854	8 Sep 94	1 Oct 94	Signal lost	51.1	58.7
Fir054	17 Sep 94	5 Oct 94	Signal lost	31.5	40.3
Usp473	12 Sep 95	11 Oct 95	Signal lost	20.1	28.0
Usp564	5 Oct 95	15 Feb 96	Exposure	92.3	110.6
Fiv034	17 Sep 95	15 Nov 95	Predation	6.0	8.3
Bur354		10 Dec 95	Exposure		
Tex262	24 Sep 95	27 Oct 95	Signal lost	30.8	85.0

[a] Fate indicated the outcome of tracking: signal loss occurred when owl transmitters could not be relocated after extensive search; radio molt refers to owls that dropped transmitters due to feather molt; exposure refers to owls that apparently starved to death; predation refers to owls that appeared to have been killed by predators, although scavenging may have occurred.
[b] Final distance was estimated as the straight-line distance from the nest to the last observed location of an owl.
[c] Total distance was estimated as the sum of the distance between all successive locations observed during dispersal.

tions and their radio signals stopped transmitting during the following summer. None of the juveniles that survived were found with mates, despite extensive surveys, before their signals terminated.

The final distance dispersed by owlets averaged 29.2 ± 22.48 km (±SD) but varied substantially (range = 1.68–92.3 km). Movement rate of individuals also varied, with periods of no movement followed by periods of rapid movement in a few days (Table 2). Four individuals averaged >7 km/d during brief periods. The total distances traveled by owls was positively correlated with number of relocations/owl (Spearman's rank correlation, $r = 0.723$). Final distance traveled was not correlated with the number of months the owls were tracked ($r = -0.093$).

The mean dispersal direction (Batschelet 1981) of all owls varied greatly and no significant directional pattern was determined within any cohort (Rayleigh's test, $P = 0.687$, 0.462, 0.104 and 0.371, 1992–95, respectively). Rayleigh's test was significant ($P < 0.05$) for five individual owls and suggested that these owls exhibited directional, versus random, movement during the portion of the dis-

Table 2. Moment rates (m/d) estimated for 20 radio-tagged Mexican Spotted Owls with $N \geq 4$, where N = number of relocations during the dispersal period.

CODE	YEAR	N	MEAN	SE	MIN (m/d)	MAX (m/d)
Ech474	1992	29	902	290	11	7476
Twi873	1992	27	301	88	12	2095
Cam784	1992	52	910	206	5	7530
Cam824	1992	15	709	180	2	2632
Ele915	1992	53	464	77	0	3641
Ele574	1992	46	619	171	0	7738
Twi374	1993	9	195	76	2	765
Spr034	1993	8	286	76	27	698
Ech414	1993	7	583	244	11	2057
Ech683	1993	4	718	320	22	1589
Ham623	1993	9	277	179	8	424
Ham262	1993	11	500	271	0	3192
Pea175	1993	15	1382	504	0	6787
Bcd824	1994	6	3209	1463	185	9367
Cam944	1994	5	6692	2073	771	2232
Fiv803	1994	5	569	384	2	2273
Soc783	1994	11	631	117	258	1451
Sco854	1994	4	3698	860	338	6038
Tex262	1995	11	1189	279	57	2844
Usp564	1995	7	738	333	48	271

persal period that we monitored. The directional movement of the remaining juveniles was apparently random and most owls appeared to wander the landscape, switching direction frequently. Three juveniles that survived for at least 1 yr eventually reversed their direction of travel back toward the natal area and two (Ele915 and Ele574, Table 1) were last observed within 8.01 and 1.68 km of their nest sites when radio signals were lost.

We observed movements by five sibling pairs in southern Utah. Dispersal date of siblings was positively correlated ($r = 0.73$) and suggested that siblings begin dispersal at similar times. When we calculated the azimuth between the nest site and final location, siblings showed a tendency to disperse at least 100° apart, suggesting they selected different travel paths during dispersal. The angle between sibling paths was even greater when the estimate "mean direction of travel" (Batschelet 1981) was used for this comparison (i.e., sibling paths were 180–209° apart).

We estimated to within 1 d when individual owls dispersed from their natal area for 26 individuals during the study (Table 1). During 1992–95, dispersal began during a 6-wk period from 1 September–15 October. Eighty-five percent of the juveniles dispersed during September and 15% in October. The mean day of dispersal did not differ among the four cohorts (ANOVA, $P = 0.063$, $F = 2.68$, df = 35), with 1992–95 cohorts dispersing during 1 September–5 October, 10–20 September, 8 September–15 October and 12 September–5 October, respectively. The overall mean day of dispersal was 17 September (±9.8 d) for all owls tracked.

During the field experiments, owls given supplemental food dispersed significantly earlier ($\bar{x}$ = 12 September ± 2.6 d) than the control owls ($\bar{x}$ = 30 September ± 12.3 d) as predicted by our second alternative hypothesis (two-sample t-test, $t = -2.75$, df = 8, $P = 0.025$). When we repeated the test with independent observations (i.e., we eliminated 2 siblings), the difference in mean dispersal date remained significant (two-sample t-test, $t = -2.92$, df = 5, $P = 0.033$). For the social hypothesis, we failed to reject the null hypothesis of no difference (paired t-test, $t = -0.954$, df = 4, $P = 0.44$) in the number of agonistic calls by adults during the pre-dispersal period (192 hr of observation during 21 nights) and the post-dispersal period (202 hr of observation during 21 nights). On average, 0.66 (±1.63) agonistic calls/hr were recorded during pre-dispersal and 0.97 (±1.74) calls/hr during post-dispersal in the vicinity of three adult pairs. Retrospective power analysis indicated that the power of the test to reject the null hypothesis did not exceed 0.20. Therefore, these results are inconclusive with respect to adult behavior toward juveniles prior to dispersal.

DISCUSSION

Factors that influence the onset of natal dispersal include endogenous mechanisms, where control is governed by genetically-based systems, and exogenous mechanisms, in which timing is a response to local factors, including food availability, body condition and social interactions (Ferrer 1993). During our study of Mexican Spotted Owls, we observed a narrow window for the onset of dispersal among four cohorts (similar to other studies, e.g., Gutiérrez et al. 1985, 1995, Ganey et al. 1998). This provided strong evidence that ontogenetic processes control the season when Spotted Owls begin dispersal.

On the other hand, the results of our feeding experiment, which showed a significantly earlier departure period for food-supplemented owls, implied that physical condition may supply the prox-

imate signal for owls to leave the natal area. Belthoff and Dufty (1998) reported that dominant screech-owls dispersed earlier than subordinates and, based on body size and mass evidence, they assumed that dominant owlets were in better physical condition than the subordinates. Ellsworth and Belthoff (1999) showed that dominant juvenile screech-owls dispersed first (in five of seven broods) and they concluded that dominance influenced the timing of dispersal but not the distances traveled to overwinter sites. Therefore, among some owls, variation in timing of natal dispersal may also be related to competitive ability.

Juvenile owls that leave the natal area in good condition may avoid use of critical muscle protein and may be more likely to survive during dispersal. Nilsson (1989) suggested that juveniles that dispersed relatively early may also have a better chance to settle in suitable habitat. Selection could favor individuals that disperse as soon as they are fit if vacant territories are limited; however, field studies of Spotted Owls do not support a relationship between dispersal date and age at first breeding (Gutiérrez et al. 1995). Furthermore, Spotted Owls do not establish territories until at least 1-yr old and few survive their first year.

Primarily due to low power and bias due to unknown effects of supplemental feeding, the result of our "Social Hypothesis" experiment was inconclusive with respect to whether juveniles were forced out of natal areas by adults. In a study using radiotelemetry to examine adult home ranges, Willey (1998) showed that during August–September adults typically moved out of natal areas to other portions of their home ranges and were far from juveniles during the onset of dispersal. Northern Spotted Owl adults also stop feeding juveniles in mid- to late August and show no evidence of aggression toward young before dispersal (E.D. Forsman pers. comm.). Thus, we believe that social interactions between adults and juveniles were not responsible for the onset of dispersal.

Results from our analysis of dispersal behavior were similar to Spotted Owls reported from a variety of landscapes. For example, Ganey et al. (1998) reported a median dispersal distance of 16.9 km (range = 0.6–72.1 km) for juveniles tracked in mixed-conifer forests versus our median of 25.7 km (range = 1.68–92.3 km) in Utah. Ganey et al. (1998) observed that Mexican Spotted Owls initiated dispersal abruptly during September and October and showed no obvious directional patterns. We observed similar patterns for four cohorts in the canyonlands of Utah.

In Arizona, New Mexico and Utah, Mexican Spotted Owls were observed moving across open low desert landscapes between islands of suitable breeding habitat (Ganey et al 1998, Stacey pers. comm., Willey 1998). Gutiérrez et al. (1996) observed movement of Mexican Spotted Owls between "Sky Island" mountain ranges in New Mexico. Observation of long-distance movement by dispersing juveniles provides evidence that widely spaced enclaves have potential connectivity and isolated populations may have genetic significance to the owl's conservation (Keitt et al. 1995, Gutiérrez and Harrison 1996, Seamans et al. 1999).

In Utah and elsewhere across their range, predation and death caused by exposure (e.g., starvation, dehydration and disease) appeared to be the primary causes of juvenile mortality during dispersal (Gutiérrez et al. 1985, Ganey et al. 1998, Miller et al. 1997, Willey 1998). In Utah, only three owls survived their first year (90% mortality) and we found it interesting that two of the three settled relatively close (1.7–8.0 km) to their natal areas. We also observed juveniles that died while moving back toward natal areas in early spring. Therefore, studies that do not follow juveniles to the place of first reproduction (i.e., recruitment into the population) may bias their estimates of mean and median dispersal distances. This bias could be nontrivial with regard to population modeling. In addition, knowledge of each individual's sex is important because dispersal may be sex-biased. In the Pacific Northwest, female Northern Spotted Owls have been observed traveling much further than males (E.D. Forsman pers. comm.). Therefore, we strongly urge that future studies of owl dispersal collect blood samples to determine sex of each juvenile.

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