HOME RANGE, HABITAT USE, SURVIVAL, AND FECUNDITY OF MEXICAN SPOTTED OWLS IN THE SACRAMENTO MOUNTAINS, NEW MEXICO

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ABSTRACT—We studied home range, habitat use, and vital rates of radio-marked Mexican spotted owls (*Strix occidentalis lucida*) in 2 study areas in the Sacramento Mountains, New Mexico. One study area (mesic) was dominated by mixed-conifer forest, the other (xeric) by ponderosa pine (*Pinus ponderosa*) forest and piñon (*P. edulis*)-juniper (*Juniperus*) woodland. Based on existing knowledge of relative use of forest types by Mexican spotted owls, we predicted that the mesic area would provide habitat of higher quality for spotted owls. Results generally supported this prediction. Median home-range size for owls in the mesic area was approximately half that of owls in the xeric area during both the breeding and non-breeding seasons ($n = 6$ owls in each area). Despite their reduced size, however, mesic-area home ranges contained twice as much mixed-conifer forest as xeric-area ranges. Owls roosted primarily (>80% of roosting locations in both seasons) in mixed-conifer forest in both study areas, and home-range size was inversely related to relative amount of mixed-conifer forest within the home range during both seasons. Both survival and fecundity rates were higher in the mesic than in the xeric area. Estimates of population trend based on observed vital rates suggested that the population in the mesic area was self-sustaining or nearly so during the period of study (1992 through 1994), but the population in the xeric area was not. Collectively, our findings suggest that habitat quality for spotted owls was higher in the mesic area than in the xeric area, and that the xeric area might function as an ecological sink. These results support the need for data linking demographic performance to habitat conditions in development of strategies for recovering threatened and endangered species.

RESUMEN—Estudiamos el rango de hogar, uso de hábitat, y las tasas vitales de los tecolotes manchados mexicanos (*Strix occidentalis lucida*) en 2 áreas de estudio en las Sacramento Mountains de New Mexico, USA. Un área de estudio (mésica) estuvo dominada por bosques de coníferas mixtas, la otra (xérica) por bosques de pino ponderosa (*Pinus ponderosa*) y bosques leñosos de pino piñonera (*P. edulis*) y enebros (*Juniperus*). Basados en el conocimiento existente del uso relativo de tipos de bosques por el tecolote manchado mexicano, predecimos que el área mésica proveería un hábitat de la más alta calidad para los tecolotes. Los resultados en general respaldan esta predicción. El tamaño medio del rango de hogar para los tecolotes en el área mésica fue aproximadamente la mitad de el de los tecolotes en el área xérica durante y fuera de la temporada de reproducción ($n = 6$ tecolotes en cada área). A pesar de sus tamaños reducidos, sin embargo, los rangos de hogar mésicos contuvieron el doble de bosques de coníferas mixtas que los rangos de hogar xéricos. Los tecolotes pasaron la noche (>80% de los lugares de descanso en ambas temporadas) principalmente en bosques de coníferas mixtas en ambas áreas de estudio, y el tamaño del rango de hogar estuvo inversamente relacionado a la cantidad relativa de bosques de coníferas mixtas dentro del rango de hogar durante ambas temporadas. Las tasas de supervivencia y fecundidad fueron más altas en el área mésica que en la xérica. Estimaciones de las tendencias poblacionales basadas en observaciones de tasas vitales sugieren que la población en el área mésica se sostuvo sola o casi se sostuvo durante el período de estudio (1992 a 1994), pero la población en el área xérica no. Colectivamente, nuestros hallazgos sugieren que la calidad del hábitat para los tecolotes manchados fue más alta en el área mésica que en la xérica, y que el área xérica puede operar como un sumidero ecológico. Estos resultados respaldan la necesidad de considerar juntos los datos de rendimiento demográfic y los de condiciones de hábitat en desarrollar estrategias para la recuperación de especies amenazadas y en peligro de extinción.

The theory of habitat selection assumes that habitats vary in quality for particular organisms, and that such variation has implications for the fitness of individuals occupying those habitats (Rosenzweig, 1981). In extreme cases, some occupied habitats might serve as population sources, producing surplus individuals, whereas others function as sinks, in which reproduction does not balance mortality (Pulliam, 1988). Because not all occupied habitats might be equal in quality for a particular species, understanding relationships between habitat composition and quality is critical to designing effective conservation strategies for threatened and endangered species.

The Mexican spotted owl (*Strix occidentalis lucida*) is widely but patchily distributed throughout the southwestern United States and northern Mexico (Gutiérrez et al., 1995; Ward et al., 1995). It is associated with mature forests throughout much of its range, although it also occurs in non-forest habitats, such as rocky canyonlands (Ganey and Dick, 1995; Gutiérrez et al., 1995), and it was listed as threatened in the USA in 1993 because of concern over the impacts of logging and stand-replacing fire on its forest habitat (United States Department of the Interior, 1993). Previous studies documented differences in home-range size (reviewed in Ganey and Dick, 1995), density, survival, and fecundity (Seamans et al., 1999) between subpopulations of Mexican spotted owls in different habitats. However, the subpopulations studied were widely separated geographically. Consequently, observed differences could have been driven by differences in local habitat quality, differences due more to biogeographic effects (e.g., differences in climate pattern or biogeographic region), or both (Ganey and Dick, 1995).

We studied movements and habitat use by radio-marked Mexican spotted owls in 2 study areas that differed in habitat composition in the Sacramento Mountains, New Mexico. This mountain range provided an opportunity to study owls in different habitats within a limited geographic area, and thus to focus on the relationship between local habitat features and habitat quality. Many Mexican spotted owls occur in montane landscapes dominated by closed-canopy mixed-conifer forest in the Sacramento Mountains, whereas others occur in montane landscapes dominated by more open

piñon (*Pinus edulis*)-juniper (*Juniperus*) woodlands (Skaggs and Raitt, 1988; Zwank et al., 1994). Mexican spotted owls are most common in mixed-conifer forests throughout their range (Ganey and Dick, 1995) and are relatively uncommon in piñon-juniper woodlands, except where such woodlands occur in rocky canyonlands (Ganey and Dick, 1995; Gutiérrez et al., 1995). In the Sacramento Mountains, Mexican spotted owls attain much higher densities in areas dominated by mixed-conifer forest than in areas dominated by drier forest and woodland types (Skaggs and Raitt, 1988; Ward et al., 1995). This implies that these habitats differ in quality for spotted owls (but see Van Horne, 1983).

Elsewhere, we have used data from these radio-marked owls in comparative analyses of roost site characteristics and structural characteristics of forest stands used (Ganey et al., 2000, 2003). Our objectives here were to: 1) estimate size and composition of spotted owl home-ranges; 2) evaluate use of cover types for roosting within home ranges of radio-marked owls; 3) estimate survival and fecundity of radio-marked owls; and 4) compare the above parameters between study areas. Based on current understanding of habitat relationships of Mexican spotted owls in general (Ganey and Dick, 1995; Gutiérrez et al., 1995) and in the Sacramento Mountains in particular (Ganey et al., 2000, 2003), we predicted that the area dominated by mixed-conifer forest would provide higher-quality habitat for spotted owls than the area dominated by piñon-juniper woodland. Following from this general prediction, we generated and tested a suite of specific predictions relative to home-range size, use of cover types, and vital rates of owls (Table 1).

METHODS—*Study Area*—This study was conducted within the Sacramento Ranger District of the Lincoln National Forest, located in the Sacramento Mountains of south-central New Mexico. This range is located near the eastern edge of the Basin and Range physiographic province and forms a montane island surrounded by a desert and semi-desert matrix (Kaufmann et al., 1998). Elevation within the range varies from 1,300 m to 3,700 m, and temperature and precipitation consequently vary greatly throughout the range. Precipitation generally increases with elevation and falls mainly in 2 seasons. Thunderstorms during July and August typically provide more than 60% of annual precipitation, with

TABLE 1—Predictions tested relative to habitat quality for Mexican spotted owls (*Strix occidentalis lucida*) in 2 study areas in the Sacramento Mountains, New Mexico. One area (mesic) was dominated by mixed-conifer forest, the other (xeric) by drier forest and woodland types generally considered less suitable for occupancy by Mexican spotted owls. All predictions are related and build on the premise that mixed-conifer forests provide higher-quality habitat for Mexican spotted owls than other forest and woodland types in this area.

Parameter estimated	Prediction tested
Use of cover types	Mixed-conifer forest used more than expected, based on relative area
Relative availability of mixed-conifer forest	Greater in mesic home ranges than in xeric home ranges
Relative availability of mixed-conifer forest	Inversely related to home-range size
Home-range size	Smaller in mesic home ranges than in xeric home ranges
Survival and fecundity	Both rates greater in the mesic area than in the xeric area
Finite rate of increase (λ)	Greater in the mesic area than in the xeric area

most of the remainder occurring during winter (December to March; Kaufmann et al., 1998). This mountain range features a long growing season, fertile soils, and productive montane forests. Major natural disturbance agents structuring these forests historically included fire and insect outbreaks. Since approximately 1900, forest structure has been intensively influenced by human activities, including logging, fire suppression, grazing, and farming within montane meadows (Kaufmann et al., 1998).

Because of the pronounced variability in elevation and topography in this range, considerable variability exists in biotic communities. We selected 2 study areas representing different habitat configurations. The first area (hereafter referred to as the mesic study area) was located along the Rio Peñasco approximately 12 km southeast of Cloudcroft, New Mexico. Montane canyons dominated topography in this area, where elevation ranged from 2,400 to 2,800 m. Montane meadows were common in canyon bottoms, whereas most canyon slopes and ridgetops were forested. The predominant forest type was a mesic mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), or both. Southwestern white pine (*Pinus strobiformis*) was prominent in most stands, and ponderosa pine (*P. ponderosa*) and quaking aspen (*Populus tremuloides*) were common.

In contrast, drier cover types dominated the second study area. This area (xeric study area) was located in and around the Sixteen Springs drainage approximately 18 km northeast of Cloudcroft and approximately 30 km from the mesic study area. Elevation in this area ranged from 2,000 to 2,500 m, and montane canyons again dominated topography. Vegetation in this area consisted of a complex mosaic of mesic and xeric forest types. Mixed-conifer forest was restricted to cooler microsites, such as

drainage bottoms and north-facing slopes. Woodlands of piñon pine and alligator juniper (*Juniperus deppeana*) dominated most ridgetops and south-facing slopes. Other slopes were dominated by ponderosa pine forest, sometimes with a prominent component of Gambel oak (*Quercus gambelii*). Gray oak (*Q. griseus*) and wavyleaf oak (*Q. undulatus*) also were present in some areas.

Radiotelemetry Methods—We captured owls ($n = 15$) using noose poles or mist nets (Forsman, 1983). Radio transmitters (Telonics Inc., Mesa, Arizona) were attached using a backpack harness constructed of 6-mm tubular Teflon ribbon. Transmitter (plus harness) packages weighed approximately 18 g. Radio signals were received using Telonics TR-4 receivers and hand-held 3-element Yagi antennas.

We monitored owls 4 to 5 days and nights per week throughout the year and located owls at all hours of the day and night. We used only one location per individual per day or night in analyses, in an attempt to reduce spatial autocorrelation between locations (Swihart and Slade, 1985) while simultaneously obtaining sufficient sample sizes to define range use adequately (Otis and White, 1999). We classified all nocturnal locations as foraging locations and all diurnal locations as roosting locations (Forsman et al., 1984). We did not use locations of incubating or brooding females in analyses, because nesting females are restricted to the nest area for approximately 2 months.

Nocturnal locations were based on triangulation of compass bearings to the radio-marked owl from ≥3 known locations (typically fixed tracking points established at 0.16-km to 0.32-km intervals along roads). We accepted locations only if ≥3 bearings formed an intersection polygon <2 ha in size. For intersection polygons ≥2 ha in size, we estimated bearings from different tracking points until a suit-

able polygon was obtained. We assumed that the owl was located at the center of the intersection polygon.

When locating owls during the day, we first estimated the location by triangulation and then visually located the owl on its roost (Carey et al., 1990). We used these paired visual and triangulated locations to evaluate accuracy in assigning triangulated locations to habitat polygons (see Use of Cover Types below). These procedures provided only a rough estimate of accuracy for nocturnal locations, however, because animal movements also affect accuracy of triangulations (Schmutz and White, 1990), and spotted owls typically do not move much during the day (Sovern et al., 1994).

Home-range Size—We estimated home-range size using program TELEM (K. S. McKelvey. 1993. Program Telem. United States Department of Agriculture Forest Service, Pacific Southwest Research Station. Albany, California). We used 95% adaptive-kernel (Worton, 1989) estimates of home-range size in all analyses.

Previous studies in different geographic areas and habitats documented seasonal differences in both home-range size and habitat use of Mexican spotted owls (Ganey and Balda, 1989). Therefore, we computed separate estimates of home-range size for the breeding (1 March to 31 August; Ganey and Balda, 1989) and non-breeding (1 September to 28 February) seasons. We pooled locations among years for seasonal home-range estimates, because geographic area used by individual owls within a season remained constant across years.

Range estimates can be biased by small sample sizes (<50; Seaman et al., 1999) or short tracking periods. Consequently, we estimated seasonal home ranges for individuals only where the cumulative number of locations was ≥80 and the owl was tracked for at least 5 months during that season. This left a sample of 6 owls on each area. We evaluated potential relationships between sample size (number of locations) and estimates of home-range size using Spearman's rank correlation coefficient (Conover, 1980:252–256). We tested the hypothesis that range size did not differ between study areas within a season using the Mann-Whitney test (Conover, 1980:216–223).

Home-range Composition—We quantified habitat composition within owl home ranges using United States Forest Service (USFS) stand maps to delineate habitat polygons. We assigned polygons to 1 of 3 broad cover types, based on ground reconnaissance of all mapped polygons. Cover types recognized were mixed-conifer forest, ponderosa pine forest, and "other," which included aspen forest, piñon-juniper woodland, and mountain meadow. We used a geographical information system (GIS; ARC/INFO, Environmental Systems Research Institute, Redlands, California) and a digital coverage of USFS-delineated forest stands to estimate area of each cover type within individual home ranges. We dropped one owl in the xeric area from this and other analyses involving habitat composition, because cover type information was not available for parts of its home range.

Numerous studies (summarized by Ganey and Dick, 1995) suggested that owls selected for mixed-conifer forests. Consequently, we focused 2 analyses specifically on mixed-conifer forest. The first tested the null hypothesis that amount of mixed-conifer forest within seasonal home ranges did not differ between study areas (Mann-Whitney test). The second assessed the relationship between proportion of home ranges consisting of mixed-conifer forest and seasonal home-range size, using linear regression. We used an arcsine-square root transformation (Zar, 1984) to normalize proportions.

Use of Cover Types—We assessed use of cover types by owls relative to the availability of those types within the home range (third-order habitat selection; Johnson, 1980). However, our evaluation of paired visual and triangulated roost locations indicated that triangulated locations could not be assigned to habitat polygons reliably (only 47.3% of 932 paired locations were mapped in the same polygon). Consequently, we restricted our analyses of cover-type use to locations based on visual observations of roosting owls. We estimated resource selection ratios for cover types following Manly et al. (1993; Design III). Analyses were stratified by season and study area.

Estimation of Survival Rates and Fecundity—All radio-marked owls were included in estimates of survival rates and fecundity. We estimated survival rates of radio-marked owls using a modification of the Kaplan-Meier method (Pollock et al., 1989). This method allows for staggered entry (i.e., not all animals are radio-marked at the same time) and inclusion of right-censored data resulting from radio failure. We estimated both annual survival rates and cumulative survival over the course of the study. For annual estimates, individuals still alive on the anniversary of the date they were radio-marked were censored and recycled back into the sample. Thus, in this analysis, the number of entries exceeded the number of individual owls (White et al., 1995). We used a log-rank test to compare survival distributions between study areas (Norušis, 1994).

We estimated fecundity for all territories containing radio-marked owls by using standard methods for demographic studies of spotted owls (Franklin et al., 1996). We assumed a 1:1 sex ratio in fledglings (Franklin et al., 1996) and estimated fecundity for each territory as mean number of female young fledged/year. We tested for differences in fecundity between study areas using the Mann-Whitney test.

We estimated the finite rate of population change (λ) for owls in both study areas after Pulliam (1988):

$$\lambda = S_a + B(S_j)$$

where S_a = adult survival, B = mean fecundity, and S_j = juvenile survival. We used point estimates of adult survival and fecundity from this study in these calculations, and set juvenile survival = 0.28 after White et al. (1995) and Ganey et al. (1998).

RESULTS—*Home Range Size and Composition*— We captured and radio-marked 9 male and 6 female owls. All owls remained within the same general area throughout the year, with no seasonal migration observed. Number of locations for owls included in home-range estimates averaged 269 ± 17.4 (*SE*) and 230.3 ± 21.3 locations for the mesic area during the breeding and non-breeding seasons, respectively. Number of locations for owls included in the xeric area averaged 208.7 ± 20.6 and 146.5 ± 27.7 locations during the breeding and non-breeding seasons, respectively. The number of locations was not correlated with range size in either study area during either season (all *P* values > 0.05). Thus, numbers of locations seemed to be adequate for estimating the utilization distribution in all cases.

Home-range size was significantly greater in the xeric than in the mesic study area during both seasons (Fig. 1; Mann-Whitney tests, *P* = 0.023 and 0.039 for breeding and non-breeding seasons, respectively). Home ranges of radio-marked owls in the mesic study area consisted of primarily mixed-conifer forest during both seasons (Fig. 2). Home-range composition was more diverse in the xeric study area. The "other" cover type dominated home ranges in this area (Fig. 2), with piñon-juniper woodlands contributing greatly to that category. Piñon-juniper woodlands comprised 31.6 ± 6.9% of breeding season home-range area and 40.5 ± 7.1% of non-breeding season home-range area in the xeric area. Although home ranges in the mesic area were approximately half as large as home ranges in the xeric area, they contained more than twice as much mixed-conifer forest as home ranges in the xeric area (breeding season, medians = 187.3 and 64.3 ha for the mesic and xeric areas, respectively, *P* = 0.004; non-breeding season, medians = 250.6 and 101.9 ha for the mesic and xeric areas, respectively, *P* = 0.009). More than 50% of home-range area consisted of mixed-conifer forest for all mesic home ranges in both seasons (Fig. 3). In contrast, mixed-coni-
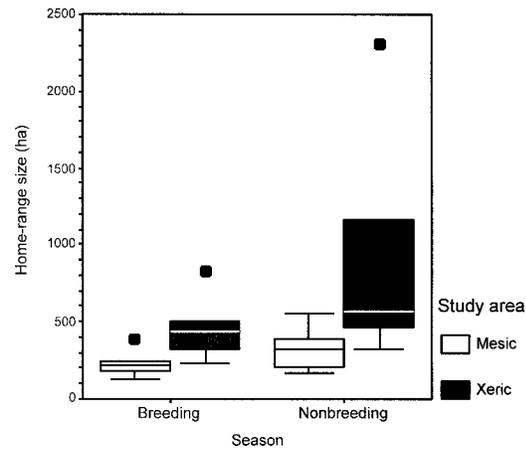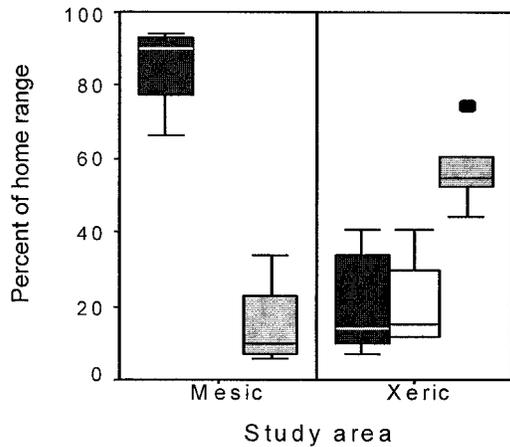

FIG. 1—Seasonal home-range size (95% adaptive kernel estimate) of radio-marked Mexican spotted owls (*Strix occidentalis lucida*) in 2 study areas in the Sacramento Mountains, New Mexico. Boxes indicate the range from the 25th to 75th percentiles, solid lines within boxes denote the median, and the whiskers denote the range excluding outliers. Outliers (observations >1.5 times the box length outside the box) are denoted by circles. Six owls in each study area met sample-size requirements for estimating home-range size (see Methods–Home-range Size).

fer forest comprised <50% of home-range area for all xeric area home ranges in both seasons. Home-range size was inversely related to the proportion of the range in mixed-conifer forest in both seasons (Fig. 3).

Use of Cover Types—Owls in both study areas roosted primarily in mixed-conifer forest in both seasons (Table 2). Use of mixed-conifer forest was significantly greater than expected in both seasons in the mesic area and during the non-breeding season in the xeric area. Owls in the xeric area also roosted primarily in mixed-conifer forest during the breeding season (Table 2), but the confidence interval around the selection ratio (0.972 to 8.351) was extremely large and included one. Selection ratios around both other cover types were significantly <1 in both study areas during both seasons (Table 2).

Survival and Fecundity—Annual adult survival rates were greater in the mesic area (0.87 ± 0.09) than in the xeric area (0.62 ± 0.14), but survival distributions did not differ significantly (log-rank test, *P* = 0.194; Fig. 4a). Estimates of cumulative survival over the study period (792 days) were 0.75 ± 0.15 and 0.29 ± 0.17
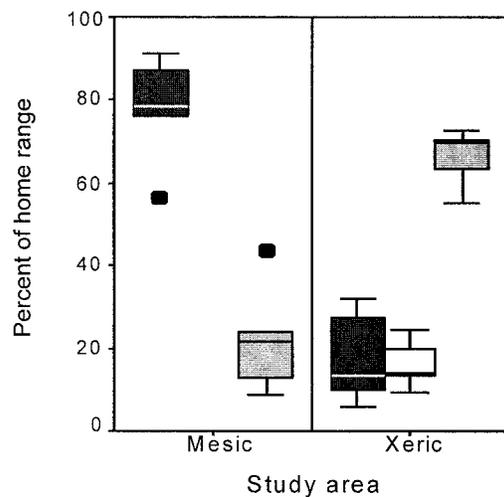
A) Breeding Season
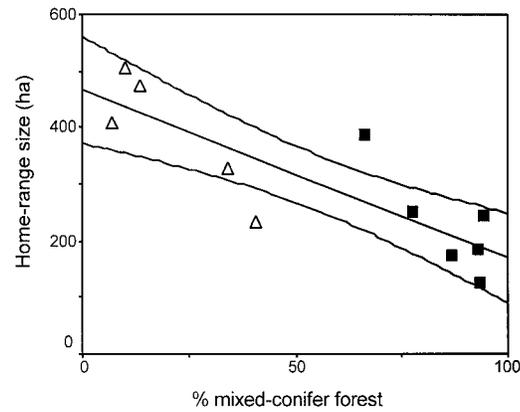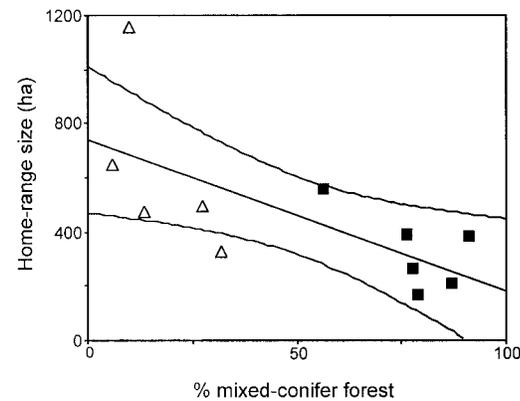

B) Nonbreeding Season

FIG. 2—Home-range composition of radio-marked Mexican spotted owls (*Strix occidentalis lucida*) in 2 study areas in the Sacramento Mountains, New Mexico. $n = 6$ and 5 owls in the mesic and xeric study areas, respectively. One owl in the xeric area was omitted due to missing data on cover-type composition within its home range. Boxes indicate the range from the 25th to 75th percentiles, solid lines within boxes denote the median, and the whiskers denote the range excluding outliers. Outliers (observations >1.5 times the box length outside the box) are denoted by dots. Cover types represented: black = mixed-conifer, white = ponderosa pine, and shaded = other.

A) Breeding Season

B) Non-breeding Season

FIG. 3—Relationship between home-range size of radio-marked Mexican spotted owls (*Strix occidentalis lucida*) and proportion of the home range consisting of mixed-conifer forest in 2 study areas in the Sacramento Mountains, New Mexico. Squares denote home ranges in the mesic study area, and triangles denote home ranges in the xeric study area. Regression line and 95% confidence limits shown. A) breeding season; adjusted $r^2 = 0.726$, $P = 0.001$, *SE* = 42.0 (intercept) and 44.6 (slope). B) non-breeding season; adjusted $r^2 = 0.598$, $P = 0.003$, *SE* = 110.1 (intercept) and 128.0 (slope). $n = 6$ and 5 owls in the mesic and xeric study areas, respectively. One owl in the xeric area was omitted due to missing data on cover-type composition within its home range.
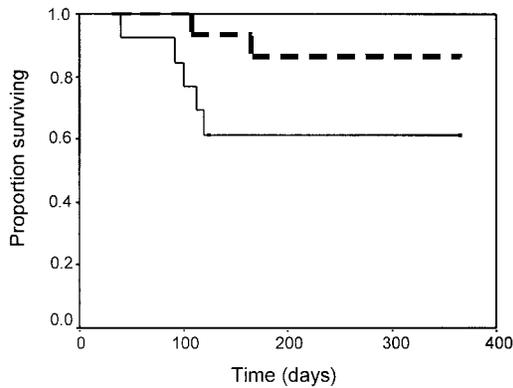
TABLE 2—Resource selection ratios for use of cover types for roosting by radio-marked Mexican spotted owls (*Strix occidentalis lucida*) in 2 study areas in the Sacramento Mountains, New Mexico, during the breeding and non-breeding seasons. Selection ratios ($\hat{w}_i$) computed following Manly et al. (1993). $n = 6$ owls in the mesic area and $n = 5$ owls in the xeric area.

Study area	Season	Cover type	Mean proportion of home range	Mean proportion of locations	$\hat{w}_i$[a]	SE_{w_i}	B_i[b]
Mesic	Breeding	Mixed-conifer	0.852	0.972	1.143 (+)	0.042	0.860
		Ponderosa pine	0.000				
		Other	0.148	0.028	0.187 (−)	0.086	0.140
Mesic	Non-breeding	Mixed-conifer	0.778	0.961	1.259 (+)	0.052	0.884
		Ponderosa pine	0.000				
		Other	0.222	0.039	0.166 (−)	0.095	0.116
Xeric	Breeding	Mixed-conifer	0.212	0.892	4.662	1.541	0.947
		Ponderosa pine	0.216	0.029	0.119 (−)	0.058	0.024
		Other	0.572	0.079	0.140 (−)	0.076	0.028
Xeric	Non-breeding	Mixed-conifer	0.178	0.802	4.949 (+)	1.452	0.886
		Ponderosa pine	0.162	0.078	0.454 (−)	0.071	0.081
		Other	0.660	0.120	0.180 (−)	0.027	0.032

[a] Ratios followed by (+) indicate positive selection for that cover type (i.e., lower limit of 95% Bonferroni confidence interval around $\hat{w}_i$ is >1). Ratios followed by (−) indicate selection against that cover type (i.e., upper limit of 95% Bonferroni confidence interval around $\hat{w}_i$ is <1).

[b] B_i = standardized resource selection ratio. These values sum to one within a study area and season, and can be crudely interpreted as denoting relative probabilities of use of cover types given equal availability of those units.

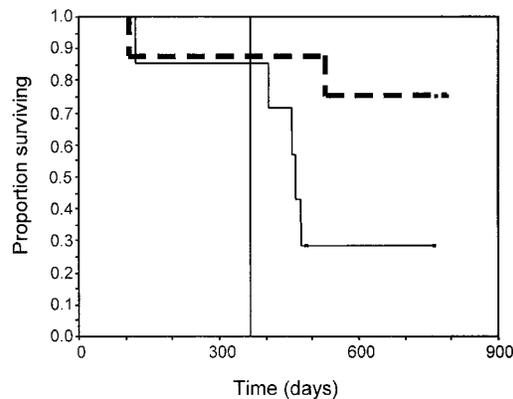## A) Annual Survival

B) Cumulative Survival

FIG. 4—Kaplan-Meier survival distributions for radio-marked Mexican spotted owls (*Strix occidentalis lucida*) in 2 study areas in the Sacramento Mountains, New Mexico. $n = 8$ owls in the mesic area (dashed line) and 7 owls in the xeric area (solid line), respectively. A) annual survival. B) cumulative survival over the period of study (1992 to 1994). Vertical reference line indicates end of the first year of radiotracking (August 1993). Note that survival distributions for the 2 areas diverge in the second winter.

for the mesic and xeric areas, respectively (log-rank test, $P = 0.057$). Visual inspection of cumulative survival distributions showed that survival distributions were similar in both study areas for the first year of radiotracking, but diverged greatly in the second winter (1993–1994; Fig. 4b). Survival remained essentially constant between years in the mesic area (e.g.,

$0.87^2 = 0.76$) but decreased markedly in the xeric area during the second winter.

We verified mortality of 6 spotted owls during the study: 2 in the mesic area and 4 in the xeric area. All mortalities occurred from December through February, and 4 occurred during winter 1993–1994 (Fig. 4b). One owl from the xeric area was recovered intact and necropsied at the National Wildlife Health Research Center (United States Fish and Wildlife Service) in Madison, Wisconsin. This owl was emaciated with no observable fat stores and marked muscle wasting, suggesting starvation as cause of death. The other 5 mortalities seemed to be attributable to avian predation, as evidenced by plucked feathers located near recovered transmitters. Two owls from the xeric area likely were killed while feeding during the day in open habitat. Both were observed feeding on rabbits (*Sylvilagus*) on the ground in meadows during the day, then found dead the next day at the same location. Diurnal foraging was rarely observed in either area outside of this time period, and diurnal foraging in meadows was never observed in the mesic area.

Annual fecundity also was lower in the xeric area than in the mesic area (mean = 0.13 ± 0.08 vs. 0.38 ± 0.11 female young fledged/territory/yr, respectively), although this difference was not significant (Mann-Whitney test, $P = 0.127$). Most pairs in the xeric area produced no young during this period.

Based on the observed vital rates, estimates of population change during the period of study (1992 to 1994) were 0.96 for the mesic area and 0.70 for the xeric area.

DISCUSSION—Our results demonstrated that: 1) owls in both areas selected mixed-conifer forests for roosting (Table 2); 2) range size was inversely related to proportion of mixed-conifer forest (Fig. 3); 3) mesic-area ranges contained more mixed-conifer forest than xeric-area ranges; 4) owls in the xeric area used larger home ranges than owls in the mesic area (Fig. 1); and 5) demographic rates were higher in the mesic area than in the xeric area (Fig. 4). Survival and reproductive rates in the mesic area seemed to be approximately adequate for a self-sustaining population, whereas vital rates in the xeric area did not seem sufficient for a

self-sustaining population during the period of the study.

Collectively, these results suggested a difference in habitat quality between study areas during the period of study. We recognize that our sample sizes were small, limiting the strength of inference possible. We would put little faith in a single line of evidence based on these sample sizes, but in this case, numerous lines of evidence suggesting differences in habitat quality between study areas vary in parallel fashion. This internal consistency among multiple indicators increased our confidence that the patterns we observed were real rather than an artifact of small samples.

Studies of northern spotted owls (*S. o. caurina*) also documented differences in range size, movement patterns, and fitness parameters among owls using different landscape configurations. In Oregon, owls in more open, fragmented landscapes used larger home ranges and traveled more widely within those home ranges than did owls in less fragmented landscapes (Forsman et al., 1984; Carey et al., 1992; Carey and Peeler, 1995), reflecting lower food availability in fragmented landscapes (Carey et al., 1992). This seems similar to our study, where owls in a study area dominated by more open forests and woodlands occupied larger ranges than owls in mesic mixed-conifer forests.

Franklin et al. (2000) demonstrated trade-offs between life history parameters and landscape configuration in mixed-evergreen forest in northwestern California. Survival rates of spotted owls were highest in closed-canopy forests, but fecundity was highest where forests were more fragmented by timber harvesting. This was apparently because the primary prey of spotted owls in the region, the dusky-footed woodrat (*Neotoma fuscipes*), was more available at the interface of late and early seral stages (Ward et al., 1998; see also Sakai and Noon, 1993), and such edges were created by clearcutting (Franklin et al., 2000). Consequently, overall fitness was highest for owls in landscapes that contained both patches of interior forest and nearby edges (Franklin et al., 2000).

No such tradeoffs in life-history parameters were evident in this study. Both survival and fecundity were lower in the xeric area than in the mesic area. Estimates of population change based on survival and fecundity rates (λ =

0.96) suggested that owls in the mesic area were producing approximately enough young for population maintenance, and 2 of 2 owls that died in this area were replaced in subsequent years. In contrast, the population in the xeric area did not seem to be self-sustaining during the period evaluated (λ = 0.70), and none of the 4 owls that died were replaced in subsequent breeding seasons in this area. This suggests that source-sink dynamics might operate at times within this mountain range, with owls persisting in the xeric area due to immigration from other areas during periods of high reproduction.

This does not mean that the xeric area is unimportant to maintenance of the overall owl population, however. For example, Howe et al. (1991) demonstrated in a modeling context that sink populations can contribute to the size and longevity of a metapopulation under some conditions. Further, if habitat in the mesic area is saturated, then owls dispersing to and reproducing in the xeric area might have higher fitness there than they would if they remained in the mesic area (Fretwell and Lucas, 1970; see also Zimmerman et al., 2003). Thus, despite providing habitat of relatively low quality, the xeric area still might contribute to overall stability of the owl population in the Sacramento Mountains.

We also recognize that survival rates and fecundity change over time, that relative habitat quality in our study areas might be dynamic, and that understanding the dynamics of this system relative to environmental variation will require longer studies involving more owls. Nevertheless, our results suggested that these areas differed in habitat quality for spotted owls during the period of study, and that source-sink dynamics might operate within this mountain range at times. Thus, our results support the idea that information on vital rates in different habitats (e.g., Franklin et al., 2000) is critical in developing appropriate conservation strategies for threatened species.

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