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DISPERSAL MOVEMENTS AND SURVIVAL RATES OF JUVENILE MEXICAN SPOTTED OWLS IN NORTHERN ARIZONA

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ABSTRACT.—We monitored dispersal movements of 19 radiotagged juvenile Mexican Spotted Owls (*Strix occidentalis lucida*) in northern Arizona during 1994 and 1995. All juveniles initiated dispersal movements in September or October during both years, with most dispersing during September. Initial dispersal movements were rapid and abrupt, but lacked a significant directional pattern. Distance from the nest to the last observed location and the most distant location reached ranged from 0.6–72.1 and 2.1–73.5 km for individual owls, respectively. These distances represent minimum estimates of dispersal capability because only one individual was tracked until it settled on a territory and paired. Owls used a variety of habitat types during dispersal, some of which differed markedly from typical nesting habitat for Mexican Spotted Owls. Four of five owls that were tracked past mid-November moved to lower elevation pinyon-juniper woodlands and at least one overwintered in pinyon-juniper woodland. Kaplan-Meier estimates of annual survival rate ranged from 20.5–28.7%, depending on whether we censored all owls with unknown fates or included suspected deaths as mortality events. Estimates differed significantly between years and confidence intervals were wide, suggesting that longer-term studies of large numbers of owls will be required to obtain accurate and precise estimates of juvenile survival. *Received 8 May 1997, accepted 21 Jan. 1998.*

Mexican Spotted Owls (*Strix occidentalis lucida*) are widely but patchily distributed throughout the southwestern United States and northern Mexico (Ward et al. 1995), apparently reflecting the disjunct distribution of the forested mountains and canyonlands they occupy (Ganey and Dick 1995). This subspecies was listed as Threatened in 1993, primarily because of concerns over the effects of loss of forested habitat on the owl (Block et al. 1995).

Recent planning efforts have demonstrated the importance of accurate estimates of juvenile survival and knowledge of dispersal patterns to understanding population processes in the Spotted Owl (Thomas et al. 1990, Noon and McKelvey 1992, Keitt et al. 1995, White et al. 1995, Forsman et al. 1996). Despite these findings, few data exist on either dispersal movements or juvenile survival rates for the Mexican Spotted Owl. Keitt and coworkers (1995: fig.1) summarized unpublished data on dispersal of Mexican Spotted Owls from two study areas (Gutiérrez et al. 1994). However, estimates of dispersal distance were based on resightings of color-banded birds on a study area of limited size. This methodology likely underestimates both dispersal distance and juvenile survival because birds that move long distances have a greater probability of leaving the study area and never being resighted (White et al. 1995, Burnham et al. 1996). The only other information on dispersal of juvenile Mexican Spotted Owls is in unpublished reports (Willey 1995, Hodgson and Stacey 1996). These studies indicated that radiotagged juveniles initiated dispersal from August–October, moved rapidly and over long distances, and sometimes crossed open habitats very different in structure from typical nesting habitat. Similar patterns were reported with respect to dispersal movements of both Northern (*S. o. caurina*) and California (*S. o. occidentalis*) Spotted Owls (Forsman et al. 1984, Gutiérrez et al. 1985, Laymon 1988, Miller 1989, Miller et al. 1997).

Estimates of annual survival rates of juvenile owls exist for all three subspecies of Spotted Owls (Noon et al. 1992: table 8G, White et al. 1995: table 2.2, Burnham et al. 1996: table 4). All of these estimates were based on mark-recapture studies and may be biased if emigration from the study area is common. Only Burnham and coworkers (1996) adjusted their estimate for emigration of marked owls from the study areas; their adjustment was based on data on the movements of radiotagged juveniles.

To provide better information on dispersal of juvenile Mexican Spotted Owls, we studied

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dispersal movements and survival of radiotagged juveniles. Our objectives were to (1) monitor movements of dispersing Spotted Owls, to document timing of dispersal, movement rates and patterns, and habitat use; and (2) estimate first-year survival rates of Mexican Spotted Owls based on observations of radiotagged juveniles.

METHODS

Study areas.—We captured and radiotagged juvenile owls in three discrete areas in northcentral Arizona. These areas were located on the (1) Mormon Lake and Long Valley Ranger Districts, Coconino National Forest; (2) Chevelon Ranger District, Apache-Sitgreaves National Forest; and (3) Williams Ranger District, Kaibab National Forest. Elevation ranged from approximately 1800–2660 m within all three study areas, and the climate in all three areas featured cold winters and warm summers.

The Coconino study area was located approximately 40 km south of Flagstaff in northcentral Arizona. Topography of this area was relatively flat with scattered cinder cones and volcanic mountains. The area consisted primarily (73%) of ponderosa pine (*Pinus ponderosa*)-Gambel oak (*Quercus gambelli*) forest, intermixed with mixed-conifer forest (14%) dominated by Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*), ponderosa pine forest (10%), pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) woodland (2.7%), and grasslands (0.7%; percentages from Gutiérrez et al. 1994).

The Chevelon study area was located approximately 60 km south of Winslow, Arizona. This area was dominated by a series of major drainages running north from the Mogollon Rim, a prominent geologic uplift, to the Little Colorado River. Vegetation in the area consisted primarily of mixed-conifer forest, ponderosa pine forest, and pinyon-juniper woodland. Mixed-conifer forest was found mainly on north-facing canyon slopes and in canyon bottoms; ridgetops and other slopes were dominated by ponderosa pine forest and/or pinyon-juniper woodland.

The Williams study area was located approximately 20 km southeast of Williams, Arizona, in the Sycamore Canyon Wilderness. Sycamore Canyon is a deeply incised drainage with vegetation similar to that on the Chevelon study area. Estimates of relative proportions of different cover types were not available for the Chevelon and William study areas.

Once owls began actively dispersing, they were followed wherever they went. Areas immediately surrounding the main study areas were generally similar in topography and vegetation to those areas. As owls moved more widely, terrain and vegetation became more diverse, ranging from high forested mountains to lowland desert in surrounding valleys.

Capturing and radiotracking owls.—The Coconino study area was shared with an ongoing study of demography of Mexican Spotted Owls (Gutiérrez et al. 1994). All territories in this area were monitored in cooperation with demography field crews to document reproductive status, identify pairs that fledged young, and determine numbers of young fledged. Information on pairs producing young within the other study areas was solicited from forest biologists. We determined the date of fledging to within 7 days for birds on the Coconino study area. All juveniles on the other two study areas were assigned the median fledging date of birds on the Coconino study area for that year.

We captured juvenile owls in August, when their tail feathers were fully grown (beginning approximately 75–80 days after hatching). We captured owls using noose poles (Forsman 1983), and attached radio transmitters (Holohil Systems Ltd., Carp, Ontario) to the central tail feathers using epoxy and dental floss (Guetterman et al. 1991). Transmitters weighed 5–6 g and had an expected battery life of 9–12 months. Because few pairs of owls bred during 1994 and 1995, we attempted to capture all known juveniles in the study areas. Juvenile owls were not sexed because Spotted Owls are monomorphic and sex cannot be determined from plumage characteristics.

Radio signals were received using ICOM (Communications Specialists, Inc., Orange, CA) and Telonics (Telonics, Inc., Mesa, AZ) receivers and a 3-element Yagi antenna. Owl locations were mapped as accurately as possible on USGS topographic maps, and date, time, and Universal Transverse Mercator coordinates were recorded.

From the time of radiotagging through late August, we attempted to locate all radiotagged juveniles visually during the day at least once a week. This schedule was agreed upon with the demography crews to minimize disturbance to the adult owls. By late August the juveniles were more independent and typically roosted away from the adults. At this time we attempted to locate owls 2–3 times per week in anticipation of the onset of dispersal. Once owls initiated dispersal, we attempted to relocate them every 3–4 days and to avoid losing contact with any individual for extended periods of time. When we were unable to efficiently locate all owls from the ground, we initiated aerial tracking flights. Aerial tracking was accomplished as described in Samuel and Fuller (1994). Ground crews attempted to visually locate owls as soon as possible following flights. In most cases ground crews were able to search for owls within 1–3 days of flights. We were not always able to locate owls between flights, however, particularly during periods of rapid dispersal. Information on mortality and the factors responsible was collected opportunistically. Accuracy of aerial locations was checked by visually locating owls from the ground on the same day as the aerial location. Mean distance between aerial and ground locations was 191.4 ± 33.1 S.E. m (range = 0–383 m, n = 15).

Timing of dispersal.—We defined dispersal as the movement of a juvenile owl from its natal area to a new area or succession of areas. We could not precisely define the natal area or the home range of the adult owls and therefore operationally determined

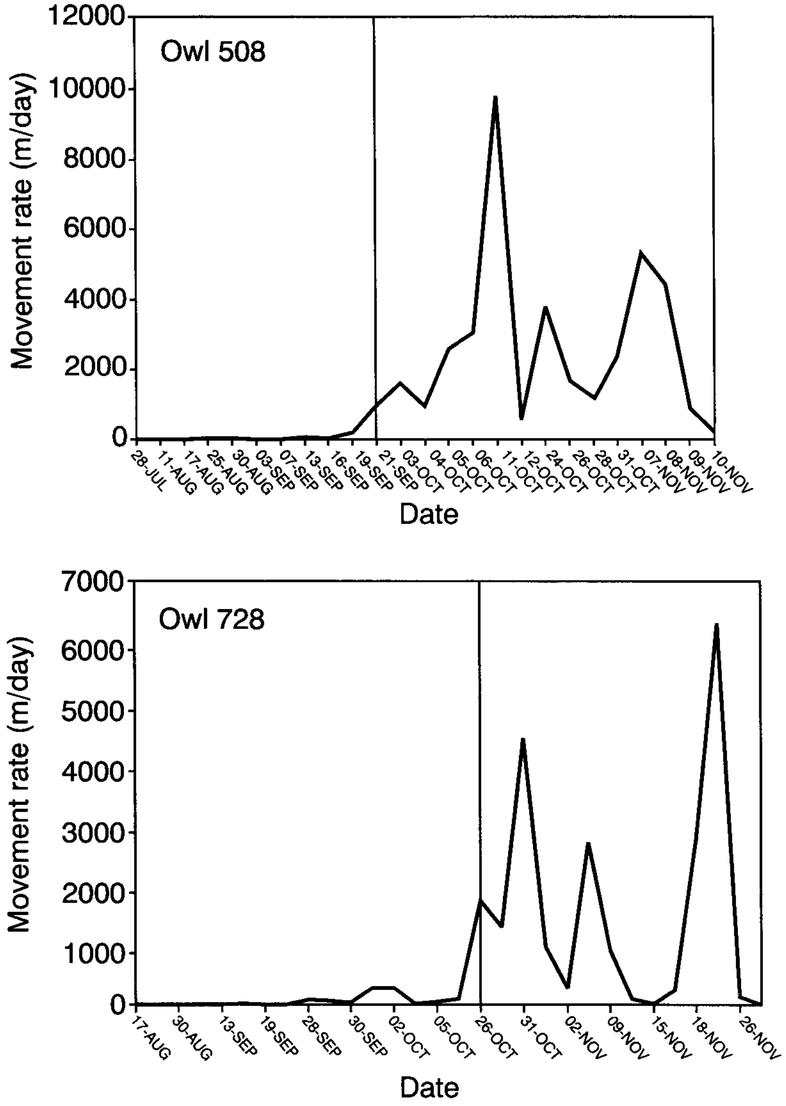

FIG. 1. Movement rates of two radiotagged juvenile Mexican Spotted Owls showing the sudden increase in movement rate indicative of the onset of dispersal. The vertical line indicates the point where dispersal was presumed to have begun. Movement rates were calculated as (distance between succcessive locations/number of days between those locations). (A) Owl 508; (B) Owl 728.

when dispersal had begun by examining the miminum movement rate between successive locations. All owls that survived to disperse showed a pattern of short-distance movements within the natal area followed by a sudden and dramatic increase in movement rate (Fig. 1). We assumed that dispersal had begun when movement rate abruptly increased above the background level. We assumed that dispersal had ceased when an owl established a territory and paired with a mate. We did not require successful breeding to consider dispersal to have ceased because even established and previously productive pairs of Spotted Owls may not breed in a given year (Forsman et al. 1984).

We estimated time on the natal territory as the number of days between fledging and dispersal. We compared time on the natal territory between years using a Mann-Whitney test (Conover 1980).

Distance and rate of dispersal.—We used locations of dispersing owls to estimate three parameters describing dispersal movements. Final dispersal distance was estimated as the straight-line distance from the nest location to the last known location for a particular owl. Because some owls moved away from and then returned toward the nest, we also estimated maximum dispersal distance as the distance from the nest to the most distant location recorded for a particular owl. Movement rate (km/day) was estimated as the distance between successive locations divided by the number of days between those locations. We compared final and maximum dispersal distances between cohorts using Mann-Whitney tests. We compared movement rates among individual owls within cohorts using a Kruskal-Wallis test (Conover 1980), using SPSS (ver. 6.1.2) statistical software on an IBM-compatible computer.

Direction of dispersal.—For each dispersing owl with more than five locations following initial dispersal, we calculated the mean direction ($\hat{a}$) of movements during dispersal and the angular deviation ($\hat{s}$) around that mean direction (Zar 1974). We used Rayleigh's z statistic (Zar 1974) to determine whether dispersal movements of each individual were random with respect to direction.

We also estimated the azimuth from the nest location to the final known location for each dispersing owl (final direction). We calculated the mean final direction and the angular deviation around mean final direction for each cohort, and used Rayleigh's z to test for directional pattern within cohorts. All circular analyses were conducted using Oriana for Windows (version 1.01; Kovach Computing Services, Pentraeth, Anglesey, Wales, U.K.).

Habitat use during dispersal.—We recorded information on cover type, type of roost perch (tree, snag, cliff, or other), and roost tree species (for tree roosts) whenever we visually located roosting owls. Cover type was recorded as: mixed-conifer forest, ponderosa pine forest, pine-oak forest, pinyon-juniper woodland, or other. We divided the sampling period into two time intervals for analysis, considering 1 August–31 October to represent a pre- and early dispersal period and 1 November–28 April to represent a later dispersal period. We compared proportional use of cover types and tree species between dispersal periods using multiresponse randomized block procedure (MRBP on an IBM-compatible; Slauson et al. 1991) with individual owl as the blocking variable. This is essentially a distribution-free analog of a blocked analysis of variance with P-values based on permutations of the actual data. Where proportional use differed between dispersal periods, we used MRBP to determine which categories differed significantly. The significance level for multiple comparisons was set at 0.05/k, where k = the number of categories tested. We restricted analyses of habitat use to a subsample of owls ($n = 7$) that were tracked in both time periods and for which at least 10 roosts were recorded.

Estimating annual survival rates.—We estimated survival rates of juvenile owls over two time intervals each year, and combined these estimates to estimate first-year survival. The first interval covered the period from fledging until we began radiotagging juvenile owls; the second covered the period following radiotagging. Consequently, our estimate of annual survival does not include any mortality that may have occurred between hatching and fledging, but we suspect that mortality is uncommon during this period. Our approach is consistent with previous studies of Spotted Owls, all of which estimated post-fledging demographic rates for owls (e.g., Franklin et al. 1996).

We assumed that juveniles that could not be relocated to radiotag had died and estimated survival from fledging until radiotagging as:

$$\hat{s}_1 = (\text{number juveniles relocated/number fledged}).$$

We estimated the variance using the normal approximation to the binomial (Zar 1974):

$$\text{var } \hat{s}_1 = [\hat{s}_1 (1 - \hat{s}_1)]/n,$$

where n = number of juveniles fledged. In a few cases on the secondary study areas we were either uncertain about how many owls fledged from a particular nest or were unable to search for the fledglings before late August. These nests were not included in survival estimates for this time period.

We estimated survival rates of radiotagged juveniles ($\hat{s}_2$) using a modification of the Kaplan-Meier (Kaplan and Meier 1958) method developed by Pollock et al. (1989). This method allows for staggered entry (i.e., not all animals are radio-tagged at the same time) and for the use of right-censored data resulting from radio failure or inability to relocate an owl once it dispersed. We used a log rank test to test for equality of survival distributions between cohorts (Pollock et al. 1989).

Because of uncertainty about the fates of some radiotagged owls, we used two models to estimate survival rates. In the first model we censored all individuals for which we could not positively document mortality. We suspected that some of these owls were dead, however, based on the circumstances surrounding transmitter recovery. In the second model we included suspected deaths as mortality events and censored all other birds of unknown fate.

We estimated annual survival of juveniles as ($\hat{s}_1 \times \hat{s}_2$). The variance in survival was estimated following Goodman (1960):

$$\begin{aligned}\text{var} = {} & [(\hat{s}_1)^2 (\text{var } \hat{s}_2)] \\ & + [(\hat{s}_2)^2 (\text{var } \hat{s}_1)] - (\text{var } \hat{s}_2 \times \text{var } \hat{s}_1).\end{aligned}$$

Calculation of P-values.—For all analyses we either calculated exact P-values or used a Monte Carlo simulation to estimate P where we could not compute an exact P-value. This method produces an unbiased and reliable estimate (Mehta and Patel 1995). All estimates of variability presented are standard errors unless otherwise noted.

RESULTS

We captured and radiotagged 24 juvenile owls ($n = 12$ in both 1994 and 1995). Five owls were lost from the sample for various reasons prior to dispersal (Table 1). Two transmitters were located on the ground with tail

TABLE 1. Dispersal dates and fates of radiotagged juvenile Mexican Spotted Owls in Arizona, 1994 and 1995.

Territory	Owl number	Dispersal date[a]	Last date known alive	Fate[b]	Final distance[c]	Maximum distance[d]	Final direction[e]	Mean direction[f]	Angular deviation[g]
Big Springs	809	18 Oct 94	7 Nov 94	RF	0.6	2.1	315.6		
Bonita	469	14 Sep 94	3 Jan 95	RF	17.3	23.5	238.6	80.9	100.7
Bonita	628	9 Sep 94	21 Oct 94	P	7.2	7.7	42.1	228.8	116.9
Circle Bar	937		11 Oct 94	S					
Coyote	659	14 Sep 94	3 Nov 94	S	0.8	22.2	35.8	322.0	132.6
Coyote	748	26 Sep 94	21 Oct 94	S	9.5	20.2	32.3	120.0	129.8
Fain Mtn	492		13 Sep 94	SL					
Fain Mtn	728	16 Oct 94	28 Nov 94	P	47.9	48.4	81.9	326.0	117.2
Lee Butte	508	20 Sep 94	10 Nov 94	S	16.3	25.2	15.4	353.5	143.1
Mayflower	611		15 Aug 94	M					
Serruchos	676	25 Sep 94	13 Oct 94	RF	27.3	28.1	158.9	150.8	99.7
Serruchos	918	20 Sep 94	20 Oct 94	P	53.1	55.7	139.2	285.4	89.3
Bonita	799	9 Oct 95	16 Nov 95	P	60.1	60.5	195.3	14.4	95.9
Hart Cyn	660	20 Sep 95	15 Jun 97	A	5.8	5.8	303.2	60.9	118.1
Hart Cyn	778		20 Sep 95	RF					
Iris	620	5 Sep 95	16 Jan 95	RF	34.9	35.1	155.1	84.7	118.1
Lake Mtn	838	28 Sep 95	5 Feb 96	P	43.0	48.9	289.9	184.5	136.4
Limpios	857	12 Sep 95	26 Apr 96	SL	72.1	73.5	269.3	55.1	110.4
Mahan Mtn	697	23 Sep 95	3 Oct 95	SL					
Mayflower	599	6 Oct 95	10 Oct 95	RF	29.4	29.4	214.8		
Mayflower	877	6 Oct 95	11 Oct 95	SL	16.5	16.5	201.3		
Mint Spring	640	18 Sep 95	2 Oct 95	SL					
Station	678	30 Sep 95	20 Nov 95	SL	3.4	18.3	142.2	162.8	107.4
Station	739		20 Sep 95	RF					

[a] Owls with no dispersal date were lost from the sample prior to dispersing.

[b] Explanatory notes for fates: RF = radio found, fate unknown; P = found dead, probable predation; S = found dead, probable starvation; SL = signal lost, fate unknown; M = molted tail feathers with attached radio; A = alive and paired.

[c] Straight-line distance (km) from the nest to the last location where the owl was observed alive or found dead. Not calculated for owls lost from the sample prior to dispersal, or for owls with fewer than 5 relocations following initiation of dispersal.

[d] Straight-line distance (km) from the nest to the location farthest from the nest. Not calculated for owls lost from the sample prior to dispersal, or for owls with fewer than 5 relocations following initiation of dispersal.

[e] Direction (°) from the nest to the last known location for an individual owl. Not estimated for owls lost from the sample prior to dispersal.

[f] Mean direction (°) of all post-dispersal movements for an individual owl. Calculated following Zar (1974); not calculated for owls with fewer than 5 post-dispersal relocations.

[g] Angular deviation around the mean direction for an individual owl. Calculated following Zar (1974); not calculated for owls with fewer than 5 post-dispersal relocations.

feathers attached and no signs of predation. We were able to verify that at least one of these radios was lost through premature molt by resighting the bird on its natal area. One owl was found dead in the natal area, and we lost the signal on another owl. For the latter owl, we are uncertain whether the radio failed or whether this owl dispersed and we were unable to locate it. The transmitter from the fifth owl was tracked to a large burrow beneath a stump. This could indicate predation. We cannot rule out scavenging following death for another reason, however, or premature molt followed by an animal dragging the radio and attached tail feathers into a burrow.

The remaining 19 owls (9 in 1994 and 10 in 1995) all dispersed from the natal area; no owls were observed to remain in their natal area. Only one owl was tracked until it settled in a territory. This 1995 juvenile moved 5.8 km downstream from its natal area along a major drainage to an historically occupied, but currently vacant, territory immediately adjacent to its natal area. The juvenile settled in this area in early October 1995 and had obtained a mate by June 1996. The mate appeared to be a 1-yr old female based on appearance of the retrices (Moen et al. 1991) and her vocalizations. This pair did not nest in 1996 but nested successfully in 1997.

One other owl was monitored through late April. This owl traveled extensively for two months following initial dispersal. It "settled" into a defined area of approximately 670 ha sometime between 22 November and 12 December 1995, and remained in this area through 26 April 1996. We lost the signal from its transmitter at that time and are uncertain whether it moved on or the radio failed. The area in which this bird settled was a canyon dominated by pinyon-juniper woodland (elevation approximately 1400 m).

All other owls either died or were lost from the sample at various times because of radio failure or inability to relocate the owl.

Timing of dispersal.—We were able to pinpoint dispersal dates of individual owls to ±3.7 days in 1994 (range = 1–9 days) and ±2.7 days in 1995 (range = 0–6 days). All owls dispersed between 9 September and 18 October in 1994, with 66.7% dispersing in September (Table 1). In 1995, all owls dispersed between 5 September and 9 October, with 70% dispersing during September.

Time spent on the natal area differed significantly between cohorts (Mann-Whitney test: Monte Carlo $P = 0.048$). Owls spent an average of 101 ± 4.8 days (range = 87–125 days) on the natal area in 1994 versus 86.8 ± 3.4 days in 1995 (range = 73–102 days). Most of this difference appeared to be attributable to only five owls. Two owls dispersed relatively late in 1994 (16 and 18 October), and three owls fledged during July in 1995, considerably later than normal for Mexican Spotted Owls (Rinkevich et al. 1995). Although these three owls were the last to disperse in 1995, all dispersed by 9 October (Table 1).

Distance and rate of dispersal.—Neither final nor maximum dispersal distance differed significantly between cohorts (Mann-Whitney tests: $P > 0.05$ for final and maximum dispersal distances). Median final dispersal distance for all owls was 16.9 km (range = 0.6–72.1 km); median maximum dispersal distance was 25.2 km (range = 2.1–73.5 km). Because only one owl was tracked until it settled and paired, we suggest that these distance estimates should be viewed as minimum estimates of dispersal capability.

Movement rates during dispersal differed significantly among owls within cohorts (Kruskall-Wallis test: Monte Carlo P-values = 0.002 for 1994, 0.006 for 1995). Movement rates also varied considerably over time for individual owls, with periods of rapid movement interspersed with periods when owls were relatively sedentary (Fig. 1). Mean and maximum movement rates of 19 individual owls ranged from 148.3–3,053.3 and 303.3–13,442.4 m/day, respectively. Because owls were not relocated daily, considerable movement likely went undetected between relocations, and estimates presented here almost certainly underestimate actual movement rates.

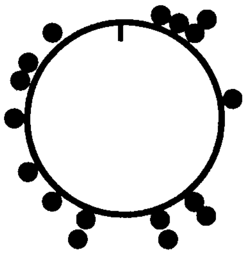

FIG. 2. Circular scattergram showing final directions from the nest to the last known location for 17 radiotagged juvenile Mexican Spotted Owls in Arizona in 1994 and 1995. Each dot represents one individual ($\hat{a} = 195°$, r = 0.093).

Direction of dispersal.—The mean directions of movement were not significant for any of the 14 owls (Rayleigh's Z: all $P > 0.05$), suggesting that movements of individual owls were not significantly concentrated around the mean direction for that individual. This was borne out by direct observation. Individual owls moved directionally at times, but these movements were interspersed with periods of wandering and/or complete reversals of travel direction.

There was no significant directional pattern to movements for either cohort, based on directions to final locations for individuals (1994: $\hat{a} = 51.3°$, $\hat{s} = 82.3°$, $P > 0.05$; 1995: $\hat{a} = 219.7°$, $\hat{s} = 60.3°$, $P > 0.05$). Because mean final direction did not differ from random for either cohort, we pooled cohorts for estimation of overall mean direction ($\hat{a} = 195.8°$, $\hat{s} = 124.7°$; Fig. 2).

Habitat use during dispersal.—We recorded perch type at 164 roost sites. Most roosts (90.0%) were in live trees, but snags (5.0%), cliffs (1.9%), and other perches such as stumps and logs (3.1%) were also used. Overall use of cover types differed significantly between early and late dispersal periods [$P = 0.021$, $n = 7$ owls (111 roost sites)], but use of individual cover types did not differ significantly [$P > 0.01$ (=0.05/5)] between dispersal periods in Bonferroni-controlled multiple comparisons (Fig. 3). We were not able

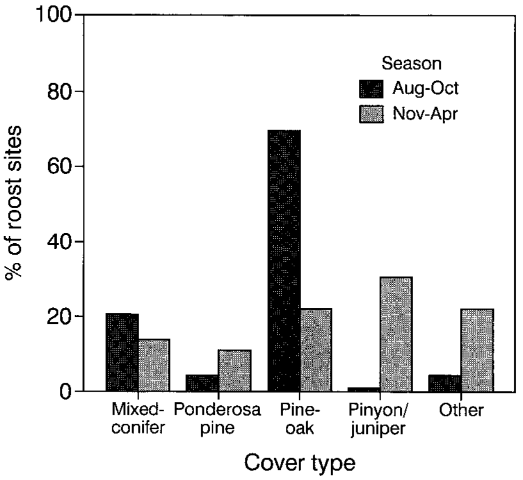

FIG. 3. Cover types used for roosting by seven juvenile Mexican Spotted Owls during dispersal. Based on 45 and 66 roost sites sampled during early and late dispersal periods, respectively. Overall use of cover types differed significantly between time periods, but use of individual cover types did not ($P > 0.01$, Bonferroni adjustment).

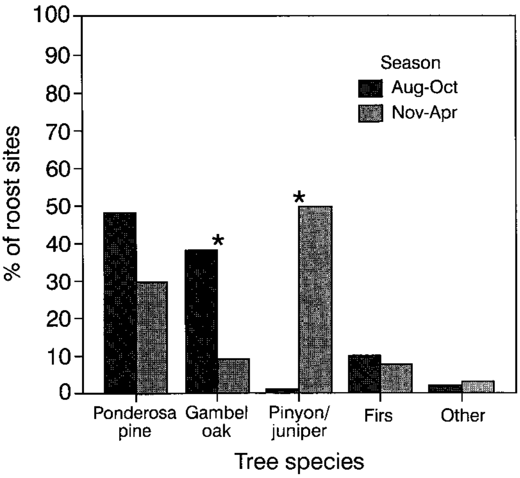

FIG. 4. Tree species used for roosting by seven juvenile Mexican Spotted Owls during dispersal. Based on 45 and 66 roost sites sampled during early and late dispersal periods, respectively. The category "firs" includes Douglas-fir and white fir. Significant differences ($P < 0.01$) indicated by asterisks.

to quantify relative availability of cover types within the areas traversed by owls, so we cannot compare habitat use to availability. In the late-dispersal period, owls roosted at significantly lower elevations than during the early-dispersal period (MRBP: $\bar{x} = 1{,}753 \pm 44.4$ m vs. $2{,}177 \pm 25.4$ m, $P = 0.017$), which is consistent with the observed differences in cover types used between periods.

Proportional use of roost tree species also differed significantly between early and late dispersal periods ($P = 0.02$). Relative to the early dispersal period, owls roosted in Gambel oak significantly less often (P = 0.004) and in pinyon pine and junipers ($P = 0.01$) significantly more often in the late dispersal period period (Fig. 4). Given the observed variation in use of cover types between dispersal periods, differences in tree species used may have reflected patterns of relative availability of trees.

Survival rates.—Survival was relatively high during the period between fledging and the onset of radiotagging activities during both years ($\hat{s}_1$; Table 2). We may have underestimated survival if any owls were alive but unlocated. Because juveniles are typically found with the adults and/or their siblings at this time (Rinkevich et al. 1995) and thus easily located, such underestimation is unlikely.

Kaplan-Meier estimates of survival rates for radiotagged owls ($\hat{s}_2$; Table 2) differed between cohorts in both models used (log rank test: $P = 0.043$ and 0.034 for models 1 and 2, respectively). Estimates of mean survival time for the 1994 and 1995 cohorts, respectively, were: model 1: 98.7 ± 14.1 vs. 270.2

TABLE 2. Estimated survival rates of radiotagged juvenile Mexican Spotted Owls in Arizona, 1994 and 1995.

Cohort	n	Model[a]	$\hat{s}_1$[b]	$\hat{s}_2$[c]	Annual survival[d]	95% confidence interval[e]
1994	12	1	0.833	0.173	0.144	0.000–0.957
		2	0.833	0.101	0.084	0.000–0.241
1995	13[f]	1	0.923	0.556	0.513	0.032–0.994
		2	0.923	0.486	0.449	0.000–0.900
Both	25	1	0.880	0.326	0.287	0.000–0.751
		2	0.880	0.233	0.205	0.000–0.561

[a] Model 1 censored all owls with unknown fates; model 2 assumed that owls with transmitters tracked to burrows were dead.

[b] Survival from date fledged through date radiotagged.

[c] Survival from date radiotagged until bird died or was censored.

[d] Annual survival = ($\hat{s}_1 \times \hat{s}_2$).

[e] Confidence intervals for annual survival computed using equation 4 from Pollock et al. (1989).

[f] Includes one owl that was alive at beginning of radiotagging operations but not captured and radiotagged.

± 58.9 days; model 2: 85.9 ± 10.9 vs. 242.4 ± 57.7 days.

Eight owls (33.3%) were confirmed dead, with another four (16.7%) suspected to be dead (radios found in burrows). Three owls found dead were emaciated and appeared to have starved. In the other five cases transmitters were found among piles of feathers and bones, suggesting predation as the cause of death. Great Horned Owl (*Bubo virginianus*) feathers were found under a tree near one recovered transmitter, but we were unable to positively identify the predator responsible. In fact, we cannot be certain that these cases represent predation, as we cannot rule out scavenging following death from other causes. It is also possible that disease or injury could have predisposed birds to death from predation or starvation. For example, one bird that apparently starved suffered an obvious eye injury approximately two weeks before dying. It appeared to become lethargic following the injury, which may have reduced its ability to hunt or avoid avian predation effectively.

DISCUSSION

Dispersal behavior.—Our attempt to monitor dispersal behavior of juvenile Mexican Spotted Owls met with limited success. Because we were able to track only one owl until it settled and paired, we are unable to comment meaningfully on the process of natal dispersal (e.g., Greenwood et al. 1979) for this owl. We are also unable to comment meaningfully on dispersal distance for the same reason. Thus, our results primarily document timing of dispersal, movement patterns, and habitat use of juvenile owls during dispersal.

With respect to timing of dispersal and movement patterns, our results were generally consistent with other studies on all three subspecies of Spotted Owls (Forsman et al. 1984, Gutiérrez et al. 1985, Laymon 1988, Miller 1989, Willey 1995, Hodgson and Stacey 1996). All owls dispersed from natal areas over a 4–5 week period in September and October. Initial dispersal movements tended to be rapid and abrupt (Fig. 1). Rapid movements sometimes continued for a period of several days or weeks interspersed with periods when owls were more sedentary. Individual owls moved directionally at times, but more often wandered or even reversed direction, and there was no significant directional pattern to movements of either cohort.

Dispersing juveniles were located in a variety of habitats ranging from high-elevation forests to pinyon-juniper woodlands and riparian areas surrounded by desert grasslands. Some juveniles remained in forests similar to typical Spotted Owl breeding habitat. For example, the juvenile that settled in an historic territory consistently roosted within the historic nest grove, suggesting that even inexperienced juveniles recognize typical breeding habitat when they encounter it. In contrast, four other juveniles that were monitored beyond mid-November moved down in elevation, with at least two establishing apparent home ranges, on which they were repeatedly located over a period of several months, in pinyon-juniper woodlands. These woodlands were very different in habitat composition and structure from known breeding habitat of Mexican Spotted Owls. This may indicate that dispersing owls were not assessing habitat suitability in the context of typical breeding habitat. Some dispersing owls settled and survived in these atypical habitats for considerable periods, and some adult Mexican Spotted Owls migrated to pinyon-juniper woodlands during the winter (Ganey et al. 1992, Rinkevich et al. 1995). Thus, some habitats not suitable for breeding may have met the needs of this owl during the nonbreeding season. If so, modeling habitat connectivity for Mexican Spotted Owls based solely on the distribution of typical breeding habitat may be inappropriate. Thomas and coworkers (1990) also recognized that habitats not suitable for breeding could meet the needs of dispersing owls, and explicitly incorporated "dispersal" habitat in their proposed conservation strategy.

Population models incorporating dispersal behavior in Northern Spotted Owls (Thomas et al. 1990, Lamberson et al. 1994; see also Doak 1989) have assumed, either explicitly or implicitly, that dispersing owls move randomly, evaluate habitats as they encounter them, and settle in the first vacant habitat of suitable quality. This is a highly efficient search pattern and model results depend strongly on this pattern (Thomas et al. 1990, Harrison et al. 1993, Lamberson et al. 1994). Our results were equivocal with respect to how well these models describe the behavior of dispersing owls. Most of the owls we monitored appeared to move randomly, but also appeared to move too rapidly to be assessing either habitat quality or occupancy status of areas traversed (see also Hodgson and Stacey 1996). However, most of these owls died. The one successful disperser we monitored used a dispersal strategy consistent with these models.

The timing of dispersal in Spotted Owls also seems to present problems in terms of assessing habitat occupancy. Calling rates of Ural (*S. uralensis*) and Eastern Screech-Owls (*Otus asio*) increase during the dispersal period (Lundberg 1980, Ritchison et al. 1988), possibly to advertise occupancy status and discourage dispersing juveniles from attempting to settle in an occupied area (Lundberg 1980, Belthoff and Ritchison 1989). In contrast, vocalizations of Mexican Spotted Owls declined in frequency during the dispersal period (Ganey 1990). Further, the adults begin to wander more widely during this period and are sometimes located considerable distances from nest areas (Ganey and Balda 1989). Thus, dispersal in Mexican Spotted Owls occurs at a time when it may be difficult for juveniles to accurately assess ocupancy status of suitable habitat.

Survival estimates.—Our estimates of first-year survival of juvenile owls fall within the range reported in studies of Northern and California Spotted Owls (Gutiérrez et al. 1985, Miller 1989, Noon et al. 1992, Burnham et al. 1996), are close to the estimate based on resightings of banded birds on the Coconino study area (28.6 ± 7.9%; White et al. 1995), and are consistent with high mortality rates reported for first-year individuals of Spotted and other owls (Southern 1970, Forsman et al. 1984, Gutiérrez et al. 1985, Korpimäki and Lagerstrom 1988, Laymon 1988, Belthoff and Ritchison 1989, Miller 1989). These estimates for Mexican Spotted Owls should be viewed as preliminary, however, for several reasons. First, fate was unknown for 58% of the radiotagged owls. Although the Kaplan-Meier estimator is able to handle right-censored data resulting from radio failure or inability to relocate owls (Pollock et al. 1989), the number of owls for which fate was unknown still argues for cautious use of survival estimates. Second, initial sample sizes were small, resulting in large confidence intervals around survival estimates. Third, variability among years was significant (Table 2). Based on these factors, we suspect that tracking of hundreds of owls over at least 10 years will be required to accurately and precisely estimate annual survival rates of juvenile owls.

The pronounced difference in survival estimates between time intervals in both years might suggest that radiotagging juvenile owls negatively affects their survival. Although we cannot rule out an effect of radiotags on survival, we suspect that such an effect was small if it existed at all. Mortality of radiotagged owls was minimal until they initiated dispersal, at which time mortality increased dramatically. Consequently, we suspect that the high mortality rate observed among radiotagged owls was due to the rigors of dispersal rather than to the effect of carrying a radio.

Predation and starvation appeared to be important causes of juvenile mortality during dispersal (see also Hirons et al. 1979, Forsman et al. 1984, Gutiérrez et al. 1985, Miller 1989). The prevalence of starvation could be due to the relative inexperience of dispersing juveniles, coupled with the difficulties of foraging in unfamiliar terrain. Predation risks may also be greater for owls travelling through unfamiliar terrain, and particularly for owls undergoing nutritional stress (Hirons et al. 1979).

Conclusions.—Better information on dispersal patterns, habitat use, and survival rates of juveniles is clearly needed. Until such information is available, our ability to model population dynamics and/or habitat connectivity will be limited. Our attempts to gather reliable information on these aspects of the ecology of Mexican Spotted Owls met with limited success. Problems with premature molt of tail feathers [also documented by Reid et al. (1996)] and suspected radio failure limited our ability to follow birds for extended periods and/or to positively determine their fate. Problems with premature molt could be addressed by attaching radios using backpack harnesses, but there is concern over the effects of backpack radios on Spotted Owls in general (Paton et al. 1991, Foster et al. 1992) and on juvenile owls in particular. These problems suggest that hundreds of owls may need to be radiotagged to ensure that adequate numbers are tracked successfully. The pronounced differ-

ence in survival estimates between years suggests that long-term studies will be required.

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