J. Raptor Res. 33(2):143–148

DIET COMPOSITION AND REPRODUCTIVE SUCCESS OF MEXICAN SPOTTED OWLS

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ABSTRACT.—We identified 3793 prey remains from 44 and 41 Mexican Spotted Owl (*Strix occidentalis lucida*) territories in Arizona and New Mexico, respectively, from 1991–95. We found no relationship between Mexican Spotted Owl reproductive success and the proportion of dietary biomass comprised of white-footed mice (*Peromyscus* spp.) or woodrats (*Neotoma* spp.). This was contrary to previously observed diet patterns in Northern (*S. o. caurina*) and California Spotted Owls (*S. o. occidentalis*) showing that mammals can comprise 88.2% of the dietary biomass in Arizona and 94.0% in New Mexico. We found that the most important prey based on relative biomass for Mexican Spotted Owls were woodrats (47.8%) and white-footed mice (17.0%). Gophers (*Thomomys bottae*) and birds occurred more frequently in owl diets in Arizona, while rabbits (*Sylvilagus* spp.), insects, and woodrats occurred more frequently in diets of New Mexico owls.

KEY WORDS: *Mexican Spotted Owl;* Strix occidentalis lucida; Neotoma *spp.; diet;* Peromyscus *spp.; reproductive success.*

Composicion de la dieta y exito reproductivo de *Strix occidentalis lucida*

RESUMEN.—Identificamos los restos de 3793 presas de 44 y 41 territorios de *Strix occidentalis lucida* en Arizona y Nuevo México respectivamente entre 1991–95. No encontramos ninguna relación en el éxito reproductivo de este buho y la proporcion de biomasa en la dieta comprendida para *Peromyscus* spp. o *Neotoma* spp. Al contrario de *S. o. caurina* y *S. o. occidentalis* en los cuales los mamíferos pueden comprender 88.2% de la biomasa en la dieta en Arizona y 94.0% en Nuevo México. Encontramos que la presa mas importante con base en la biomasa relativa para *Strix occidentalis lucida* fue *Neotoma* spp. (47.8%) y *Peromyscus* spp. (17.0%). *Thomomys bottae* y aves ocurrieron mas frecuentemente en las dietas de los buhos de Arizona, mientras que *Sylvilagus* spp., insectos y ratas de bosque ocurrieron mas frecuentemente en las dietas de los buhos de Nuevo México.

[Traducción de César Márquez]

The Spotted Owl (*Strix occidentalis*) is a medium-sized forest owl of western North America that eats a variety of prey but primarily small and medium-sized rodents (Forsman et al. 1984, Ganey 1992, Verner et al. 1992, Gutiérrez et al. 1995). Previous dietary studies have suggested that, when breeding, Northern (*S. o. caurina*) and California Spotted Owls (*S. o. occidentalis*) take larger prey items than when they are not breeding (Barrows 1987, Thraillkill and Bias 1989, White 1996). Northern Spotted Owls also appear to concentrate their foraging based on the distribution of large prey (Carey and Peeler 1995, Ward et al. 1998). Finally, when older forests that contain large prey are widely distributed, home-range size increases (Carey et al. 1992).

Since none of this has been adequately studied and documented in the Mexican Spotted Owl (*S. o. lucida*), we have been studying the demography of two Mexican Spotted Owl populations in the southwestern U.S. Because most of the owls in these populations were color marked, we were able to collect representative prey remains from egested pellets in most of the owl territories over several years. Therefore, we could address the population's breeding response to variation of important prey species. Additionally, we were able to assess individual territory breeding response in relation to variation in the diet. An ancillary result of our analysis was an enumeration of the diet from these two populations. Collectively, our results will be important to the conservation of this endangered subspecies because the relationship between demography and prey is an essential element of any conservation strategy.

STUDY AREAS

Our studies are located in Arizona and New Mexico. The U.S. Forest Service chose the study areas based on previous occupancy by owls and their access. The study areas are at opposite ends of the Upper Gila Mountains

Forest Province (Bailey 1980). This province has the highest known number of Mexican Spotted Owls and is considered key to the subspecies conservation (USDI 1995).

The Arizona study area (AZ) encompassed 635 km^2 and was located in central Arizona on the Coconino Plateau. Elevations ranged from 1800–2660 m. The New Mexico study area (NM) encompassed 323 km^2 and was located in westcentral New Mexico in the Tularosa Mountains. Elevations ranged from 1900–2900 m. Based on random vegetation points ($N = 141$ for AZ and $N = 130$ for NM), dominant forest cover types were pine-oak (82.2% of AZ and 30.8% of NM), mixed-conifer (14.4% of AZ and 28.5% of NM) and piñon-juniper woodland/grassland (3.4% of AZ and 40.7% of NM). Both areas were characterized by warm summers and cold winters with two distinct periods of precipitation with winter snow and summer monsoon thundershowers.

METHODS

We surveyed owls by imitating their calls and listening for a response at established calling points and along transects ≤0.8-km apart throughout both study areas (Forsman 1983, Franklin et al. 1996). We located owls during daytime visits to check for reproductive activity by feeding live mice (*Mus musculus*) to individuals (Franklin et al. 1996). One or two visits were conducted at a territory to estimate its nesting status and, if found nesting, two or more visits were conducted to estimate the number of young fledged. Nonreproduction (no young fledged) was inferred for a territory if during a single daytime survey, one owl ate four mice or took ≥2 mice and cached the last mouse (Franklin et al. 1996).

Regurgitated pellets were collected from 1 April–20 August 1991–95, which encompassed the breeding period from incubation to the fledging of young (Gutiérrez et al. 1995). Pellets were collected opportunistically below owl roosts and nests. Although no random or systematic survey design was used to collect pellets, we assumed the prey remains we identified reflected the true diet composition of the owls. We combined pellets collected on the same day from the same site into one sample unless some pellets were markedly older; in which case older pellets were separated from more recent pellets.

We used skull, appendicular skeletons, beaks, and feathers to identify mammalian and avian remains. Remains were identified using keys in Findley et al. (1975), Hoffmeister (1986) and Dalquest and Stangl (1983), and by comparison with collections at the Humboldt State University Vertebrate Museum and the Museum of Southwestern Biology (MSB) at the University of New Mexico. We estimated the number of prey items in a sample by counting pairs of mandibles, skulls, or appendicular remains, whichever gave the highest count (Forsman et al. 1984). We used mandibles, legs, and exoskeletons to identify and enumerate insects.

We estimated diet composition for each owl site by multiplying counts of each prey species by species-specific body mass. Mean body mass of individual species was estimated from known weights of specimens at the MSB. Most MSB specimens we used were collected within the counties of the study areas or adjacent counties. We attempted to use at least 50 museum specimens for each prey species to estimate mean weight. Comparison with reference collections indicated rabbit (*Sylvilagus* spp.) remains were probably all small individuals or juveniles. Thus, we used an average weight of juvenile rabbits from the MSB. We did not attempt to age other prey items. We used an estimate of 1.0 g for each insect.

Diet of individual owls probably varies owing to differences in territory composition (vegetation and prey), competition, sex, breeding status, and possibly learned or inherent individual preference. Biases in dietary patterns likely are introduced by lumping prey remains across individuals or territories which have unequal sample sizes. To avoid such bias, we estimated owl diet composition by considering diet composition on a territory by territory base, or by using the aggregate percentage of individual prey remains. The aggregate percentage equaled the proportion of an individual prey species from an individual territory averaged over all territories (Swanson et al. 1974). We compared the frequency of occurrence of the most important prey groups in the diet (arbitrarily defined as groups that comprised >10% of the diet by number or weight) between the study areas using *t*-tests (Zar 1984), using each territory in each year as the sample. For inclusion into the analysis, we only considered territories with >20 prey remains in a year.

We examined the relationship between owl reproductive success and diet following two approaches. The two null hypotheses we tested were: (1) H_O: There was no population response in reproductive output to composition of the diet, and (2) H_O: There was no individual (territory) response in reproductive success to composition of the diet. We used the aggregate percentages of white-footed mice (all *Peromyscus* species) and woodrats (all *Neotoma* species) by year and study area as the samples for the population approach. We used the percentages of white-footed mice and woodrats for individual territories by year as the samples for the individual approach. We only considered white-footed mice and woodrats because they were the only two prey items that comprised >10% of the dietary biomass on both study areas. We arbitrarily used 20 prey remains within a year as the cutoff point for a territory to enter the analyses.

We used analysis of covariance (ANCOVA; Zar 1984) to test for a population response, with the mean number of young fledged by pairs as the dependent variable, study area as a categorical factor and the aggregate percentages of white-footed mice, and woodrats as the covariates. We used logistic regression (Hosmer and Lemeshow 1989) to test for an individual response in reproductive success to diet. The response variable was divided into unsuccessful territories (zero young fledged) and successful territories (≥1 young fledged). The predictor variables were year, study area, the proportion of the diet comprised of white-footed mice, and the proportion of the diet comprised of woodrats. We tested the significance of predictor variables using the Wald statistic (Hosmer and Lemeshow 1989). We excluded territories occupied by single (unpaired) owls for both analyses

RESULTS

We identified 16 species of mammals, 13 species of birds, and 3 families of insects among 3793 prey remains from 44 and 41 Spotted Owl territories in AZ and NM, respectively (Table 1). Mammals comprised 69.2% of owl diet by number and 91.9% by mass. The most important mammalian prey groups were woodrats (16.1% by frequency and 47.8% by mass), white-footed mice (38.6% and 17.0%), northern pocket gopher (*Thomomys bottae*, 3.6% and 11.5%), and rabbits (1.8% and 10.1%). Birds comprised 5.4% of the diet by frequency and 7.5% by mass (Table 1). No single bird species accounted for >2.0% of the diet. Insects accounted for 25.4% of the diet by frequency and 0.6% by mass. Mean prey mass for both study areas combined was 42.5 g.

Woodrats (t = 2.60, df = 76, P = 0.01), rabbits (t = 2.10, df = 76, P = 0.04) and insects (t = 2.10, df = 76, P = 0.04) occurred more frequently in NM owl diets while gophers (t = 2.17, df = 76, P = 0.03) and birds (t = 2.05, df = 76, P = 0.04) occurred more frequently in AZ owl diets. The frequency of occurrence of white-footed mice was not different (t = 1.59, df = 76, P = 0.12) between study areas. Mean prey mass was 36.3 g for AZ and 47.3 g for NM.

We collected 20 or more prey remains in a year from 32 territories in AZ and 46 territories in NM. There was no population response in reproductive output to composition of the diet (ANCOVA model F = 0.85, df = 3,6, P = 0.52). There was no indication of a pattern among the individual terms in the model (study area F = 0.06, df = 1,6, P = 0.82; white-footed mice F = 1.72, df = 1,6, P = 0.24; woodrats F = 0.50, df = 1,6, P = 0.51).

To test for an individual response in reproductive success to composition of the diet, the basis for calculating log odds for the logistic model were AZ for the study area effect and 1991 for the year effect. The logistic model adequately fit the data based on a goodness-of-fit test (χ^2 = 76.59, df = 70, P = 0.28). There were differences in individual territory reproductive success among years, but not between study areas or in relation to the proportion of the diet composed of white-footed mice or woodrats (Table 2).

DISCUSSION

Mexican Spotted Owls in our study took a wide variety of prey, but concentrated on small mammals, especially woodrats, similar to the Northern and California Spotted Owl subspecies (Forsman et al. 1984, Verner et al. 1992). However, except in the canyonlands of southern Utah, the Mexican Spotted Owl appeared to depend more on small rodents such as white-footed mice and voles (*Microtus* spp.; Ganey 1992, Young et al. 1997) than the other Spotted Owl subspecies (Gutiérrez et al. 1995).

Regional differences in diet have been noted within the ranges of all three subspecies (Forsman et al. 1984, Ganey 1992, Verner et al. 1992), and dietary differences between our study areas may reflect differences in prey abundance, prey availability, or prey selection. We could not address the latter two possibilities given the nature of our study. However, the habitat preferred by gophers (gentle topographic relief with deeper soils) was more abundant in AZ while habitat preferred by rabbits (piñon-juniper woodland) was more abundant in NM (Findley 1975, Hoffmeister 1986). The Mexican woodrat (*N. mexicana*) has been associated with montane coniferous forest and rock outcrops (Cornely and Baker 1986, Hoffmeister 1986), and in New Mexico reaches its highest abundance in montane mixed-coniferous forests (Findley et al. 1975). There appeared to be an abundance of montane coniferous forest on both study areas.

In contrast to previous studies of California and Northern Spotted Owls (Barrows 1987, Thrailkill and Bias 1989, White 1996), breeding owls in our study did not consume larger prey than nonbreeding owls. There were three possible reasons for this difference. First, the Mexican Spotted Owl may be different ecologically from the two coastal subspecies. The Mexican subspecies may depend on the overall abundance of prey within the landscape to successfully reproduce, or may respond to other environmental cues such as predator abundance, or intra- or interspecific competition.

A second possible explanation is that the prey remains we collected did not accurately reflect the true diet of the owls. This should not have contributed to the differences in findings because our protocol for pellet collection was similar to those for studies of the two coastal subspecies. A further concern was that reproducing males may have taken larger prey back to the nest and consumed smaller prey at the point of capture. Under such a scenario, prey remains in pellets might not represent the general diet. Bull et al. (1989) found such a pattern for Great Gray Owls (*S. nebulosa*). However, based on pellet egestion rates, we believe that pellets collected below Spotted Owl roosts and nests accurately depicted overall diet. In an exper-

Table 1. Mexican Spotted Owl diet composition in central Arizona and westcentral New Mexico, 1991–95.

		ARIZONA			NEW MEXICO		
PREY SPECIES OR GROUP	MASS (g)[a]	*N*	NUMBER %	MASS %	*N*	NUMBER %	MASS %
Sylvilagus spp.	232.4	7	0.4	2.8	63	2.9	14.3
Spermophilus lateralis	173.9	1	0.1	0.3	0	0.0	0.0
Tamiasciurus hudsonicus	218.5	5	0.3	1.8	3	0.1	0.6
Neotoma mexicana	121.3	143	8.8	29.3	288	13.3	34.2
N. albigula	146.9	21	1.3	5.2	22	1.0	3.2
Neotoma spp.	134.1	38	2.3	8.6	100	4.6	13.1
Neotoma total		202	12.4	43.2	410	19.0	50.5
Thomomys bottae	114.4	89	5.5	17.2	49	2.3	5.5
Eutamias spp.	63.2	4	0.2	0.4	7	0.3	0.4
Microtus mogollonensis	30.8	47	2.9	2.4	82	3.8	2.5
M longicaudus	34.9	4	0.2	0.2	43	2.0	1.5
Microtus spp.	32.9	3	0.2	0.2	87	4.0	2.8
Peromyscus maniculatus	16.9	403	24.7	11.5	409	18.9	6.8
P boylii	21.4	141	8.6	5.1	148	6.8	3.1
P. difficilis	22.0	0	0.0	0.0	96	4.4	2.1
Peromyscus spp.	20.1	82	5.0	2.8	186	8.6	3.7
Peromyscus total		626	38.4	19.4	839	38.8	15.6
Zapus princeps	25.3	0	0.0	0.0	1	0.0	0.0
Sorex spp.	5.3	7	0.4	0.1	14	0.6	0.1
Eptesicus fuscus	16.4	1	0.1	0.0	8	0.4	0.1
Lasionycteris noctivagans	9.0	0	0.0	0.0	4	0.2	0.0
Myotis spp.	6.7	6	0.4	0.1	5	0.2	0.0
Unidentified bats	10.7	5	0.3	0.1	2	0.1	0.0
Mammal total		1007	61.7	88.2	1617	74.8	94.0
Cyanocitta stelleri	107.7	8	0.5	1.5	10	0.5	1.1
Colaptes auratus	132.9	5	0.3	1.1	4	0.2	0.5
Accipiter striatus	128.8	1	0.1	0.2	0	0.0	0.0
Unidentified large avian	123.1	15	0.9	3.1	16	0.7	1.9
Myadestes townsendi	31.6	0	0.0	0.0	1	0.0	0.0
Otus flammeolus	50.0	3	0.2	0.3	2	0.1	0.1
Glaucidium gnoma	62.5	3	0.2	0.3	4	0.2	0.2
Unidentified medium avian	48.1	43	2.6	3.5	23	1.1	1.1
Parus gambeli	11.0	0	0.0	0.0	8	0.4	0.1
Dendroica coronata	12.3	0	0.0	0.0	1	0.0	0.0
Junco hyemalis	19.2	0	0.0	0.0	3	0.1	0.1
Sialia mexicana	24.5	2	0.1	0.1	2	0.1	0.0
Sitta carolinensis	17.5	0	0.0	0.0	4	0.2	0.1
Tachycineta spp.	16.7	0	0.0	0.0	1	0.0	0.0
Catharus guttatus	25.4	1	0.1	0.0	0	0.0	0.0
Unidentified small avian	17.9	26	1.6	0.8	20	0.9	0.4
Aves total		107	6.6	10.9	99	4.6	5.6
Cerambycidae	1.0	263	16.1	0.4	275	12.7	0.3
Gryllacridae	1.0	47	2.9	0.1	77	3.6	0.1
Scarabacidae	1.0	4	0.2	0.0	16	0.7	0.0
Unidentified insect	1.0	203	12.4	0.3	78	3.6	0.1
Insect total		517	31.7	0.9	446	20.6	0.4
No. prey items		1631			2162		

[a] Prey weights were estimated from specimens at the Museum of Southwestern Biology, Albuquerque, New Mexico.

Table 2. Results of logistic regression for test of individual Mexican Spotted Owl territory response in reproductive success to diet. Data from central Arizona and westcentral New Mexico, 1991–95.

PREDICTOR VARIABLE	PARAMETER ESTIMATE	SE OF PARAMETER	WALD χ^2	
			VALUE	P
Study Area	−0.508	0.565	4.58	0.03
Year				
1992	1.677	1.722	2.05	0.15
1993	2.254	1.163	3.75	0.05
1994	3.019	1.215	6.18	0.01
1995	3.125	1.352	5.34	0.02
White-footed mice	1.693	2.292	0.55	0.46
Woodrats	1.298	1.579	0.67	0.41

imental study of Barred Owls (*S. varia*), Duke et al. (1980) estimated that pellet egestion occurred on average 16.24 hr (SD = 3.48) after meal consumption. Thus, pellets collected below Spotted Owl roosts probably represented food consumed from the previous night, regardless of where it was consumed. In addition, we observed nesting females egesting pellets away from nests, often in the vicinity of male roosts, making pellets collected at roosts of nesting owls a reflection of the pair's diet.

A third possible reason is the different statistical methods used to compare owl diets. We used an aggregate percentage method to estimate population level responses to diet and territories to estimate individual pair response to diet. Previous studies have lumped all prey remains across territories before estimating diet. Thus, there was little information on the contribution of individual territories to the total number of prey remains. Consequently, the observed patterns may have been the result of one or a few territories consuming unique prey items and contributing most of the prey remains to the final tally (Swanson et al. 1974).

A difficult question in estimating diet following our methods is what should be the required minimum number of prey items for including a territory in the analysis. We arbitrarily chose 20 prey remains for the cutoff, but more prey remains would have led to a higher precision in diet estimates. For example, if white-footed mice comprise 20% of the diet ($\hat{p} = 0.20$), the estimated coefficient of variation (CV) given a sample size of 20 is 45%, and given a sample size of 200 the CV is 14%. Although the latter CV estimate is obviously preferred, collecting 200 prey remains from a territory during the breeding season would be nearly impossible due to logistical constraints. Our choice of 20 prey remains was a tradeoff between precision of diet estimates and sample size considerations. However, simulations using different cutoff points revealed our results were somewhat unstable. An increase or decrease of 10 prey remains from our cutoff point (10 or 30 prey remains to be included in the analysis) resulted in significant associations between reproductive success and white-footed mice in the diet. Because of this instability, we chose to infer no patterns of associations, recognizing that future studies with larger samples or more sophisticated analyses might detect such patterns. Thus, future studies should first consider the sampling effort required to obtain sufficient samples to adequately describe variation among individuals.

ACKNOWLEDGMENTS

We would like to thank D. Olson, E. Forsman, D. Holt, A. Franklin, Z. Peery, K. White, and P. Carlson for helpful comments. We thank D. Olson, C. May, and our many field assistants who collected pellets. We also thank an anonymous reviewer for one of the most cogent and helpful reviews we have received. B. Gannon at the Museum of Southwestern Biology and T. Lawlor at the Humboldt State University Vertebrate Museum provided access to collections at their institutions. This study was funded by the USFS (contract #s 53-82FT-4-07, 53-82FT-1-04, and 53-82-FT-3-07 to R.J.G.).

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Received 23 May 1998; accepted 30 January 1999