

ARE RED-TAILED HAWKS AND GREAT HORNED OWLS DIURNAL-NOCTURNAL DIETARY COUNTERPARTS?

CARL D. MARTI¹ AND MICHAEL N. KOCHERT²

ABSTRACT.—Red-tailed Hawks (*Buteo jamaicensis*) and Great Horned Owls (*Bubo virginianus*) are common in North America where they occupy a wide range of habitats, often sympatrically. The two species are similar in size and have been portrayed as ecological counterparts, eating the same prey by day and night. We tested the trophic similarity of the two species by comparing published dietary data from across the United States. Both species ate primarily mammals and birds, and mean proportions of those two prey types did not differ significantly between diets of the two raptors. Red-tailed Hawks ate significantly more reptiles, and Great Horned Owls significantly more invertebrates. Dietary diversity was not significantly different at the level of prey taxonomic class, and diet overlap between the two species averaged 91%. At the prey species level, dietary overlap averaged only 50%, and at that level Red-tailed Hawk dietary diversity was significantly greater than that of Great Horned Owls. Mean prey mass of Red-tailed Hawks was significantly greater than that of Great Horned Owls. Populations of the two species in the western United States differed trophically more than did eastern populations. We conclude that, although the two species are generalist predators, they take largely different prey species in the same localities resulting in distinctive trophic characteristics. Received 19 December 1994, accepted 15 May 1995.

Red-tailed Hawks (*Buteo jamaicensis*) and Great Horned Owls (*Bubo virginianus*) have been portrayed as ecological counterparts that take the same kinds of prey by day and night (Bent 1938, Craighead and Craighead 1956, Austing 1964, Austing and Holt 1966, Springer and Kirkley 1978). Both are widespread, common raptors in North America (Johnsgard 1988, 1990), and both occupy a wide range of habitats, often sympatrically. They are similar in size (Red-tailed Hawk mean mass = 1126 g; Great Horned Owl mean mass = 1354 g; Dunning 1984), and both are considered to have generalized diets, i.e., they do not specialize on specific prey types (Errington et al. 1940, Steenhof and Kochert 1985).

Coexisting species segregate their feeding niches primarily by differences along three dimensions: the habitat used for foraging, the kind of food eaten, and the time of day that foraging occurs (Cody 1968, Schoener 1974, Jaksić 1988). Schoener (1974) considered time of activity to be the least influential of these niche dimensions, and Jaksić (1982) concluded that time of activity was not adequate to separate niches of hawks and owls. However, judging from the similarity in body size and habitat

¹ Dept. of Zoology, Weber State Univ., Ogden, Utah 84408-2505.

² Raptor Research and Technical Assistance Center, National Biological Service, Boise, Idaho 83705.

usage between Red-tailed Hawks and Great Horned Owls (Hagar 1957, McInville and Keith 1974, Houston 1975, Petersen 1979, Minor et al. 1993), time of foraging activity seems likely to be the most important factor differentiating the niches of the two.

Our objective was to determine if trophic characteristics of the two species support the contention that they are dietary counterparts. We tested whether time of activity produced substantial differences in trophic characteristics between the two raptors.

METHODS

We searched the literature for dietary data with the requirement that the geographic area and date of data collection potentially enabled both species to exploit the same prey resources. Additionally, we required that each sample contained at least 100 prey items, and had vertebrate prey identified to genus or species, and most invertebrate prey to order. For geographic analyses, we considered samples from New York, New Jersey, Connecticut, Ohio, Wisconsin, and Michigan as representing eastern populations, and samples from Wyoming, Utah, Idaho, Montana, Washington, and California as representing western populations. We calculated the following trophic estimators from the selected data sets: (1) Food-niche breadth (FNB) as estimated by Levins' (1968) modification of Simpson's index ($FNB = 1/\sum p_i^2$, where p_i = the frequency of each prey type in a diet) was calculated at both coarse and fine resolution. The coarse level (FNB_c), where prey categories were taxonomic classes, provided an indication of the versatility of the predator, i.e., larger values at this level indicate that the predator is capable of detecting, capturing, and handling diverse kinds of prey (Greene and Jaksic 1983). The fine resolution (FNB_p), where prey categories were species or genera for vertebrate prey and order for invertebrate prey, provided greater discrimination between the two raptors' diets. (2) Geometric mean prey mass (GMPM; Sokal and Rohlf 1981, p. 42) was estimated using prey weights in Steenhof (1983).

Overlap between diets of the two raptors was assessed by Pianka's index (1973): $O = \sum p_i \sum q_i / (p_i^2 \sum q_i^2)^{1/2}$, where p_i = the frequency of a prey type in one of the raptor's diet and q_i = the frequency of the same prey type in the other raptor's diet. Overlap was also calculated at coarse and fine resolutions using the same criteria as for FNB. Paired *t*-tests were used to compare means of trophic estimators.

RESULTS

The thirteen data sets meeting our selection criteria (Appendix 1) revealed that both Red-tailed Hawks and Great Horned Owls fed largely on vertebrates in five taxonomic classes, but they also consumed small numbers of arthropods. Mammals were numerically dominant in all of the Great Horned Owl diets, and in all but one Red-tailed Hawk diet (Fig. 1; Orians and Kuhlman 1956). Avian prey was second in numeric importance overall for both species (Fig. 1), but was exceeded by reptiles in four studies on the Red-tailed Hawk (Fitch et al. 1946, Knight and Erickson 1976, Fitzner et al. 1981, Marti et al. 1993b), and by arthropods in three studies on the Great Horned Owl (Fig. 1; Fitch 1947, Smith and

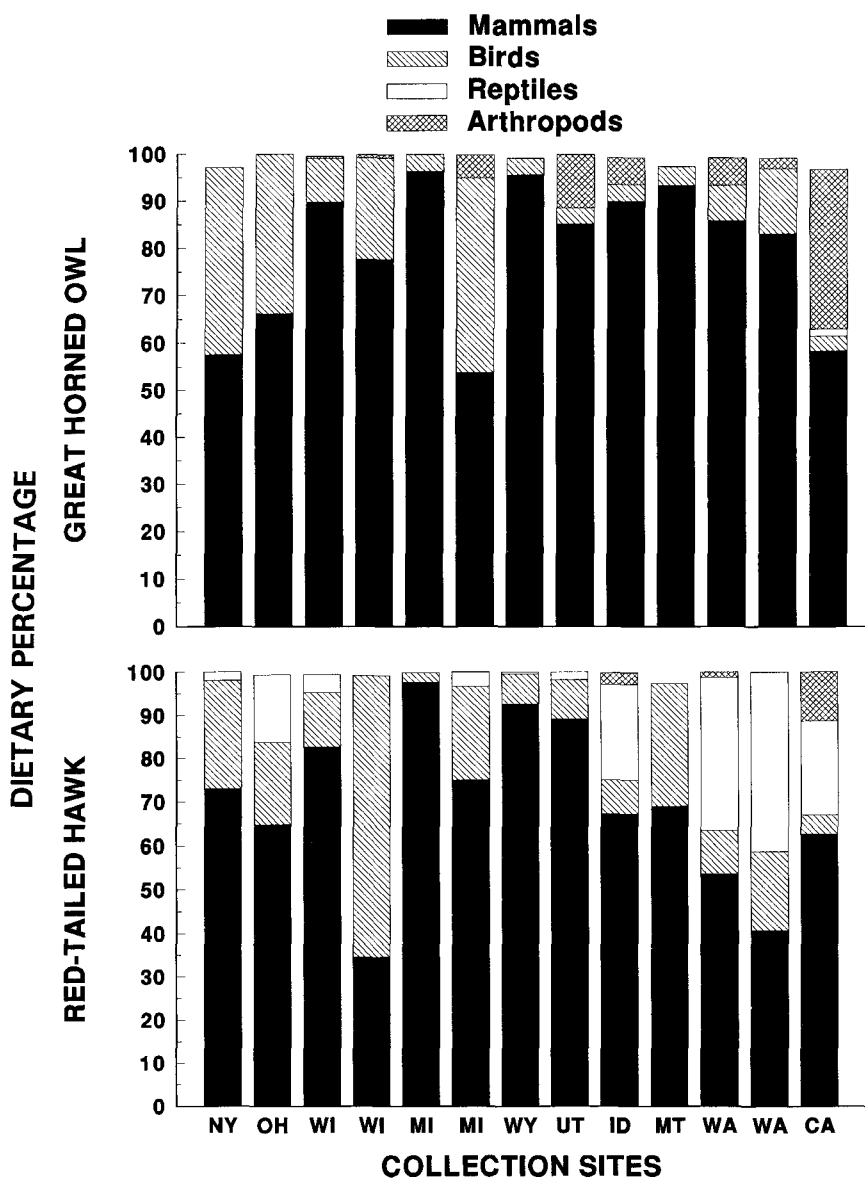


FIG. 1. Proportions by number of major prey types in diets of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

TABLE 1
SUMMARY AND COMPARISON OF TROPHIC CHARACTERISTICS OF GREAT HORNED OWLS AND RED-TAILED HAWKS (CALCULATED FROM DATA SOURCES IN APPENDIX I)

Trophic characteristic	Great Horned Owl		Red-tailed Hawk		<i>r</i> ^a	<i>P</i>
	Mean	SD	Mean	SD		
Food-niche breadth (class)	1.51	0.42	1.78	0.49	1.81	0.10
Food-niche breadth (species)	5.44	3.28	6.66	4.58	2.36	0.04
Geometric mean prey mass, g	76.0	64.7	175.0	137.4	3.00	0.01
% mammals in diet	79.5	15.3	69.4	18.9	1.73	0.11
% birds in diet	14.2	14.2	17.7	16.3	0.77	0.46
% reptiles in diet	0.4	0.8	11.4	14.5	2.80	0.02
% amphibians in diet	0.1	0.4	0.2	0.3	0.25	0.81
% fishes in diet	0.5	1.0	0.2	0.5	1.43	0.18
% arthropods in diet	5.0	9.3	1.2	3.2	2.15	0.05
Mean overlap in prey class (SD)		0.91 (0.1)				
Mean overlap in prey species (SD)		0.50 (0.3)				

^a Paired *t*-tests, *N* = 13.

Murphy 1973, Marti et al. 1993b). Although both raptors occasionally ate amphibians and fish, neither was important in their diets (Table 1).

The heavy reliance on mammalian prey by both raptors resulted in high dietary overlap between them at the prey class level (Fig. 2). Dietary overlap at the prey species level was considerably lower indicating that the two often ate different mammal species at the same localities (Fig. 2). The most common prey for Red-tailed Hawks typically was a diurnal mammal while for Great Horned Owls it was a nocturnal mammal (Table 2).

FNB_{cl} was also quite similar between the two species demonstrating that they have corresponding capabilities in detecting and capturing prey at the broad category of taxonomic class (Fig. 3). Mean differences between FNB_{cl} in paired samples of Red-tailed Hawks and Great Horned Owls were not significant (Table 1). FNB_{cl} of the Red-tailed Hawk was larger than the Great Horned Owl FNB_{cl} in eight of the paired samples, but the converse was true in five. FNB_{sp} of the Red-tailed Hawk was significantly greater than that of the Great Horned Owl (Table 2). Ten of the 13 paired FNB_{sp} values were higher for the hawk (Fig. 4), showing that it usually preyed upon a greater diversity of prey species than did the owl. Red-tailed Hawks took larger prey on average in 11 of the 13 paired samples (Fig. 5), and the GMPM of the Red-tailed Hawk overall was significantly larger than that of the Great Horned Owl (Table 1).

In dietary samples from eastern populations, none of the trophic char-

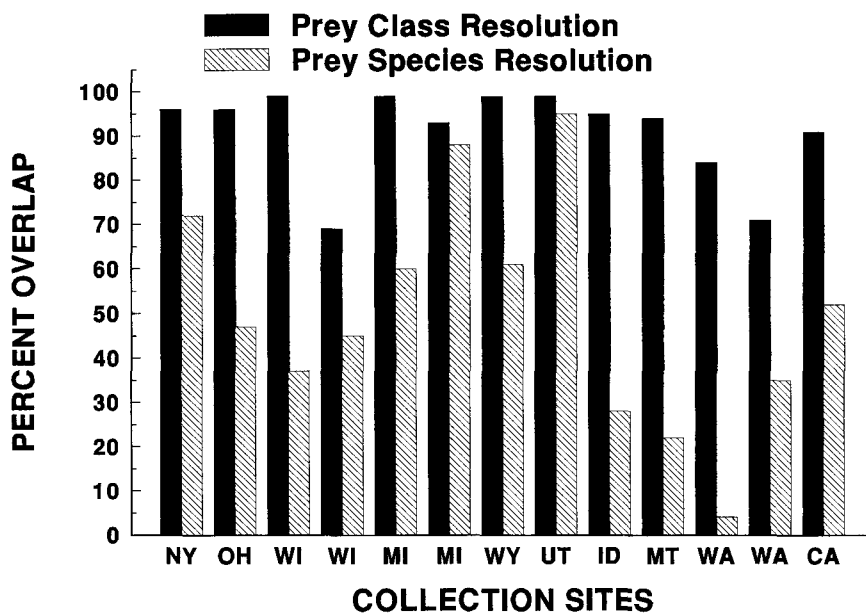


FIG. 2. Overlap between diets of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

TABLE 2

MOST COMMON PREY FOR GREAT HORNED OWLS AND RED-TAILED HAWKS (CALCULATED FROM DATA SOURCES IN APPENDIX I)

Location ^a	Most common prey in diet	
	Great Horned Owl	Red-tailed Hawk
1	<i>Peromyscus</i>	<i>Tamias</i> and <i>Sciurus</i>
2	<i>Microtus</i>	<i>Tamias</i>
3	<i>Peromyscus</i>	<i>Spermophilus</i>
4	<i>Peromyscus</i>	<i>Phasianus</i>
5	<i>Peromyscus</i>	<i>Microtus</i>
6	<i>Microtus</i>	<i>Microtus</i>
7	<i>Microtus</i>	<i>Spermophilus</i>
8	<i>Lepus</i>	<i>Lepus</i>
9	<i>Microtus</i>	<i>Spermophilus</i>
10	<i>Peromyscus</i>	<i>Spermophilus</i>
11	<i>Perognathus</i>	<i>Spermophilus</i>
12	<i>Microtus</i>	<i>Coluber</i>
13	<i>Neotoma</i>	<i>Spermophilus</i>

^a See Appendix I for geographic location and source of data.

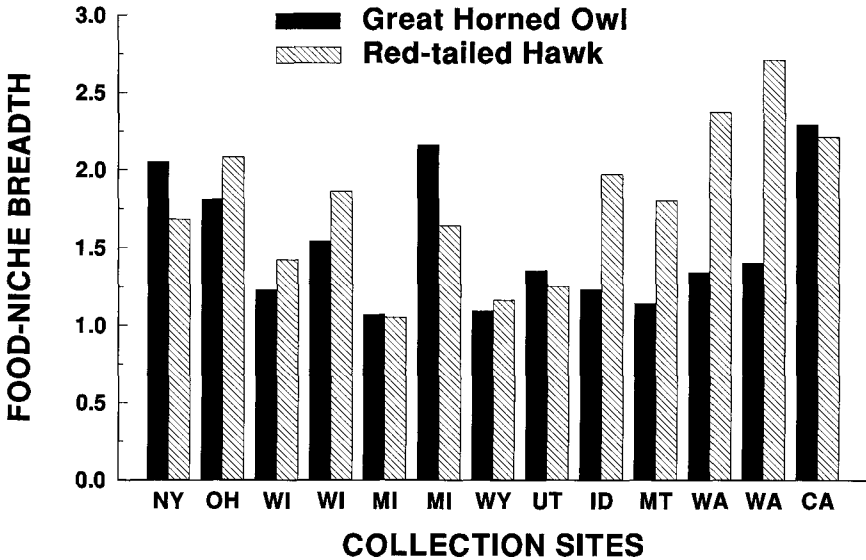


FIG. 3. Dietary diversity at the coarse level of prey discrimination (FNB_{c1}) in diets of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

acteristics we measured was significantly different between the two species (Table 3). In the West, though, five of the seven trophic characteristics did differ significantly. GMPM diverged most with Red-tailed Hawks taking significantly larger prey. Dietary overlap at the prey species level also was much less in the West indicating a stronger divergence in the kinds of prey eaten (Table 3). Despite the geographic variation in interspecific differences between Red-tailed Hawks and Great Horned Owls, intraspecific trophic characteristics were not significantly different, east versus west, except for birds in diets of Great Horned Owls (Table 4).

DISCUSSION

Red-tailed Hawks and Great Horned Owls appear to use similar habitats, although we do not know of any studies that simultaneously examined microhabitat use by the two species. Numerous investigators found them breeding in the same habitat (e.g., Hagar 1957, McInville and Keith 1974, Houston 1975, Petersen 1979, Minor et al. 1993). Nests of the two species averaged only 51 m apart where nest sites were limited and clumped (Houston 1975), but even in more homogeneous habitats the two often nested within 200–300 m of each other (Hagar 1957, McInville and Keith 1974, Minor et al. 1993). Great Horned Owls commonly use

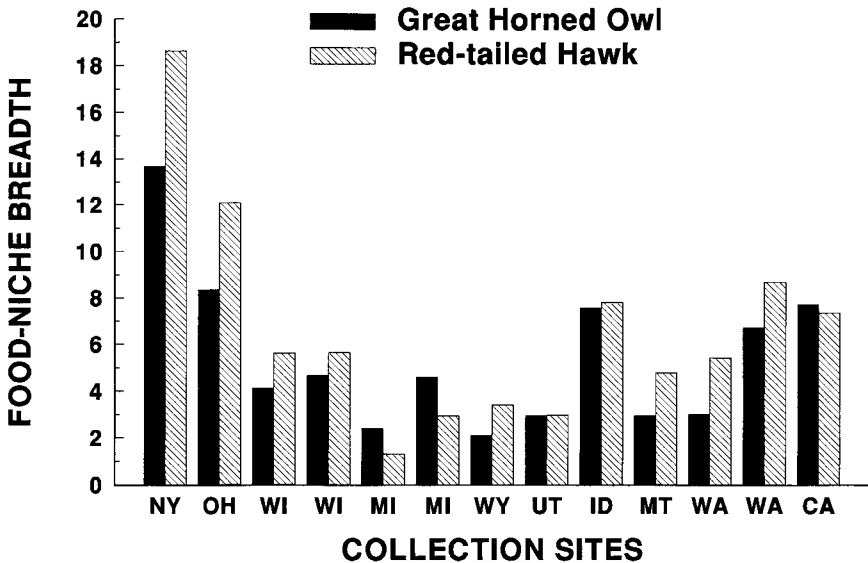


FIG. 4. Dietary diversity at the fine level of prey discrimination (FNB_{sp}) in diets of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

nesses constructed by Red-tailed Hawks (Orians and Kuhlman 1956, Hagar 1957, Houston 1975, Petersen 1979, Minor et al. 1993).

Both of these raptors are dietary generalists and highly opportunistic predators capable of taking the same prey over a large range in size and type. They have the potential to have high overlap in diet, and on a continent-wide basis we found that diets of co-occurring populations did overlap extensively at the coarse level of prey discrimination (taxonomic class of prey). At the fine level (prey species), however, their diets on average overlapped only 50%—a large niche separation. Both species have been reported to feed on carrion (Sooter 1942, Stalmaster 1980, Preston and Beane 1993). How this behavior might affect the trophic parameters we measured cannot be evaluated because the data on it are limited and mostly anecdotal.

Trophic differences between the two species were much more pronounced in the West than in the East. A previous broad-scale analysis of the trophic structure of raptor assemblages (Marti et al. 1993a) concluded that, on a regional basis, both the Red-tailed Hawk and Great Horned Owl consumed far more species of prey and had broader food-niche breadths in the western United States than in the central or eastern U.S. That same pattern held for entire assemblages of many raptor species

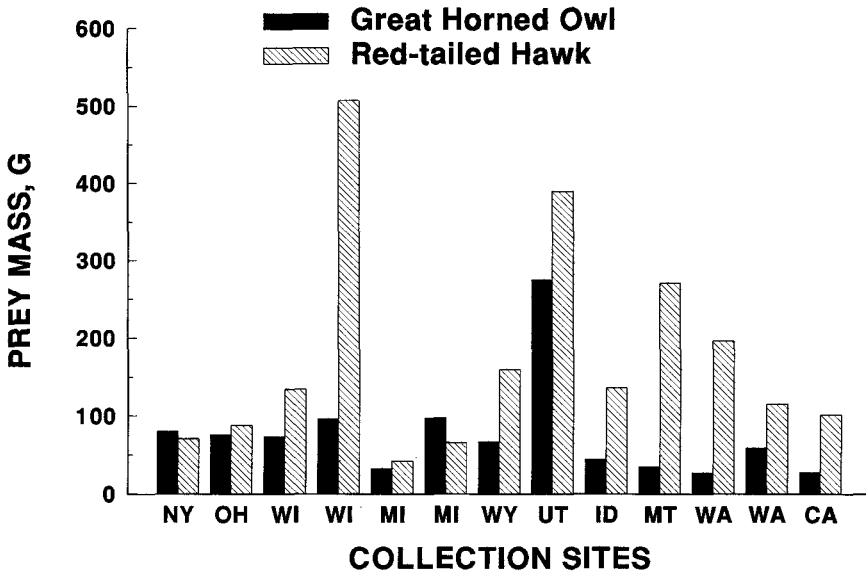


FIG. 5. Geometric mean prey mass of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

(Marti et al. 1993a). The species density of both birds and mammals increases from east to west in North America (Cook 1969, Pagel et al. 1991), and, at least for mammals, the size of geographic ranges decreases toward the West. These patterns could help explain why raptor food-niche breadths calculated for large regions should be broader in the West than in the East. Our present much finer scale analysis found that food-niche breadth was narrower for both Red-tailed Hawks and Great Horned Owls in the West compared to the East. A possible explanation is that greater diversity of available prey in the West may permit local populations of these two raptors to increase their diet segregation in that region.

Jaksić (1982) believed that time of activity, in general, did not result in diet differences sufficient to separate the niches of hawks and owls. Carothers and Jaksić (1984) proposed that interference competition rather than exploitation competition was the force causing the diel difference in activity between hawks and owls. Time of activity, however, does seem to be the niche dimension that causes the greatest divergence in diets of Red-tailed Hawks and Great Horned Owls. Our findings show that diets of the two species at the same locality are similar to each other in most trophic characteristics, but that these two raptors concentrate their pre-

TABLE 3
TROPIC CHARACTERISTICS OF GREAT HORNED OWLS (GHO) VERSUS RED-TAILED HAWKS (RTH) IN EASTERN AND WESTERN POPULATIONS (CALCULATED FROM DATA SOURCES IN APPENDIX I)

Trophic characteristic	Eastern U.S.		Western U.S.	
	GHO	RTH	GHO	RTH
Food-niche breadth (class)				
Mean (SD)	1.64 (0.44)	1.62 (0.36)	1.41 (0.41)	1.92 (0.57)
Paired- <i>t</i> (<i>P</i>) ^a	0.15 (0.89)		2.44 (0.05)	
Food-niche breadth (species)				
Mean (<i>P</i>)	6.30 (4.10)	7.70 (6.49)	4.70 (2.48)	5.77 (2.22)
Paired- <i>t</i> (<i>P</i>)	1.32 (0.24)		2.44 (0.05)	
Geometric mean prey mass, g				
Mean (<i>P</i>)	75.2 (23.8)	151.1 (177.0)	76.1 (88.9)	195.4 (102.9)
Paired- <i>t</i> (<i>P</i>)	1.10 (0.32)		5.03 (0.002)	
% mammals in diet				
Mean (SD)	73.6 (17.3)	71.2 (21.4)	84.6 (12.4)	67.8 (18.4)
Paired- <i>t</i> (<i>P</i>)	0.25 (0.81)		2.39 (0.05)	
% birds in diet				
Mean (SD)	24.3 (15.5)	24.2 (21.4)	5.6 (3.9)	12.1 (8.4)
Paired- <i>t</i> (<i>P</i>)	0.01 (0.99)		2.16 (0.07)	
% reptiles in diet				
Mean (SD)	0.1 (0.2)	4.2 (5.8)	0.7 (1.0)	17.6 (17.1)
Paired- <i>t</i> (<i>P</i>)	1.71 (0.15)		2.66 (0.04)	
% arthropods in diet				
Mean (<i>P</i>)	1.0 (2.0)	0 (0)	8.5 (11.9)	2.2 (4.2)
Paired- <i>t</i> (<i>P</i>)	— (—)		2.05 (0.09)	
Mean overlap in prey class (SD)	0.92 (0.1)		0.90 (0.1)	
Mean overlap in prey species (SD)	0.58 (0.2)		0.42 (0.3)	

^a N = 13.

dation on a different array of species by being active at different times of the day.

Other sympatric predators (raptors, mammals, and snakes) that eat the same species taken by Red-tailed Hawks and Great Horned Owls must also be considered when attempting to understand and compare the niches of Red-tailed Hawks and Great Horned Owls. Only four predator assemblages in North America containing both Red-tailed Hawks and Great Horned Owls have been analyzed for such effects (Jaksić 1988, Marti et

TABLE 4
TROPIC CHARACTERISTICS OF EASTERN VERSUS WESTERN POPULATIONS OF GREAT HORNED OWLS AND RED-TAILED HAWKS^a

Trophic characteristic	Great Horned Owl					Red-tailed Hawk					
	Eastern		Western		P	Eastern		Western		P	
	\bar{x}	(SD)	\bar{x}	(SD)		t	\bar{x}	(SD)	\bar{x}		(SD)
Food-niche breadth (class)	1.64	(0.44)	1.41	(0.41)	0.86	1.62	(0.36)	1.92	(0.57)	0.74	0.47
Food-niche breadth (species)	6.30	(4.10)	4.70	(2.48)	1.01	7.70	(6.49)	5.77	(2.22)	1.12	0.29
Geometric mean prey mass	75.2	(23.8)	76.1	(88.9)	0.01	151.1	(177.0)	195.4	(102.9)	0.56	0.58
% mammals in diet	73.6	(17.3)	84.6	(12.4)	1.33	71.2	(21.4)	67.8	(18.4)	0.31	0.76
% birds in diet	24.3	(15.5)	5.6	(3.9)	3.10	24.2	(21.4)	12.1	(8.4)	1.39	0.19
% reptiles in diet	0.1	(0.2)	0.7	(1.0)	1.33	4.2	(5.8)	17.6	(17.1)	1.81	0.10
% arthropods in diet	1.0	(2.0)	8.5	(11.9)	1.50	0	—	2.2	(4.2)	—	—

^a Calculated from data sources in Appendix I.

al. 1993b). In two assemblages (Idaho and Wisconsin) the two species were in different feeding guilds, but in the other two (Michigan and California) they were in the same guild (in California they were in different subgroups within one guild). The small number of such studies does not provide much insight into what trophic patterns might arise out of interactions among a wider range of predators. But, those analyses may indicate that trophic relationships between Red-tailed Hawks and Great Horned Owls are also affected by the presence of other predators.

The high overlap in habitat use and prey between Red-tailed Hawks and Great Horned Owls could certainly lead to exploitation competition. Competition and its effects, however, have been notoriously hard to quantify in most bird populations (Wiens 1989). We know of only two studies on competition in raptors that have detected reduced reproductive success in the presence of a potentially competing species (Nilsson 1984, Korpimäki 1987). Interference competition between Red-tailed Hawks and Great Horned Owls may be largely avoided by differences in time of activity. However, Great Horned Owls begin nesting about one month earlier than co-existing Red-tailed Hawks (Orians and Kuhlman 1956, Seidensticker and Reynolds 1971, McInville and Keith 1974, Minor et al. 1993) and may thus interfere with the hawks' access to breeding areas by appropriating nests. The ultimate form of interference competition—one species killing the other—has been reported between these two species, mostly based on circumstantial evidence. The majority of instances were Great Horned Owls preying on nestling Red-tailed Hawks (Hamerstrom and Hamerstrom 1951, Craighead and Craighead 1956, Luttich et al. 1971, Petersen 1979), but one adult Red-tailed Hawk may have been killed by a Great Horned Owl (Houston 1975). Red-tailed Hawk predation on nestling Great Horned Owls was suspected by Fitch (1940) and Orians and Kuhlman (1956).

Our analysis suggests that time of activity may be the most important factor that prevents or reduces the degree of competition between these two species by permitting sympatric populations to prey upon somewhat different prey arrays. Our results further support the contention that many raptors are very versatile in diet, and that diets in local areas are, to a large extent, the result of opportunism.

The answer to the question—are these two species diurnal-nocturnal dietary counterparts—is strongly affected by the scale used to compare them. At a coarse level, the two are much alike in habitat use and predatory capability, and could be considered to be day-night equivalents. At a fine level, dietary differences are much more pronounced. Thus, Red-tailed Hawks and Great Horned Owls, by being active at different times,

interact with different arrays of prey species, and are not day-night feeding equivalents.

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APPENDIX I

SOURCES AND CHARACTERISTICS OF DATA SETS USED FOR ANALYSES

Location	Habitat type	Length of study (years)	Season of data collection	Source
1 New York, New Jersey, Connecticut	Deciduous forest	12	Breeding	Bosakowski and Smith (1992)
2 Ohio	Farmland	3	Breeding	Springer and Kirkley (1978)
3 Wisconsin	Farmland	3	All year	Errington (1932, 1933)
4 Wisconsin	Farmland	3	Breeding	Orians and Kuhlman (1956)
5 Michigan	Farmland	2	Winter	Craighead and Craighead (1956)
6 Michigan	Farmland	2	Breeding	Craighead and Craighead (1956)
7 Wyoming	Mountain valley ^a	1	Breeding	Craighead and Craighead (1956)
8 Utah	Shrub-steppe	4	Breeding	Smith and Murphy (1973)
9 Idaho	Shrub-steppe	17	Breeding	Marti et al. (1993b)
10 Montana	Mountain valley ^a	3	Breeding	Seidensticker (1968, 1970)
11 Washington	Shrub-steppe	6	Breeding	Fitzner et al. (1981)
12 Washington	Shrub-steppe	2	Breeding	Knight and Erickson (1976, 1977)
13 California	Grassland/chaparral	3	All year	Fitch et al. (1946), Fitch (1947)

^a Mostly riparian and shrub-steppe with some upland forest and pasture.