

PREY ECOLOGY OF MEXICAN SPOTTED OWLS IN PINE–OAK FORESTS OF NORTHERN ARIZONA

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Abstract: We studied Mexican spotted owl (*Strix occidentalis lucida*) diets and the relative abundance and habitat associations of major prey species in a ponderosa pine (*Pinus ponderosa*)–Gambel oak (*Quercus gambelii*) forest in north-central Arizona, USA, from 1990 to 1993. The owl's diet was comprised of 94% mammals by biomass and consisted of primarily the deer mouse (*Peromyscus maniculatus*), brush mouse (*P. boylii*), Mexican woodrat (*Neotoma mexicana*), and Mexican vole (*Microtus mexicanus*). Spotted owl prey in our study area were smaller on average than prey in other locations, and the total biomass of potential prey was less than that reported in other areas within the owl's geographic range. Although all prey populations exhibited seasonal fluctuations in relative abundance, only the deer mouse exhibited significant temporal variation in population abundance. The general pattern was for prey populations to rise during spring, peak during summer, decline in fall, and reach a winter low. Deer mice exhibited the greatest amplitude in population change as evidenced by the shift from a high of 12.2 mice/ha (SE = 2.3) during summer 1991 to a low of 3.3 mice/ha (SE = 0.7) during winter 1991–1992. Woodrats and brush mice used areas on slopes >20° with relatively more rocks and shrub cover than found in other areas. In contrast, deer mice were found in forests with relatively open understories and little Gambel oak. Conservation measures for the Mexican spotted owl must include management directed at sustaining or increasing prey numbers rather than assuming that managing for owl nesting and roosting habitat will provide favorable conditions for the prey as well. Management practices that increase and sustain shrub and herbaceous vegetation should receive the highest priority. This can be accomplished by thinning small diameter trees, using prescribed fire, and managing grazing pressures.

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Key words: brush mouse, deer mouse, diet, habitat selection, Mexican spotted owl, Mexican woodrat, *Neotoma mexicana*, north-central Arizona, *Peromyscus boylii*, *P. maniculatus*, ponderosa pine–Gambel oak forest, prey abundance, prey habitat, *Strix occidentalis lucida*.

The Mexican spotted owl occurs within canyons and forested highlands of the southwestern United States, extending south into Mexico's Sierra Madre Occidental and Sierra Madre Oriental (Gutiérrez et al. 1995, Ward et al. 1995). The subspecies was listed as threatened in 1993, prompting development of a recovery plan (U.S. Fish and Wildlife Service 1995). The recovery plan included a set of measures to protect, develop, and sustain owl habitat. Whereas specific forest structural targets were proposed for nesting and roosting habitat, the recovery plan provided little guidance for foraging habitat because little was known of its attributes.

Most information on spotted owl nest and roost habitat is based on visual observations of owls (Ganey and Dick 1995, Seamans and Gutiérrez 1995, Ganey et al. 2000, May and Gutiérrez 2002), whereas most information on foraging habitat is inferred indirectly from radiotelemetry (Ganey and Balda 1994, Ganey et al. 1999). Nocturnal telemetry to identify foraging locations is based on

triangulating 3 or more fixes resulting in a polygon that might be up to 3 ha and assumes that the bird is actually within the polygon (Carey et al. 1989, 1992; Hodgson 1996). Realistically, telemetry data provide little more than a general index of where birds forage; thus, limited inferences can be made about foraging habitat (Ganey et al. 2003). Descriptions of foraging habitat, however, may be refined with additional information on prey. In particular, information on prey habitat could aid in descriptions of owl foraging habitat and could be used to identify habitat attributes to be manipulated to sustain or enhance prey populations.

Little is known about the prey ecology of the Mexican spotted owl (Ward and Block 1995). Although various studies have quantified the owl's diet based on prey remains (Duncan and Sidner 1990, Ganey 1992, Tarango 1994, Young et al. 1997, Delaney et al. 1999, Seamans and Gutiérrez 1999), no published study has compared diet composition with the availability or occurrence of potential prey items. Furthermore, little specific information exists on habitat associations of key prey within spotted owl home ranges; nor do we understand temporal fluctuations in prey abun-

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dance and how those relate to prey selection by the spotted owl (but see Ward 2001).

We conducted a study in a ponderosa pine–Gambel oak forest of northern Arizona to increase our understanding of Mexican spotted owl prey ecology. We took a multifaceted approach that included examination of owl pellets to evaluate diets, live trapping of small mammals to assess population characteristics of potential prey, and measurements of habitat to assess habitat features correlated to prey abundance. We collected data year-round from fall 1990 through winter 1992–1993. Our objectives were to (1) characterize the diets of Mexican spotted owls, (2) contrast spotted owl diets with the relative occurrence of prey, (3) examine spatial and temporal variation in relative abundances of key prey, and (4) describe habitat associations of key prey species.

STUDY AREA

We conducted our study in a 7,000-ha area within the watersheds of Bar-M and Woods canyons, Coconino National Forest, about 40 km south of Flagstaff, Arizona, USA. The dominant vegetation was ponderosa pine forest with a woody understory consisting of Gambel oak, alligatorbark juniper (*Juniperus deppeana*), New Mexican locust (*Robinia neomexicana*), and buckbrush (*Ceanothus fendleri*). Various grasses and forbs comprised the herbaceous understory. Elevation ranged from 2,090 to 2,280 m. Topography was flat to rolling, with canyons and volcanic cones contributing some variation in slope and aspect. Primary land uses included timber harvest, livestock grazing, and recreation. Natural fire was the primary historical disturbance agent influencing forest structure. Fire regimes were disrupted since the late 1800s, thereby altering forest ecology. The combined effects of fire suppression, logging, and livestock and wildlife herbivory had altered structure and composition of the vegetation within much of the study area from what existed prior to European settlement (Covington and Moore 1994).

METHODS

Diets of Spotted Owls

We collected regurgitated pellets from 7 pairs of spotted owls from July 1990 through July 1993. All owls studied carried radio transmitters and were relocated by telemetry (Ganey et al. 1999). We collected pellets at roost sites where we observed the owls, so pellets were easily identified with the pair that produced them.

We lumped all pellets collected during a visit to a roost site because remains of a given prey item may appear in more than 1 pellet (Forsman et al. 1984). We bagged the collections, labeled them with the site name and date, and froze them for later identification. We identified and enumerated prey remains following Forsman et al. (1984) and DeRosier and Ward (S. DeRosier and J. P. Ward, Jr. 1994. Protocol for analyzing pellets regurgitated by Mexican spotted owls, unpublished report. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Flagstaff, Arizona, USA.). We keyed remains to species, where possible, using skulls and appendicular skeletal parts. If identification to species was not possible, we identified remains to the lowest taxon possible. Counts represent minimum numbers of individuals. The methods we used were comparable with other studies of spotted owl diet based on pellet analysis (Forsman et al. 1984, 2001; Ganey 1992; Seamans and Gutiérrez 1999). We recognize that pellets may provide a biased estimate of owl diets given variable digestibility of different prey (e.g., arthropods vs. small mammals). We assumed that items found in pellets reflected the true proportions of prey species in the diet. The degree to which this assumption was violated is unknown.

Trapping Design

The large home-range size of Mexican spotted owls on our study area (95% adaptive kernel estimate: mean = 895 ha, SE = 119 ha, $n = 12$; Ganey et al. 1999) presented sampling difficulties for characterizing prey abundance and habitat associations. An ideal situation would be to sample across enough owl home ranges to capture adequate spatial variation while sampling with enough intensity within each home range to characterize prey relationships for a given pair. Given logistical constraints imposed by limited funding and resources, we strove to achieve a balance by using the following design.

We used large and small trapping grids to sample prey populations. Large grids consisted of 100 trapping stations in a 10 × 10 array (10 rows by 10 columns) with 20-m spacing between stations; small grids consisted of 20 trapping stations in a 2 × 10 array with 20-m spacing between stations. Larger grids sampled 4-ha portions of owl foraging habitat and were used to estimate population density and habitat characteristics. The smaller, 0.8-ha grids provided additional information on prey habitats and relative abundances and allowed

us to sample across a larger area given funding and personnel limitations. All grids were located within general areas used by foraging spotted owls as identified by clusters (≥ 3) of radiotelemetry locations (Ganey et al. 1999, 2003). Given that triangulated telemetry are imprecise and inexact (Hodgson 1996, Ganey et al. 1999), we could only define general foraging areas and not specific foraging locations. However, because we used a cluster of locations to define these areas, we assumed (confidently) that they were representative of owl foraging habitat. Specific placement and orientation of a grid within the general foraging area was determined randomly. We sampled 2 large and 3 small grids within the home ranges of each of 4 pairs of spotted owls throughout the study. For statistical analyses, we treated all grids as independent samples; they were not blocked by owl pair. All grids were placed >400 m apart to increase the probability of independence among grids. We assumed that 400 m was adequate separation given the relatively small home ranges of the small mammals under study (McNab 1963). During our trapping efforts, no individuals were captured on more than 1 grid, which validated our assertion of independence.

We placed large ($8 \times 9 \times 23$ cm) Sherman live traps at each grid station and placed extra-large ($10 \times 18 \times 60$ cm) Sherman live traps at alternate stations. We used extra-large traps to ensure that they were large enough to capture larger prey such as woodrats (*Neotoma* spp.) and species of Scuridae. We trapped grids from 3 to 7 nights during each trapping session. Our goal was to trap a grid until $>90\%$ of all captures were recaptures. We truncated our efforts, however, during inclement weather to minimize trap mortalities. We attempted to trap throughout the year to assess temporal patterns in prey populations, but harsh weather conditions greatly limited sampling efforts during the winter of 1990–1991. Each grid was trapped for 5 to 7 sessions during the study; total trapping effort (adjusted for closed and unoccupied traps, or those otherwise unavailable for occupancy) was about 50,000 trap nights. We baited traps with rolled oats and chicken scratch; cotton was placed in the trap for insulation. We placed a cedar shingle on top of each trap to provide additional protection against snow and rain, and during cold weather we placed traps in a sleeve made of closed-cell foam pad to further insulate animals. We identified the species, age, sex, and reproductive condition of captured animals, and then they were marked, weighed, and released.

Habitat Sampling

We sampled habitat characteristics within circular plots of 5-m radius centered at each trapping station ($n = 1,040$). We estimated cover by grass, forb, rock, dead-and-downed woody debris of 3 size classes (<1 cm, 1–10 cm, >10 cm in diameter), and live woody vegetation in 4 height strata (<1 m, 1–2 m, 2–5 m, >5 m) as the percentage of 10 point intercepts (at 1-m intervals along a randomly oriented transect centered on the trap station) covered by each variable (Heady et al. 1959). We sampled all trees >10 cm diameter at breast height (dbh) and 2 m tall within the plot. Tree diameters were measured with a dbh tape; heights were measured with a clinometer. We measured the height of all shrubs and slash piles found within the plot with a meter stick. Mid-point diameters and lengths of logs (>10 cm dbh and 2 m long) or parts of logs that had ≥ 2 m of their length within the plot were measured with a measuring tape. We recorded numbers of trees and shrubs by species. We measured slope with a clinometer and aspect with a compass.

Data Analysis

Diet Composition.—We quantified owl diets using measures of relative frequency and biomass. To estimate biomass, we multiplied the number of individuals identified in pellets by the average mass for that species. If available, we used mean masses of small mammals trapped to estimate biomass contributions of particular prey species. Lacking site-specific data on mass for other species, we used estimates from the literature or estimates derived from specimens at the Museum of Vertebrates, Northern Arizona University (Appendix 1).

We found few pellets during the winter months; thus, our analyses of diet composition include only March through November. Most of our data were collected from 4 pairs of owls ($\sim 85\%$ of the pellets) with additional data from another 3 pairs ($\sim 15\%$ of the pellets); thus, we pooled data to characterize general descriptions of owl diets.

Population Dynamics of Primary Prey Species.—We used program CAPTURE (Otis et al. 1978, White et al. 1982) to estimate prey density for the 10×10 grids. Using CAPTURE allowed us to estimate capture probabilities, effective sampling area, and sampling variances. In cases where the number of individuals captured for a grid was insufficient for calculating density, we estimated density as the minimum number known alive/effective grid size. For these situations, we estimated effective grid size by averaging grid sizes from other

grids and trapping occasions. We calculated the average population density by season for each species to evaluate general temporal trends.

We used 2-way analysis of variance (Steel and Torrie 1980:195–239) to test for spatial and temporal variation in biomass of the primary prey and of all prey combined. The spatial units were owl home ranges; temporal units were broken into the owl breeding (Mar–Aug) and nonbreeding (Sep–Feb) seasons from 1991 to early 1993.

Owl Diets and Prey Occurrence.—We compared diets of 4 pairs of spotted owls with the relative occurrence of nocturnal rodents on their home ranges. Relative occurrence was estimated from trapping results and was defined as the number of unique animals captured per 100 trap nights for each sampling array during each trapping session. We included diet and trapping data only for March–November, 1991 and 1992, because most pellets were collected and most small mammal trapping occurred during those periods. Because of sample size limitations, we averaged trapping data to provide a single estimate of prey occurrence for each owl home range for this period.

We used exact χ^2 goodness-of-fit tests (Mehta and Patel 1995) to evaluate whether spotted owls consumed small mammals in proportion to their occurrence as estimated by trapping results. The first analysis included only 2 groups of small mammals (woodrats and white-footed mice) because we seldom caught individuals in other taxa. Our second analysis focusing on white-footed mice tested the hypothesis that spotted owls consumed deer mice and brush mice in proportion to their occurrence. We could not identify the species of some white-footed mice found in pellets. Thus, we assigned unidentified specimens to species in the same proportions as the specimens that had been identified, assuming that unidentified specimens occurred in the same proportions as identified specimens.

Habitat Relationships of Primary Prey Species.—We restricted habitat analyses to 3 species (Mexican woodrat, deer mouse, brush mouse) that were well represented in spotted owl diets and sampled adequately by live traps. We first related an index of a species' relative abundance to grid-level habitat values using simple correlations and multiple linear regression analyses (Draper and Smith 1981). We rarely captured enough individuals in the 2×10 arrays to apply program CAPTURE (Otis et al. 1978, White et al. 1982) and estimate densities. Consequently, we used catch-per-unit effort of unique individuals (i.e., we only used the

initial capture of an individual captured on multiple occasions) as an index of relative abundance (see Carey 2000). We felt justified in doing so because density estimates derived from CAPTURE (methods described above) for the larger grids were highly correlated to the relative abundance index for all 3 species (deer mouse: $r = 0.88$, $df = 48$, $P < 0.001$; brush mouse: $r = 0.86$, $df = 32$, $P < 0.001$; Mexican woodrat: $r = 0.81$, $df = 33$, $P < 0.001$). To standardize use of data from the 2×10 and the 10×10 grids, we used only 2 outer and adjoining perimeter lines from the 10×10 grids. We averaged relative abundance for each species found on each trapping array during the study. Our objective was to describe prey habitat relationships; thus, we treated each 2×10 array as an independent sample, resulting in a sample size of 20 sampling arrays (i.e., 5 arrays/home range pooled across 4 home ranges).

We obtained grid-level habitat values for each 2×10 array by averaging and pooling values across trap stations. To screen variables, we first examined the product-moment correlations of each variable with relative abundance of each prey species, as well as intercorrelations among habitat variables. For the multiple regression analysis we selected variables that (1) showed strong negative or positive correlations ($|r| > 0.5$) with the relative abundance of 1 or more species, and (2) measured unique habitat characteristics relative to other variables (e.g., ground cover compared to tree measurements). As an exploratory analysis to identify habitat associations, we used all-possible-subsets regression (Draper and Smith 1981:296–302) to evaluate models consisting of up to 5 variables based on the amount of variance (R^2) explained by the model. We limited the number of independent variables to 5 to ensure an adequate sample size to variable ratio (Tabachnick and Fidell 1983:92).

RESULTS

Diets of Spotted Owls

We identified 1,125 prey items from pellets of spotted owls (Table 1). Mammalian prey dominated the diets in terms of biomass, comprising approximately 94% of spotted owl diets. Birds and insects contributed little in terms of prey biomass. Mean prey weights for all prey items were 40.1 g (SE = 1.8) overall or 60.0 g (SE = 2.4) when considering only vertebrate prey. Of mammals, the deer mouse was taken most frequently followed by the brush mouse, Mexican woodrat, pocket gopher, and Mexican vole, respectively. Owls occa-

Table 1. Diet composition of Mexican spotted owls in ponderosa pine-Gambel oak forests in northern Arizona, USA, 1990–1993. Shown are relative contributions of various prey items in terms of frequency, biomass, and mean proportion.

Prey type ^a	Entire study area				Individual territories (% of prey items)			
	% of prey items ($\Sigma = 1,125$) ^b	% of biomass ($\Sigma = 45,129$ g)	Mean proportion	CV of mean	Gash Mountain ($\Sigma = 403$)	Lee Butte ($\Sigma = 249$)	Limpios Tank ($\Sigma = 185$)	T-Six Tank ($\Sigma = 145$)
Woodrats	7.8	27.8	10.2	0.55	1.0	14.1	11.9	6.2
White-footed mice	37.3	17.3	46.6	0.35	24.8	37.3	50.3	47.6
Botta's pocket gopher	5.5	15.5	6.3	0.62	6.9	4.0	2.7	2.1
Mexican voles	1.9	1.1	1.1	1.18	2.2	3.2	1.6	0.7
Rabbits	0.8	7.8	0.5	1.20	0.8	0.4	1.1	1.4
Bats	0.9	0.3	1.0	1.30	0.8	0.4	2.2	0.0
Unidentified mammals					6.2	11.6	13.5	6.2
Small	2.6	1.4	2.2	0.98				
Medium	5.9	19.0	5.3	1.22				
Large	0.5	3.6	0.3	0.13				
Aves spp.	3.0	5.2	2.7	0.89	2.2	3.6	3.2	2.8
Insecta spp.	33.7	0.9	23.3	0.84	55.1	25.3	13.5	33.1

^a See Appendix 1 for scientific names.

^b Relative frequency averaged across 7 pairs of owls.

sionally took cottontails (*Sylvilagus* spp.), chipmunks (*Tamias* spp.), ground squirrels (*Spermophilus* spp.), bats, birds, and shrews (Table 1), and they consumed substantial numbers of arthropods (>33% of all prey items identified). Identifiable insect taxa included Coleoptera and Orthoptera; many samples were not identified even to the ordinal level.

Prey Population Dynamics

Populations of trapped prey species exhibited seasonal fluctuations (Fig. 1). Generally, populations rose during spring, peaked during summer, declined in fall, and reached a winter low. The deer mouse showed the greatest amplitude in population change as evidenced by the shift from a high of 12.2 animals/ha (SE = 2.3) during summer of 1991 to a low of 3.3 animals/ha (SE = 0.7) in winter 1991–1992. Although both brush mouse and Mexican woodrat populations showed seasonal variation, the magnitude of the fluxes was not as great as for the deer mouse (Fig. 1). Total prey biomass varied significantly between seasons ($F_{3,100} = 3.17$; $P = 0.028$). The deer mouse, however, was the only species to exhibit significant temporal biomass shifts between owl breeding and nonbreeding seasons ($F_{3,100} = 11.49$, $P < 0.001$), largely because of the pronounced population peak in summer of 1991 (Fig. 1).

Spotted Owl Diets and Prey Occurrence

Two of 4 pairs of spotted owls consumed woodrats and white-footed mice in proportion to their relative occurrence as estimated by trapping

results. These 2 pairs, however, did not consume the 2 species of white-footed mice in proportion to occurrence. Owls at Gash Mountain ate more brush mice than expected ($\chi^2 = 41.06$, $df = 1$, $P < 0.0001$), whereas the owls at T-Six Tank took more deer mice ($\chi^2 = 10.46$, $df = 1$, $P = 0.0008$). At the remaining 2 sites, owls consumed more woodrats and fewer white-footed mice than expected (Lee Butte, $\chi^2 = 26.59$, $df = 1$, $P < 0.0001$; Limpios Tank, $\chi^2 = 7.23$, $df = 1$, $P = 0.0097$). The Limpios Tank pair consumed the 2 species of white-footed mice in proportion to their occurrence ($P > 0.05$), whereas the Lee Butte pair ate more deer mice and fewer brush mice than expected ($\chi^2 = 6.36$, $df = 1$, $P = 0.0079$).

Prey Habitat Relationships

We captured the Mexican woodrat at least once at 202 (19.4%) of the 1,040 trap stations, the brush mouse at 281 stations (27.1%), and the deer mouse at 337 stations (32.4%; Table 2). Few woodrats were captured at Gash Mountain (Table 2).

Results of product-moment correlations between grid-level habitat variables and relative abundances of the 3 prey species reduced the data set to 11 variables for use in the multiple regression analyses. Numerous shrub variables exhibited significant correlations with prey abundance whereas tree variables rarely did. Ground cover and other variables were intermediate between shrub and tree categories in achieving significant correlations. The 11 variables selected for use in multiple regressions included 4 shrub variables (density of oak shrubs, density of pine shrubs, pine

shrub height, vegetation cover 1–2 m above ground), 2 tree variables (density of oak trees, dbh of pine trees), 3 ground cover variables (rock cover, exposed soil, and cover by downed woody debris 10–30 cm in diameter), slope, and stump density.

Seven variables were significantly ($P < 0.05$) and positively related to the relative abundance of woodrats (Table 3). The 3 variables with the strongest relationships were vegetation cover at 1–2 m above ground ($r = 0.73$, $df = 18$), density of oak shrubs ($r = 0.64$, $df = 18$), and rock cover ($r = 0.49$, $df = 18$). These correlations were heavily influenced by 2 arrays found within the T-Six home range. Multivariate models derived from all-possible-subsets regression for the woodrat consisted of combinations of shrub variables with rock cover and slope. The 5-variable model that included Gambel oak shrub density, vegetation cover 1–2 m above the ground, Gambel oak tree density, rock cover, and number of stumps explained 82% of the variation in the relative abundance of woodrats ($F_{5,14} = 12.9$, $P < 0.0001$).

For brush mice, 9 variables were significantly ($P < 0.05$) correlated with relative abundance (Table 3), and all correlations were positive. The 5 variables with the strongest relationships to brush mouse abundance in univariate models were vegetation cover at 1–2 m above ground ($r = 0.84$, $df = 18$), density of oak shrubs ($r = 0.58$, $df = 18$), density of all shrub species ($r = 0.57$, $df = 18$), slope ($r = 0.50$, $df = 18$) and rock cover ($r = 0.49$, $df = 18$). The 5 variable all-possible-subsets regres-

sion model that included number of pine shrubs, vegetation cover 1–2 m above ground, slope, rock cover, and number of stumps accounted for 80% of the variation in relative abundance of the brush mouse ($F_{5,14} = 10.9$, $P = 0.0002$).

Four variables including vegetation cover 1–2 m ($r = -0.63$, $df = 18$), vegetation cover 2–5 m ($r = -0.52$, $df = 18$), height of pine shrubs ($r = -0.49$, $df = 18$), and stumps ($r = 0.77$, $df = 18$) were significantly correlated to relative abundance of deer mouse (Table 3). The 5 variable all-possible-subsets regression model including number of pine

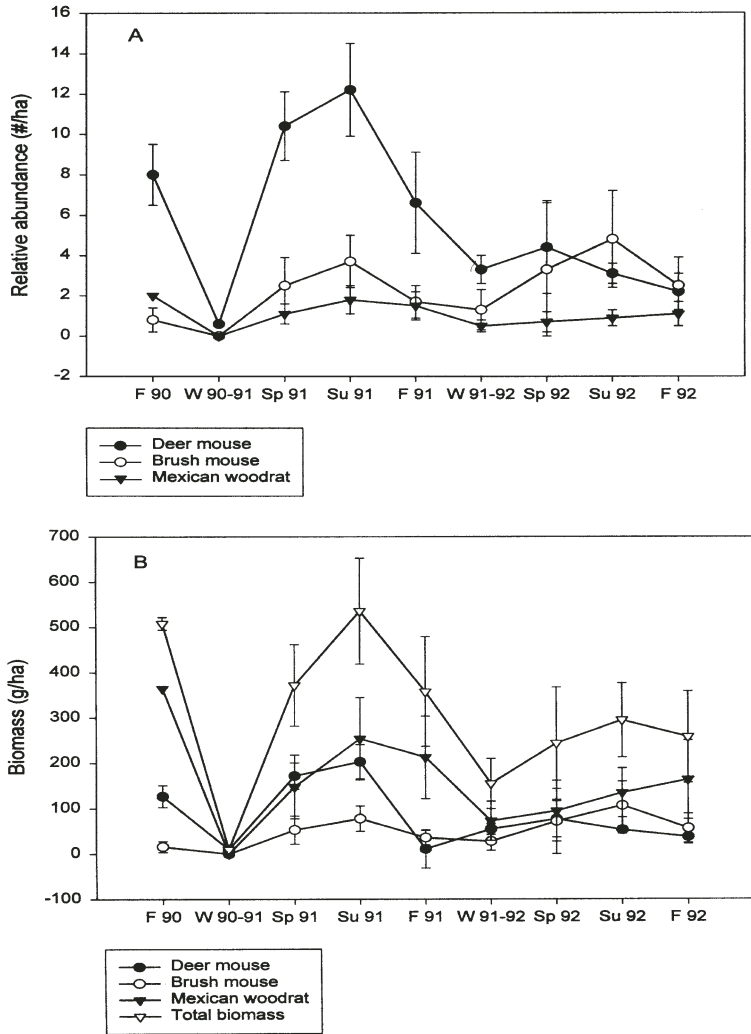


Fig. 1. Temporal variability in relative abundance for the deer mouse, brush mouse, and Mexican woodrat from a ponderosa pine–Gambel oak forest, north-central Arizona, USA, 1990–1992. Shown are (a) seasonal density estimates (number/ha) for each species, and (b) seasonal biomass estimates (g/ha) for each species and all species combined. Error bars represent standard errors. Only 1 grid was trapped during the 1990–1991 winter.

Table 2. Minimum number of prey captured within home ranges of 4 pairs of Mexican spotted owls in ponderosa pine-Gambel oak forests of north-central Arizona, USA, 1990–1993.

Species ^a	Gash Mountain		Lee Butte		Limpios Tank		T-Six Tank	
	No. of individuals	% ($\Sigma = 745$)	No. of individuals	% ($\Sigma = 923$)	No. of individuals	% ($\Sigma = 869$)	No. of individuals	% ($\Sigma = 803$)
Deer mouse	488	65.5	571	61.9	529	60.9	237	29.5
Brush mouse	12	1.6	213	23.1	140	16.1	344	42.8
Mexican woodrat	5	0.7	86	9.3	114	13.1	127	15.8
White-throated woodrat	0	0.0	1	0.1	10	1.2	5	0.6
Mexican vole	5	0.7	5	0.5	6	0.7	2	0.2
Rock squirrel	11	1.5	21	2.3	24	2.8	16	2.0
Golden-mantled ground squirrel	37	5.0	0	0.0	1	0.1	0	0.0
Gray-collared chipmunk	187	25.1	2	0.2	2	0.2	9	1.1
Cliff chipmunk	0	0.0	24	2.6	43	4.9	63	7.8
No. trap stations	260		260		260		260	
No. trap nights/days	11,626		13,470		12,904		11,811	

^a See Appendix 1 for scientific names.

shrubs, vegetation cover 1–2 m above ground, Gambel oak tree density, rock cover, and stump density explained 89% of the variation in deer mouse abundance ($F_{5,14} = 18.2$, $P < 0.001$).

DISCUSSION

Diets of Spotted Owls

Although spotted owls consumed a wide variety of prey taxa, their diet was dominated by the few

nocturnally active mammalian taxa of the appropriate size (Table 1). Three or 4 groups of mammals contributed most of this biomass. This is consistent with other studies of spotted owls that have also documented a few dominant prey taxa (Ganey 1992, Verner et al. 1992, Ward and Block 1995, Seamans and Gutiérrez 1999, Forsman et al. 2001, Ward 2001). However, the taxa dominating the diet of spotted owls appear to vary among areas or habitats. For example, Mexican spotted

owls inhabiting rocky canyons of Arizona and Utah preyed primarily on woodrats (Rinkevich 1991, Ganey 1992, Ward and Block 1995, Willey 1998), whereas owls in ponderosa pine-Gambel oak forest on our study area preyed primarily on white-footed mice (Table 1). This was also the prey type we captured most frequently during live trapping (Table 2).

The mean prey mass recorded in this study was lower than values reported in the literature for other areas. For example, mean prey mass ranged 54–150 g for northern spotted owls (*S. o. caurina*) in various parts of Oregon (Forsman et al. 1984), was >100 g for

Table 3. Simple correlations between habitat variables and prey abundance on 2×10 trap grids ($n = 20$) for key Mexican spotted owl prey species in pine-oak forests of north-central Arizona, USA, 1990–1992. We only report correlations where $P < 0.10$.

Variable	Mexican woodrat		Brush mouse		Deer mouse	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Shrubs						
Density, all species	0.46	0.037	0.57	0.009		
Density, pine					-0.40	0.085
Density, oak	0.64	0.022	0.58	0.008		
Density, locust			0.38	0.094		
Species richness	0.41	0.076	0.56	0.011		
% cover at 0–1 m	0.47	0.036	0.61	0.004		
% cover at 1–2 m	0.73	0.001	0.84	0.001	-0.63	0.003
% cover at 2–5 m	0.45	0.048	0.57	0.009	-0.52	0.018
Height, pine					-0.49	0.029
Height, oak			0.44	0.056		
Trees						
Density, oak			0.39	0.092		
Dbh, pine					0.39	0.089
Snag density, oak			0.48	0.033		
Slope	0.45	0.044	0.50	0.024		
Ground cover						
Bare ground	-0.43	0.058				
Rock	0.49	0.028	0.49	0.027		
Dead wood 1–10 cm diam.	-0.39	0.088				
Dead wood >10 cm diam.	-0.44	0.051	-0.41	0.072	0.41	0.070
Density, stumps	-0.39	0.085			0.77	0.001

spotted owls in California (Barrows 1980), and ranged from 63 to 118 g for Mexican spotted owls in 5 geographic regions in Arizona (Ganey 1992). The lower prey mass we observed may be partially due to the large numbers of insects eaten (Table 1), but the estimate of mean mass based on only vertebrate prey (60.0 g, SE = 2.4) still falls low in the range of reported values.

Relatively low prey biomass may be directly related to the large owl home-range sizes on our study area compared to those used by Mexican spotted owls in other locations (Ganey and Dick 1995) and may indirectly influence population trend. Zabel et al. (1995) demonstrated that home ranges of northern spotted owl were inversely related to prey biomass and the abundance of large prey items such as woodrats. Low prey biomass might also influence owl reproduction (Ward 2001) and ultimately population trend (Seamans et al. 1999). Ward (2001) observed less variation in owl reproduction when woodrats comprised a larger proportion of the diet. Seamans et al. (1999) found pronounced inter-annual variation in owl reproduction, and demonstrated a link between reproduction and population trajectory.

Spatial and Temporal Trends in Prey Populations and Biomass

During winter, the quantity and total biomass of prey diminished (Fig. 1). Ganey et al. (1999) found that home ranges of the spotted owls that we studied increased in size during the nonbreeding season. Given less available food, owls may have needed to hunt over larger areas to find enough food to survive. Similarly, Carey and Peeler (1995) postulated that seasonal and home-range adjustments for northern spotted owls were in response to fluctuating prey numbers. Foraging over a larger area probably requires greater energy, especially when coupled with the higher energetic costs associated with winter survival.

An alternative strategy would be to migrate to a different site that provides more food. This strategy was apparently employed by both mates from Gash Mountain (representing 2 of 13 birds tracked by radiotelemetry), who migrated down slope to pinyon-juniper woodlands. This migration entailed a 40-km move in distance and a drop of about 920 m in elevation (Ganey et al. 1992). We conducted limited prey sampling (about 1,200 trap nights of effort) in this area and captured 5 species of small mammals. These species represented the same genera documented in the owl diet and provided almost 1,200 g/ha of

potential food. Prey biomass on that pair's breeding home range averaged about 315 g/ha throughout the year and only 155 g/ha during winter. Further, we captured fewer woodrats at Gash than within the other home ranges (Table 2). Given low prey biomass within the Gash home range, the altitudinal migration may have been food-driven. If 15% of the birds (2 out of 13) migrating was representative of high-elevation conifer forests of the Southwest, then altitudinal migration may be conducted by a substantial proportion of the population. Further supporting this idea, 2 of 8 owls tracked by Ganey and Balda (1989) disappeared from study areas during winter and returned in spring. Wintering areas were never determined, but altitudinal migration was suspected (Ganey and Balda 1989). In addition, Mexican spotted owls have been observed in low-elevation habitats on other occasions during winter (Ganey and Dick 1995, Gutiérrez et al. 1995, Johnson 1997, Willey 1998). Hamer (1988), Laymon (1989), and Verner et al. (1992) have noted altitudinal migrations by northern and California spotted owls that entailed birds moving down slope during winter. Whether or not these altitudinal migrations were food driven is unknown, but this hypothesis may be supported somewhat by our data.

Prey Habitat Relationships

Identifying and understanding the ecology of key prey of the spotted owl is important when designing and implementing conservation measures for this threatened species (Ward and Block 1995). Providing appropriate habitat for the owl must include providing habitat for its prey base. This should not be restricted to providing habitat for 1 prey species but should include habitat for the suite of species that the owl consumes. Providing habitat for multiple prey species may help buffer the owl against short-term declines in the population of any 1 species (Ward 2001).

Many of our results of prey-habitat relationships are consistent with those reported by other investigators. Hoffmeister (1986) noted a disjunct pattern in Mexican woodrat distribution that corresponded to a disjunct habitat distribution, and Sureda and Morrison (1999) and Ward (2001) found them closely associated with rocks and shrub cover. This is consistent with our observations of larger woodrat populations where appropriate habitat elements (rocks and shrub cover) were present in sufficient amounts. Ward (2001) found that woodrat biomass was cor-

related with the density of large (≥ 30 cm diameter) logs, a relationship not supported by our data. Brush mice exhibited habitat relationships similar to woodrats in that population numbers were influenced by the patchy distribution of key habitat elements such as oak shrub cover and rocks. Ward (2001) found that brush mice in the Sacramento Mountains of New Mexico also were found in association with oak brush and rocks. Deer mice were more ubiquitous but tended to occur in forest stands that exhibited sparse woody vegetation cover 1–5 m above the ground and high stump density. Stumps typically were the result of thinning small pines (< 23 cm dbh), thereby opening up the understory.

Surprisingly, downed logs were not a strong predictor of habitat use by any of the 3 species studied. Often, logs are important habitat components for many small mammal species (Maser et al. 1979, Szaro et al. 1987, Ward 2001, Laudenslayer et al. 2002). We found that woodrat and brush mouse abundances were weakly and negatively correlated ($r = -0.44$, $df = 18$; and $r = -0.41$, $df = 18$, respectively), and deer mouse abundances were weakly and positively ($r = 0.41$, $df = 18$) correlated with log cover (Table 3). We offer 2 possible explanations for the weak relationships. First, ponderosa pine is a fire-adapted ecosystem (Biswell 1972). As such, frequent, low-intensity fires occurring at 2–12 year intervals were part of the evolutionary ecology of ponderosa pine forests (Moir et al. 1997). Under such a fire regime, large log volumes were not likely to accumulate, assuming that many logs would burn during each fire. Given inherently low log volumes, small mammals indigenous to ponderosa pine forests may not require large log volumes. Second, fire exclusion over the past century has allowed logs to accumulate on the forest floor. Log volume averaged $15.8 \text{ m}^3 \text{ ha}^{-1}$ ($SE = 1.5$) across our study area, ranging from 8.9 ($SE = 2.4$) to 23.9 ($SE = 3.6$) $\text{m}^3 \text{ ha}^{-1}$ for the 4 spotted owl home ranges. These log volumes may exceed threshold log requirements of any of the species we studied; thus, dependence on logs by prey was not readily apparent.

MANAGEMENT IMPLICATIONS

A few pieces of evidence suggest that spotted owls within the area we studied in Arizona may be vulnerable to population declines because of prey size and abundance. First, prey is, on average, smaller than that taken on other areas within the owls' geographic range (see Barrows 1980, Forsman et al. 1984, and Ganey 1992 for comparisons). Second,

total available biomass is less than that found in other vegetation types used by Mexican spotted owls (Ward and Block 1995). Third, we demonstrated temporal variation in prey abundance which might influence owl reproduction and the owl population's trajectory. Given the importance of prey, management of the Mexican spotted owl in ponderosa pine–Gambel oak forests should therefore incorporate active management for prey, especially larger prey such as woodrats, rather than assuming that provision of owl nest and roost habitat will provide for prey habitat needs.

Management for prey habitat should emphasize elements closely correlated with prey population numbers and habitat elements that are in short supply. For the species that we studied, these elements include rock outcrops, shrub cover, and herbaceous vegetation. Obviously, the distribution of rocks will be impossible to manipulate across the landscape. However, the presence of rocks might indicate where management efforts should be focused, especially for woodrats and brush mice. Thinning small diameter trees using both prescribed fire and mechanical treatments would open the tree canopy, releasing understory vegetation for increased growth. Cutting small diameter trees should be emphasized given that large trees are important and rare attributes of spotted owl habitat and therefore should be retained (U.S. Fish and Wildlife Service 1995). Thinning of oaks should be avoided given their importance to spotted owls and prey (Seamans and Gutiérrez 1995, U.S. Fish and Wildlife Service 1995, May and Gutiérrez 2002). Reducing densities of small trees likely will enhance deer mouse and Mexican vole habitat. The deer mouse uses areas with little woody cover within 5 m of the ground. Thinning small trees would reduce pine cover in this stratum, thereby improving deer mouse habitat. Thinning also would benefit vole habitat by opening the canopy and increasing grass and forb cover. We suspect that recent changes in forest structure, namely increased forest canopy and reduced herbaceous production, probably have reduced the amount, quality, and distribution of vole habitat. Few voles were found in pellets (Table 1) or captured in live traps (Table 2). Voles are a major component of Mexican spotted owl diets in many other parts of their range, especially in mesic habitats (Ganey 1992, Ward and Block 1995, Young et al. 1997, Ward 2001). Forest and range management practices that promote herbaceous growth could lead to increased vole populations.

Woodrats and brush mice were closely associated with shrub cover as provided by New Mexican locust, Gambel oak, and buckbrush. Thinning and prescribed fire would promote establishment, sprouting, and growth of these plants. Emphasis for management of these shrubs should be on sites that support the establishment and growth of these shrub species. We found that they primarily occurred on slopes $>20^\circ$ and close to rock outcrops, which is where we captured many of these animals.

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Appendix 1. Prey taxa identified in the diets of Mexican spotted owls in north-central Arizona, USA, 1990–1993. Mass estimates used in biomass calculations and sources for mass estimates.

Prey taxa ^a	Mass estimate (g)		Other estimate (g)	Source ^b
	1991	1992		
Mammals				
Merriam's shrew (<i>Sorex merriami</i>)			5.1	2
Pallid bat (<i>Antrozous pallidus</i>)			18.0	2
Big brown bat (<i>Eptesicus fuscus</i>)			15.0	2
Fringed myotis (<i>Myotis thysanodes</i>)			7.0	5
Unidentified bats			14.2	2, wm ^c
Chipmunks (<i>Tamias</i> spp.)	58.3	62.9	60.6	1, wm ^c
Mexican vole (<i>Microtus mexicanus</i>)			24.1	1
White-throated woodrat (<i>Neotoma albigula</i>)	143.9	134.7	139.3	1
Mexican woodrat (<i>N. mexicana</i>)	140.5	146.1	143.3	1
Unidentified woodrat (<i>Neotoma</i> spp.)	140.7	145.4	143.1	1, wm ^c
Brush mouse (<i>Peromyscus boylii</i>)	21.4	22.3	21.8	1
Deer mouse (<i>P. maniculatis</i>)	16.6	17.4	17.0	1
White-footed mouse (<i>Peromyscus</i> spp.)	18.1	18.9	18.5	1, wm ^c
Squirrels (<i>Spermophilus</i> spp.)			186.6	1, wm ^c
Cottontail rabbits (<i>Sylvilagus</i> spp.)			390.6	4 ^d
Botta's pocket gophers (<i>Thomomys bottae</i>)			113.0	2
Small mammal	18.7	19.5	19.1	1, wm ^c
Medium mammal	129.2	132.0		1, wm ^c
Large mammal			288.3	1, wm ^c
Birds				
Small birds			30.0	3
Medium birds			70.0	3
Large birds			121.5	5
Insects				
Coleoptera			1.0	6
Orthoptera			1.0	6
Unidentified insect			1.0	6

^a Common and scientific names for mammals follow Hoffmeister (1986).

^b Sources: (1) animals captured on the study area (estimated by year where sufficient captures/year allowed); (2) specimens in the Northern Arizona University Museum of Vertebrates; (3) Forsman et al. (1984); (4) Steenhof (1983); (5) J. P. Ward, Jr., unpublished data; and (6) Ganey (1988).

^c wm = weighted mean. We calculated wm based on relative proportions of prey taxa identified in the diet. For example, the weighted mean of white-footed mice was calculated assuming that brush mice and deer mice were represented in the unidentified white-footed mice in proportion to their representation in the sample of white-footed mice that could be identified to species. Where sufficient data were available to estimate mass for a given year, weighted means were computed using year specific mass estimates and proportions of prey species in the diet that year. Species included in estimates of weighted mean were: bats = pallid bat, big brown bat, and fringed myotis; chipmunks = cliff chipmunk (*Tamias dorsalis*) and grayneck chipmunk (*T. cinereicollis*); unidentified woodrat = white-throated woodrat and Mexican woodrat; white-footed mouse = brush mouse and deer mouse; squirrels = golden mantled squirrel (*Spermophilus lateralis*) and rock squirrel (*S. variegatus*); small mammal = chipmunks, voles, and white-footed mice; medium mammal = pocket gophers and woodrats; and large mammal = rabbits and squirrels.

^d Estimate assumed 60% juveniles and 40% adults (Ganey 1988).