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Dietary Overlap Between Sympatric Mexican Spotted and Great Horned Owls in Arizona

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Abstract

We estimated diet composition of sympatric Mexican spotted (*Strix occidentalis lucida*, $n = 7$ pairs of owls) and great horned owls (*Bubo virginianus*, $n = 4$ pairs) in ponderosa pine (*Pinus ponderosa*)-Gambel oak (*Quercus gambelii*) forest, northern Arizona. Both species preyed on mammals, birds, and insects; great horned owls also ate lizards. Mammals dominated the diet of both species. Mammals comprised 63 and 62% of all prey items identified in diets of spotted and great horned owls, respectively, and 94 and 95% of prey biomass. Both species primarily preyed on a few groups of small mammals. Observed overlap in diet composition between species (0.95) was greater than expected based on null models of diet overlap, and the size range of prey taken overlapped entirely. Mean prey mass was similar for both species (great horned owl, 47.0 ± 7.4 g [SE], $n = 94$ items; spotted owl, 40.1 ± 1.8 g, $n = 1,125$ items). Great horned owls consumed larger proportions of diurnally active prey than spotted owls, which primarily consumed nocturnally active mammals. Our results, coupled with a previous analysis showing that these owls foraged in the same general areas (Ganey and others 1997), suggests that they could compete for food resources, which are assumed to be limiting in at least some years. They may minimize the potential for resource competition, however, by concentrating foraging activities in different habitats (Ganey and others 1997) and by foraging at different times, when different suites of prey species are active.

Key words: Arizona, diet, food niche breadth, great horned owl, Mexican spotted owl, niche overlap, null models, overlap, prey

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Cover: A radio-marked Mexican spotted owl roosting in a Gambel oak tree.

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Introduction

The Mexican spotted owl (*Strix occidentalis lucida*) occurs in forested mountains and canyonlands throughout the southwestern United States and the mountains of Mexico (Gutiérrez and others 1995; Ward and others 1995). This owl was listed as threatened in the United States under the Endangered Species Act of 1973 (USDI 1993). The recovery plan for the Mexican spotted owl (USDI 1995) listed competition with other species as one biological factor in need of further investigation in evaluating the status of this owl.

Throughout much of the range of the Mexican spotted owl, the most likely competitor is the great horned owl (*Bubo virginianus*; USDI 1995). This owl is sympatric throughout the range of spotted owls and both owls are active at night. Thus, they might interact directly and compete for food prey (Gutiérrez and others 1995; Houston and others 1998). The great horned owl also may prey on spotted owls (Forsman and others 1984; Ganey 1988:185; Gutiérrez and others 1995).

Despite the potential for competition between these species and predation by great horned owls on spotted owls, little is known about interspecific interactions between the two. Anecdotal evidence suggests that spotted owls sometimes avoid areas occupied by great horned owls. For example, Phillips and others (1964) reported that great horned owls colonized an area previously occupied by spotted owls in Arizona following a fire that opened up the forest canopy. Spotted owls were not heard in this area in subsequent years. Similarly, once great horned owls moved into areas previously occupied by spotted owls in New Mexico, Johnson and Johnson (1985) seldom heard spotted owls in those areas.

In contrast, Ganey and others (1997) reported considerable spatial overlap between home ranges of sympatric, radio-marked spotted and great horned owls in Arizona (fig. 1). On average, spotted owls shared 51.0% of their breeding-season home range and 74.1% of their non-breeding-season home range with great horned owls ($n = 6$ spotted owl and 3 great horned owl home ranges). The figures for proportions of great horned owl home

ranges shared with spotted owls were similar (57.4 and 70.5% for breeding- and non-breeding-season home ranges, respectively; Ganey and others 1997: table 2). These were minimum estimates of spatial overlap, because not all of the owls inhabiting the area were radio-marked. Both species of owls foraged in the same forest types, and sometimes in the same forest stands, although these stands were not necessarily used at the same time (Ganey and others 1997: tables 3 and 6).

This overlap between species in area used, coupled with similarity in activity period (both primarily nocturnal; Gutiérrez and others 1995; Houston and others 1998), suggests that these species could compete for resources such as food. Because available food is assumed (but not proven) to limit spotted owl reproduction in at

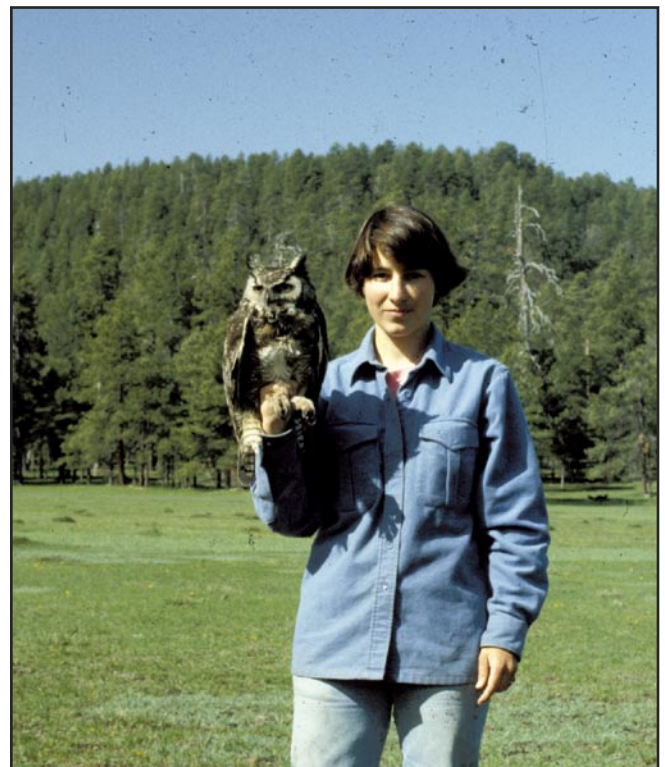


Figure 1. Biologist Sandra Miller prepares to release a radio-marked great horned owl. This owl was captured using a balchatri beneath the large snag in the background.

least some years (Verner and others 1992; Ward 2001), this interaction could have important implications in terms of fitness for spotted owls. In conjunction with studies of movements of both owl species (Ganey and others 1997) and trophic ecology of spotted owls (Block and others 2005), we had an opportunity to estimate diet composition for radio-marked spotted and great horned owls that foraged in the same areas. Elsewhere, we described aspects of the diets of spotted owls in this study area (Block and others 2005; Ward and Block 1995). Here, we also describe diet composition for great horned owls, and estimate diet overlap between these two species.

Methods

Study Area

The study area was located within the Bar-M and Woods Canyon watersheds, Coconino National Forest, approximately 26 km south of Flagstaff, north-central Arizona. Elevation in this area ranged from 1800-2500 m. Topography was relatively gentle with rolling terrain broken by scattered volcanic buttes and small canyons. Most of the study area consisted of ponderosa pine (*Pinus ponderosa*)-Gambel oak (*Quercus gambelii*) forest with scattered meadows or parks. Alligatorbark juniper (*Juniperus deppeana*) was present in many stands, particularly on warmer, drier sites. Small pockets of quaking aspen (*Populus tremuloides*) also occurred throughout the study area, and small numbers of narrowleaf cottonwood (*P. angustifolia*) and box-elder (*Acer negundo*) occurred in some canyons. New Mexican locust (*Robinia neomexicana*) and buckbrush (*Ceanothus fendleri*) were common understory shrubs, and the herbaceous layer consisted of various species of grasses and forbs.

Primary land uses within the study area historically included livestock grazing, timber harvest, and recreation (Block and others 2005). The primary natural disturbance agent influencing forest structure historically was fire. Natural fire regimes in this area were disrupted in the late 1800s, however, when effective fire suppression began (Covington and Moore 1994). The combined effects of fire suppression, livestock grazing, and timber harvest resulted in profound changes in forest structure, and a general decline in the herbaceous vegetation (Covington and Moore 1994) that provides food and cover for many species of small mammals preyed on by spotted and great horned owls (Ganey and others 1997; Reynolds and others 1996).

Diets of Spotted and Great Horned Owls

We collected regurgitated pellets from seven pairs of spotted owls and four pairs of great horned owls on the study area from July 1990 through July 1993. Pellets were collected opportunistically at roost sites where we observed the owls. All pellets collected during a visit to a roost site were lumped, because remains of large vertebrates can appear in more than one pellet (Forsman and others 1984). Collections were bagged, labeled with the site name and date, and frozen for later identification of prey remains. Prey remains were identified and enumerated following Forsman and others (1984) and Ganey (1988). Remains were keyed to species where possible, using skulls, appendicular skeletal parts, or other identifiable remains (e.g., insect exoskeletons). Where identification to species was not possible, we identified remains to the lowest taxon possible. All counts represent minimum numbers of individuals.

We quantified dietary composition using measures of relative frequency and biomass (Marti 1987). Where possible, we used mean masses of small mammals trapped on the study area (Block and others 2005) in estimating biomass contributions for particular prey species. Where we did not have site-specific data on prey mass, we used mass estimates from the literature (see table 1 for mass estimates and sources for those estimates). We compared diet composition between species using chi-square tests (Conover 1980). Where results indicated significant differences, we examined adjusted standardized residuals to determine which prey categories caused those differences. These residuals are normally distributed with a mean of zero and variance of 1, and can be interpreted as Z-scores. We applied a Bonferroni correction to account for the multiple comparisons made (Hoaglin and others 1985).

We also computed three standard trophic estimators for interspecific comparisons: food niche breadth (FNB), mean prey mass, and overlap in diet between the two species (Marti 1987). We estimated FNB, an index of diversity in the diet, using Levin's (1968) modification of Simpson's (1949) index: $FNB = 1/\sum p_i^2$, where p_i = the proportion of prey type i in the diet. This index incorporates both richness (the number of prey types in the diet) and evenness (how uniformly those prey types are represented in the diet), with higher values reflecting wider dietary breadth (Marti 1987). We used this index rather than other available diversity indices because it is used commonly in the comparative literature on raptor diets (Marks and Marti 1984; Marti and others 1993; Marti and Kochert 1995). For comparisons with

Table 1. Prey taxa identified in the diets of Mexican spotted and great horned owls in north-central Arizona, mass estimates used in biomass calculations, and sources for mass estimates (from Block and others 2005).

Prey taxa ¹	Mass estimate (g)	Source for mass estimate ²
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 ³
Chipmunks (<i>Tamias</i> spp.)	60.6	1, wm ³
Mogollon vole (<i>Microtus mogollonensis</i>)		1
White-throated woodrat (<i>Neotoma albigula</i>)	139.3	1
Mexican woodrat (<i>N. mexicana</i>)	143.3	1
Unknown woodrat (<i>Neotoma</i> spp.)	143.1	1, wm ³
Brush mouse (<i>Peromyscus boylii</i>)	21.8	1
Deer mouse (<i>P. maniculatis</i>)	17.0	1
White-footed mouse (<i>Peromyscus</i> spp.)	18.5	1, wm ³
Squirrels (<i>Spermophilus</i> spp.)	186.6	1, wm ³
Cottontail rabbit (<i>Sylvilagus</i> spp.)	390.6	4 ⁴
Pocket gopher (<i>Thomomys bottae</i>)	113.0	2
Unidentified mammals		
Small mammal	19.1	1, wm ³
Medium mammal	130.1	1, wm ³
Large mammal	288.3	1, wm ³
Birds		
Small birds	30.0	3
Medium birds	70.0	3
Large birds	121.5	5
Reptiles		
Unidentified lizard	17.0	4
Insects		
Coleoptera	1.0	6
Orthoptera	1.0	6
Unidentified insect	1.0	6

¹ Common and scientific names for mammals follow Hoffmeister (1986), except for Mogollon vole (after Frey 2004; Frey and LaRue 1993).

² Sources: 1) animals captured on the study area (Block and others 2005); 2) specimens in the Northern Arizona University Museum of Vertebrates; 3) Forsman and others (1984); 4) Steenhof (1983); 5) J. P. Ward, Jr., unpublished data; and 6) Ganey (1988).

³ Wm = weighted mean. Weighted means were calculated 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. Species included in estimates of weighted means 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; Large mammal = rabbits and squirrels.

⁴ Estimate assumed 60% juveniles and 40% adults (Ganey 1988).

the literature, we also computed a standardized FNB estimate: $FNB_{ST} = (B_{obs} - B_{min}) / (B_{max} - B_{min})$, where B_{obs} = observed FNB, $B_{min} = 1$, and B_{max} = the number of prey types used in computing B_{obs} (Marti and others 1993). This estimate is independent of the number of prey types included, and is useful for comparing diets among different areas that may vary in number of prey types available.

We estimated mean prey mass for each species as (total biomass/total prey items). We estimated mean prey mass both with and without insect prey included, and used Mann-Whitney tests (Conover 1980) to compare prey mass between species.

We estimated overlap in diet composition between owl species using Pianka's (1973) index: $O = \sum p_i q_i / (\sum p_i^2 \sum q_i^2)^{1/2}$, where p_i and q_i represent the

proportions of prey type *i* in the diets of the two species, respectively. This index ranges from 0 (no overlap in diet) to 1 (complete overlap).

To provide a frame of reference for evaluating dietary overlap, we compared observed overlap in diet between these species with null models of dietary overlap generated using the niche overlap module in EcoSim (Gotelli and Entsminger 2004). This module allowed us to simulate diets based on observed diet composition, and provides four possible randomization algorithms to generate null models. Based on recommendations in Winemiller and Pianka (1990) and Gotelli and Entsminger (2004), we used randomization algorithms 2 and 3. Algorithm 2 retains zero states in the observed diet data, but relaxes constraints on observed niche breadth when reshuffling data within species. Retaining zero states means that any prey type not observed in the diet of a particular species will not be included in the simulated diet for that species. In relaxing niche breadth, the program replaces the observed utilization distribution with a uniform value between 0 and 1. This results in a broad utilization spectrum, and liberal estimates of diet overlap in the simulations (Gotelli and Entsminger 2004). In algorithm 3, observed niche breadth is retained in the simulations, but zero states are reshuffled. This option thus maintains the observed dietary breadth of both species, but reshuffles the observed values among prey categories within species. This option is the recommended default (Gotelli and Entsminger 2004). We

ran 1,000 simulations for each algorithm, and accepted the default assumption that all prey types were equally available to both species, because we lacked good estimates of prey availability. Where this assumption is untrue, simulations will overestimate overlap between species (Gotelli and Entsminger 2004).

Results

We identified 1,125 and 94 prey items from pellets of spotted and great horned owls, respectively (table 2). The lower number of prey remains from great horned owls reflected both the lower number of great horned owls radio-marked and behavioral differences between owl species. Spotted owls generally could be approached closely, facilitating location of roost sites and pellet collection. In contrast, great horned owls often flew from their roost sites before we could approach closely, making it more difficult to locate roost sites and collect pellets. They also tended to re-use roost sites less often than did spotted owls, with the result that concentrations of pellets typically did not accumulate at great horned owl roost sites.

Both species of owl consumed a variety of prey groups (table 2). Both owls preyed primarily on mammals, although both also ate birds and insects, and great horned owls occasionally preyed on lizards. Mammals comprised 63 and 62% of the diets of spotted and great

Table 2. Diet composition of Mexican spotted and great horned owls in ponderosa pine-Gambel oak forest, northern Arizona. Shown are relative contributions of various prey items in terms of frequency and biomass. Data on spotted owl diet from Block and others (2005). *N* = 1,125 prey items for spotted owls and 94 prey items for great horned owls

Prey type	Mexican spotted owl		Great horned owl	
	% of prey items	% of biomass	% of prey items	% of biomass
<i>Neotoma</i> spp.	7.8	27.8	5.3	16.2
<i>Peromyscus</i> spp.	37.3	17.3	25.5	9.8
<i>Thomomys bottae</i>	5.5	15.5	10.6	25.6
<i>Microtus mogollensis</i>	1.9	1.1	10.6	5.4
<i>Sylvilagus</i> spp.	0.8	7.8	1.1	8.8
Bats	0.9	0.3	0.0	0.0
Unidentified mammals				
Small ¹	2.6	1.4	2.2	1.8
Medium	5.9	19.0	2.1	5.9
Large	0.5	3.6	4.2	21.5
Birds	3.0	5.2	2.1	3.2
Reptiles	0.0	0.0	3.2	1.2
Insects	33.7	0.9	33.0	0.7

¹ Small category includes Merriam's shrew (*Sorex merriami*). Otherwise, see Appendix 1 for size range included in categories, and for mass estimates used to estimate biomass.

horned owls, respectively, based on prey numbers, and 94 and 95% of the diets based on prey biomass. The principal mammal species consumed included the deer mouse (*Peromyscus maniculatis*), brush mouse (*P. boylii*), Mexican woodrat (*Neotoma mexicana*), pocket gopher (*Thomomys bottae*), and Mogollon vole (*Microtus mogollonensis*). Although both species of owls preyed on the same prey types (table 2), they consumed these prey types in different proportions ($P < 0.001$, test based on frequency of prey). Examination of adjusted standardized residuals indicated that significant differences in consumption occurred for reptiles, voles, and pocket gophers, with great horned owls taking more of all three prey types than spotted owls.

Both species of owl occasionally took cottontail rabbits (*Sylvilagus* spp.), chipmunks (*Tamias* spp.), and squirrels (*Spermophilus* spp.), and spotted owls occasionally took bats and Merriam's shrews (*Sorex merriami*). Both species of owls also consumed substantial numbers of insects. Identifiable insect taxa included beetles (Coleoptera) and orthopterans (Orthoptera); many were not identified even to the ordinal level.

Food niche breadth was greater for the great horned owl than for the spotted owl (table 3). This difference was due to the evenness component of this index, because richness did not vary between species ($n = 12$ prey groups included in the analysis, with 11 groups represented in the diet of each species; see table 2).

Mean prey mass averaged 47.0 ± 7.4 (SE) g for great horned owls and 40.1 ± 1.8 g for spotted owls when all prey were included. For all non-insect prey ($n = 63$ and 746 items for great horned and spotted owls, respectively), mean prey mass was 69.7 ± 9.8 g for great horned owls and 60.0 ± 2.4 g for spotted owls. Prey mass did not differ significantly between species in either of the above comparisons (Mann-Whitney tests, both P -values > 0.255).

Dietary overlap was 0.95, indicating substantial similarity in the diets of these species. Comparisons with null models indicated that observed overlap between species was greater than expected by chance. For randomization algorithm 2, mean simulated overlap was 0.69, and observed overlap was greater than simulated overlap in all 1,000 simulations (i.e., $P = 0.000$, 12 prey groups included in analysis; table 2). For randomization algorithm 3, mean simulated overlap was 0.036 ($P = 0.003$).

Discussion

We evaluated diet composition of these species based on analysis of remains from regurgitated pellets. Estimates of diet composition based on pellet contents can be biased, however, and the nature of the bias can vary among species. For example, pellets containing small remains such as insect parts may decompose rapidly, and some species may dismember large prey rather than swallowing it whole, so that pellets may not contain remains of a significant portion of prey consumed (Marti 1987). In general, analysis of remains from pellets is considered an excellent technique for estimating diet composition of medium-sized owls, but less suitable for large owls consuming large prey (Marti 1987). Although great horned owls were significantly larger than spotted owls in our study area (mean mass = $1,054 \pm 80.7$ g for five great horned owls and 602 ± 20.6 g for 13 spotted owls; $P < 0.001$), both species appeared to concentrate on relatively small prey (table 2), most of which could be consumed whole without requiring dismemberment. Consequently, we assume that analysis of remains from pellets was a suitable technique for both species, and that any inherent biases were similar between species.

Table 3. Estimates of food niche breadth (FNB) for great horned and spotted owls in North America. Species level FNB estimates were sensitive to the number of prey species included, whereas standardized FNB estimates were independent of the number of prey species (Marti and others 1993).

Species	Species-level FNB		Standardized FNB	
	This study	North America ¹	This study	North America ¹
Great horned owl	5.56	5.32-21.55	0.46	0.07-0.42
Spotted owl	3.85	8.13	0.29	0.13

¹ Estimates for the great horned owl show the range across four regions (Alaska and Canada, Western North America, mid-central North America, and east-central North America). Estimates for the spotted owl included data from all three subspecies of spotted owl, and from sites throughout the range of the spotted owl. Source: Marti and others (1993).

We have less confidence in our estimate of diet composition for great horned owls than for spotted owls, based on both the low numbers of great horned owl territories sampled and prey items located. However, all metrics of diet composition for great horned owls were similar to metrics reported elsewhere (see below). Further, our sample size for great horned owls (94 prey items) was almost double the minimum sample size ($n = 50$ observations per species) recommended by Ricklefs and Lau (1980) for estimating niche overlap. Thus, despite small sample size for great horned owls, available evidence does not suggest systematic bias in our estimate of either diet composition of great horned owls, or diet overlap between species.

Although both species of owls consumed a wide variety of prey taxa, a few taxa dominated the diet of both species (table 2). Mammals clearly dominated the diets of both owls in terms of biomass, with a few groups of mammals (3-4 groups; table 2) contributing most of this biomass. This is consistent with other studies of spotted owls, which also documented a few dominant prey taxa in most areas (Forsman and others 2001, 2004; Verner and others 1992; Ward and Block 1995). Spotted owls in ponderosa pine-Gambel oak forest preyed primarily on white-footed mice (table 2), the most abundant prey type in the study area (Block and others 2005).

Diet composition of spotted owls in this study also was extremely similar to diet composition reported in a previous study from the same area. In that study, mammals comprised 62% of the spotted owl diet by frequency and 88% by biomass, a similar range of prey types was identified, and proportions consumed were similar to our results for most taxa (Seamans and Gutiérrez 1999: table 1).

The observed diet composition of great horned owls also was generally consistent with results of other studies. The general pattern that emerges in the literature is that great horned owls are opportunistic generalist predators. Diet composition again varies among geographic areas and habitats (reviewed in Houston and others 1998), but typically includes the primary taxa identified here. No previous studies have reported diet composition of great horned owls from our study area.

Food niche breadth was greater in great horned owls than in spotted owls in this study (table 3). Observed FNB of great horned owls in this study was similar to mean FNB reported for this species (5.44) by Marti and Kochert (1995), and within the range reported for great horned owls from four regions throughout North America (table 3). In contrast, observed FNB for spotted

owls was lower than the value reported for this species by Marti and others (1993). However, Marti and others (1993) included spotted owls from throughout the western U.S. in their estimate. Because of geographic differences in prey types available, this could greatly inflate the richness component of the index relative to our study area. Consequently, it is more meaningful to compare standardized FNB estimates, which are independent of the number of species in the diet. Our standardized estimates were greater for both species of owls than values in the literature (table 3). Thus, owls in our study area did not show extreme dietary specialization relative to other populations studied, but the great horned owl showed greater dietary breadth than did the spotted owl.

Mean prey mass did not differ significantly between species. Mean prey mass for great horned owls in our study area fell within the range of values reported in the literature from different regions. Mean prey mass for great horned owls (reviewed in Houston and others 1998) ranged from 28 g in California (Rudolph 1978) to 266 g in Chile (Jaksic and Yañez 1980). In contrast, our mean prey mass for spotted owls was lower than most values reported in the literature. Mean prey mass was >100 g for spotted owls in California (Barrows 1980), and ranged from 90-142 g for northern spotted owls in seven geographic regions in Oregon (Forsman and others 2004), from 75-111 g for northern spotted owls in three geographic regions in Washington (Forsman and others 2001), and from 63-118 g for Mexican spotted owls in five geographic regions in Arizona (Ganey 1992). Our mean prey mass was comparable to that previously estimated for this area, however (36.3 g; Seamans and Gutiérrez 1999).

Overlap between spotted and great horned owls in diet composition was relatively high, and was consistently greater than simulated overlap estimates from null-model analysis. This was true even though our simulated estimates of diet overlap were biased high due to (1) our assumption of equal resource probability, and (2) our relaxation of observed niche breadth in randomization algorithm 2 (Gotelli and Entsminger 2004).

This high observed overlap in diet suggests that both species preyed on similar taxa. Diet composition may indicate some differences in foraging behavior between species, however. For example, the greater numbers of lizards, pocket gophers, and voles taken by great horned owls could indicate a greater incidence of diurnal or crepuscular foraging by this species than by spotted owls. Diurnal foraging by great horned owls has been reported elsewhere (reviewed in Houston and



Figure 2. *top*) A portion of the study area occupied by both Mexican spotted and great horned owls. Typical foraging habitat for great horned owls appears in the foreground. Great horned owls often hunted meadow edges bordered by large trees and snags. Spotted owls typically foraged in the interior forests on the butte behind the meadow. *bottom*) Interior view of pine-oak forest typically used by foraging spotted owls. Note relatively dense forest cover, presence of oak understory, and numbers of down logs.

others 1998), whereas spotted owls appear to forage largely at night (Delaney and others 1999; Forsman and others 1984, 2004; Ganey 1988; Gutiérrez and others 1995; Sovern and others 1994; but see Laymon 1991; Miller 1974).

Diet composition also suggests some differences in habitats used for foraging. For example, great horned owls took more pocket gophers than did spotted owls. Pocket gophers were widespread within the study area, but appeared to be most numerous in and around meadows and open drainage bottoms, where soils were deepest. We frequently heard or observed great horned owls calling from or perched in large trees

overlooking such areas (fig 2). In contrast, radio-marked spotted owls were seldom observed to use such areas, and concentrated their activity in forests with canopy cover >40% (Ganey and others 1997).

In summary, our results suggest that spotted and great horned owls in our study area preyed on the same types of animals. Both species preyed primarily on a few types of small mammals, overlap in diet composition was greater than expected by chance, and overlap in the size of prey taken appeared to be complete. Further, Ganey and others (1997) noted that home ranges of spotted and great horned owls overlapped spatially, and that radio-marked owls of both species foraged in at least some of the same forest stands. The fact that both species take similar prey types from the same areas suggests that they could compete for food resources. Prey availability is assumed to limit reproduction and/or survival of both spotted and great horned owls in some years (Adamcik and others 1978; Rohner 1995; Rohner and Hunter 1996; Verner and others 1992; Ward 2001), and this appears to be true both for many other owls (Korpimäki and Norrdahl 1991; Lundberg 1981; Southern 1970) and for raptorial birds in general (Newton 1979). Further, prey numbers in this area may be lower than historical levels due to changes in forest structure and especially reductions in herbaceous vegetation (Block and others 2005; Covington and Moore 1994; Ganey and others 1997; Reynolds and others 1996). Despite these considerations, however, prey limitation has not been demonstrated conclusively for either species in this area, nor can we document shifts in prey use by either species in the presence of the other. Consequently, we can not conclusively demonstrate that these owls compete for limiting food resources.

There also is evidence suggesting that these owls may partition resources to some extent, despite the observed overlap in space and food use. For example, great horned owls tended to consume more diurnally active prey than did spotted owls, suggesting potential differences in activity periods. Finally, great horned owls concentrated foraging activity in areas with canopy cover <40%, whereas spotted owls concentrated foraging activity in areas with >40% canopy cover (Ganey and others 1997: table 5), and great horned owls foraged in and around meadows which were used rarely by spotted owls (Ganey and others 1997: table 6). These differences in habitat use, activity period, and type of prey taken (diurnally active versus nocturnally active) could allow these owls to minimize potential competition for food.

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