

Dietary shifts of sympatric buteos during a prey decline

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Summary. Diets of nesting Red-tailed Hawks (*Buteo jamaicensis*) and Ferruginous Hawks (*Buteo regalis*) were sampled before and after a decline in the hawks' principal prey species. Diets of pairs that shared their foraging ranges with interspecifics were contrasted with those of pairs whose home ranges did not overlap with interspecifics. Current theory predicts that diets should diverge during prey shortages and that overlap should be especially reduced in ranges shared with interspecifics. Species composition of the two hawks' diets diverged during the prey shortage, but the divergence was most pronounced in hawks that did not share foraging ranges with interspecifics. In contrast to predictions, the two species converged on similar-sized prey during the prey shortage. Available data on differences in habitat composition and prey availability at the sample sites did not explain the deviations from the predicted response. Although our findings on diet shifts differ from those of most other studies, the implications are consistent with observations of others who have studied assemblages of mammal-feeding raptors. We conclude that diet composition of the hawks we studied was not directly affected by interspecific competition and that shifts in diet overlap during prey shortages do not necessarily imply that interspecific competition is occurring.

Although interspecific competition has long been recognized as an important factor that shapes the niches of sympatric species (Hutchinson 1957; MacArthur 1972; Cody 1974), the mechanisms of food-niche divergence have rarely been documented in natural situations. Resource overlap measures are, by themselves, ambiguous (Colwell and Futuyma 1971; Lawlor 1980), but changes in resource overlap may sometimes reveal the effects of interspecific competition.

Two approaches have been used to assess niche shifts and the influencing role of interspecific competition. The first examines resource utilization patterns of species, contrasting niches in situations where potential competitors are present with niches where competitors are absent (Huey et al. 1974; Schoener 1975; Werner and Hall 1976; Diamond 1978; Alatalo 1981; Schmitt and Coyer 1983). If interspecific competition is influencing resource utilization patterns, overlap should be reduced in situations where po-

tential competitors are present. Findings have suggested that competition is associated with niche shifts both in ecological time through interaction of individuals (e.g. Alatalo 1981) and in evolutionary time through differential selection pressure (e.g. Diamond 1978). One problem with this approach is that divergence in resource use may be due solely to differences in resource availability; many investigations have contrasted resource utilization patterns in widely separated areas where resource availability differs greatly. A lack of divergence, on the other hand, may be due to resources not being limited at the time data were collected (Wiens 1977).

The second approach, recently revived by Schoener (1982), contrasts resource utilization patterns during periods of prey abundance with those during prey shortages. If interspecific competition favors or has favored resource partitioning during so-called "lean" (Schoener 1982) or "crunch" periods (Wiens 1977), then resource utilization by ecologically similar species should diverge as resources become scarce (Lack 1946; Svardson 1949; Schoener 1982). A number of studies (e.g. Werner 1977; Smith et al. 1978; Dunham 1983 and others cited in Schoener 1982) have demonstrated reduced interspecific dietary overlap during periods of resource shortage. Evidence has come mainly from studies of seasonal differences in resource use (e.g. Baker and Baker 1973; Opdam 1975), which can be confounded by variations in taxonomic composition and diversity of available resources. Additional evidence has come from shifts observed during less regular drought periods (Smith et al. 1978; Dunham 1983). Experimental population studies (reviewed by Schoener 1983) have shown that year-to-year variability in competition is especially pronounced in drought situations. But merely finding that resource use by species differs, even if the differences are greater during crunch periods, does not necessarily imply that the differences result from interspecific competition.

Foraging shifts can result from either genetic changes or behavioral plasticity (Werner and Hall 1976; Thomson 1980; Alatalo 1980, 1981). Evidence to implicate interspecific competition as a major force in the evolution of genetically fixed resource niches (Alatalo 1980) is difficult to obtain. The role of present competition in effecting niche changes is more easily assessed. If competition is the proximal cause of niche divergence, then decreased dietary overlap during food shortages should be most clear in individuals whose foraging ranges overlap with those of potential competitors. If overlap decreases as much or more in un-

Table 1. Comparison of morphological characteristics of *Buteo regalis* (BR) and *Buteo jamaicensis* (BJ). Ratios are calculated from the means shown or from the midpoints of ranges provided by Brown and Amadon (1968)

Characteristic	BJ	BR	(BR/BJ)	Source ^a
♂ mass (g)	1,028	1,059	1.03	1
♀ mass (g)	1,224	1,231	1.01	1
♂ culmen (mm)	25.1	27.7	1.10	1
♀ culmen (mm)	26.9	28.4	1.06	1
♂ wing length (mm)	337–396	421–440	1.17	2
♀ wing length (mm)	370–427	427–450	1.10	2
♂ tail length (mm)	197–240	231–246	1.09	2
♀ tail length (mm)	215–254	239–252	1.05	2
tarsal length (mm)	77–93	81–92	1.02	2
food pad length (mm)	89	81	0.91	This study

^a 1 = Snyder and Wiley 1976

2 = Brown and Amadon 1968

shared foraging ranges, then some other factor may be implicated. As yet, no field studies of vertebrates have examined changes in food-niche overlap in relation to both temporal changes in prey abundance and the spatial presence of a potential competitor.

Interspecific competition is expected to be more important at higher trophic levels (Menge and Sutherland 1976). Hairston et al. (1960) predicted that interspecific competition for food should be especially important for predatory birds and noted that coexistence is usually facilitated by niche diversification. Bird-eating accipiter hawks typically exhibit low dietary overlap and distinct morphological separation (Lack 1946; Storer 1966; van Beusekom 1972; Opdam 1975; Reynolds and Meslow 1984; Schoener 1984), but the sympatric buteos of North America do not. Two North American buteos, the Red-tailed Hawk (*Buteo jamaicensis*) and the Ferruginous Hawk (*Buteo regalis*), are excellent subjects for the study of resource partitioning, interspecific competition, and niche shifts because: 1) they typically show high dietary overlap (Schmutz et al. 1980; Cottrell 1981; Jaksić and Braker 1983); 2) they are closely related (Brown and Amadon 1968); 3) ratios of linear morphological characters are below Hutchinson's (1959) proposed minimum ratio of 1.3, and ratios of body mass are far below the expected value of 2.1 (Table 1); 4) they do not maintain interspecific territories (Schmutz et al. 1980; Cottrell 1981; Knight and Smith 1982); 5) predation on them is minimal and therefore should not confound resource utilization patterns; and 6) both buteo species are known to be food-limited, at least at some levels of prey abundance (Howard and Wolfe 1976; Woffinden and Murphy 1977; Phelan and Robertson 1978; Smith and Murphy 1978, 1979; Thuroff et al. 1980; Smith et al. 1981).

Diets of these two sympatric buteos were studied in southwestern Idaho before and after a severe decline in the hawks' main prey species. We sampled diets at different levels of prey abundance and contrasted responses of individuals that shared their foraging ranges with interspecifics against those whose ranges did not overlap with interspecifics. The purpose of the analysis was to determine: 1) whether diet divergence occurred during periods of low prey availability, and 2) whether divergence was associated with

the presence of potential competitors. We also examined the available data to determine if deviations from the predicted response could be explained by differences in habitat composition or prey availability.

Methods

From 1975 to 1978, nesting *Buteo regalis* and *Buteo jamaicensis* pairs were studied in a 100,000-ha area within the Snake River Birds of Prey Area in southwestern Idaho, USA (42°50' N, 115°50' W). Vegetation in the area is characteristic of a shrubsteppe community in an Upper Sonoran life zone, with big sagebrush (*Artemisia tridentata*), shadscale (*Atriplex confertifolia*), and winterfat (*Ceratoides lanata*) vegetation associations. The principal physiographic feature is the Snake River Canyon with basalt cliffs ranging from 2 to 125 m in height. Topography above the canyon is generally flat or slightly rolling with a few isolated buttes. Elevation ranges from 770 m in the canyon bottom to 1000 m at the rim. Annual precipitation averages 20 cm and occurs mainly in winter; summers are hot and dry (USDI 1979).

Relative densities of each of the major prey species were estimated by other investigators during the study period. Townsend ground squirrel (*Spermophilus townsendii*) abundances were estimated from live-trapping grids (Smith and Johnson 1985) and hole count transects (USDI 1979). Densities of small rodents other than ground squirrels were estimated from a combination of live-trapping and snap-trapping (USDI 1979). Spotlighting transects (Smith and Nydegger in press) and counts by survey crews (USDI 1979) were used to census black-tailed jack rabbits (*Lepus californicus*). Snake and lizard populations were assessed from drift fence captures (Diller and Johnson 1982), and passerines were censused using walking transects (Emlen 1971). These studies established habitat affinities for the major prey species as well as yearly changes in overall abundances.

Homogeneous vegetation stands in the study area were identified from aerial photographs and inventoried on the ground (USDI 1979). Habitat types were identified on the basis of physiognomic and taxonomic characteristics of the vegetation as well as habitat affinities of prey species. Prey abundance estimates (PAE's) for specific areas were calculated for each of five prey groups based on habitat/density relationships developed by USDI (1979), Diller and Johnson (1982), Smith et al. (1984), and Nydegger and Smith (in press). PAE's served as indexes to relative differences in geographic availability of prey and were independent of yearly changes in prey populations.

A severe drought occurred in the area during the winter of 1976–77. Precipitation from November to April was lower than in the 70 previous years for which records were kept (USDI 1979). In the spring of 1977, Townsend ground squirrels failed to reproduce, apparently because of the lack of available green vegetation (Smith and Johnson 1985). Squirrel densities in April 1977 were only 25% of those observed in 1975–76, and adult ground squirrels estimated two months earlier than normal in 1977. Spring densities in 1978 were 50% lower than 1975–76 densities, reflecting the absence of yearlings in the population (Smith and Johnson in press). Snake species that depend on ground squirrels for food were also affected by the drought. Western rattlesnake (*Crotalus viridis*) reproduction and growth rates declined significantly in 1977 and 1978, apparently due to

the lack of ground squirrels. In addition, activity of both rattlesnakes and gopher snakes (*Pituophis melanoleucus*) decreased markedly in 1977 (Diller and Johnson 1982). Cyclic fluctuations masked any possible effects of the drought on black-tailed jack rabbit populations; rabbit numbers in 1977–78 were 15% higher than in 1975–76. Our sampling methods detected no significant changes in populations of other prey species during the study period. Exceptionally tall growth of annual plants in the unusually wet spring of 1978, however, may have concealed prey from raptors, further reducing the availability of most prey species in 1978. In this analysis, we considered 1975 and 1976 to be “normal” prey years; 1977 and 1978 were classed as “low” prey years.

Diets of both hawk species were sampled from 1975 to 1978 by collecting prey remains and pellets from nests with young. Prey remains were collected approximately once every four days during the brood-rearing period. A “collection” consisted of all remains and pellets collected from a particular nest on a particular day. The original purpose of sampling was to assess possible effects of land use changes on raptors (USDI 1979). For this later analysis we used data from a smaller area and a more restricted number of nesting pairs to minimize variability in habitat composition and relative prey abundance around nests. All pairs of hawks used in the analysis nested on cliffs within the canyon, and we excluded pairs if more than 20% of their generalized foraging range (see below) was irrigated farmland. The analysis was based on 158 collections at 25 nests, which yielded 602 prey items (Table 2).

Fresh prey remains were identified, marked by removing the head, feet, and tail, and left in the nest. Inedible remains and pellets were collected and analyzed in the laboratory. Species, size, and sex of prey items were ascertained by comparison with study skins and taxonomic keys. Number of individual prey in each collection was calculated from a maximum count of body parts (femurs, toenails, and/or mandibles) as outlined by Mollhagen et al. (1972). Prey remains identified in pellets were compared with the tally of fresh prey individuals and partially eaten prey identified during the previous collection. If remains in a pellet might have originated from a prey individual that had already been counted, the possible duplicate was excluded from the total. Weights were assigned to individual prey according to their size and sex class, based on average weights reported by Steenhof (1983).

Home ranges of radioed *Buteo jamaicensis* individuals on the study area averaged 15 km² (USDI 1979), and nests were usually near the center of the home range. Although we had no data on *B. regalis* foraging ranges from our study area, individuals in southeastern Idaho foraged in all directions from the nest, using home ranges that averaged 20 km² (Wakeley 1978). Two *B. regalis* individuals spent approximately 75% of their foraging time within 1500 m of the nest (calculated from Figs. 2 and 3 in Wakeley 1978). Based on these patterns, we assumed that pairs nesting within 1500 m of an interspecific pair's nest used “shared” foraging ranges, whereas those nesting farther than 1500 m from an interspecific pair's nest were assumed to have “unshared” ranges. We had complete data on nest locations of both species but did not collect prey remains from all nests in the study area. Therefore, while all pairs with “shared” ranges nested near an interspecific, we did not always have diet data from the interspecific pairs near

Table 2. Sampling intensity for eight subsamples of nesting hawks in southwestern Idaho

	Number of nests	Number of collections	Number of prey items
Normal years (1975–76)			
Shared ranges			
<i>B. jamaicensis</i>	4	20	69
<i>B. regalis</i>	3	17	53
Unshared ranges			
<i>B. jamaicensis</i>	3	17	79
<i>B. regalis</i>	2	8	44
Low prey years (1977–78)			
Shared ranges			
<i>B. jamaicensis</i>	3	21	100
<i>B. regalis</i>	4	26	68
Unshared ranges			
<i>B. jamaicensis</i>	4	35	134
<i>B. regalis</i>	2	14	55
Total	25	158	602

which they nested. Both “shared” and “unshared” ranges were distributed throughout the area; they were not concentrated at one end or the other. Habitat composition in a 20 km² circular area around each sample nest was calculated according to procedures described by Steenhof (1982). In each of these generalized foraging ranges, a prey abundance estimate (PAE) was calculated for each of five prey groups. Our experimental design and sample sizes are shown in Table 2.

Diet breadth was calculated using Levins' (1968) formula:

$$B = \frac{1}{\sum p_i^2}$$

where p_i represents the proportion of the diet contributed by the i th taxon. Values of this index range from 1 to n . Overlap in taxonomic composition of the diet was calculated using Pianka's (1973) formula:

$$O = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where p_{ij} and p_{ik} are the proportions of the i th taxon in the diets of the j th and k th species. Values of this index range from 0 (no overlap) to 1 (complete overlap).

In calculations of diet breadth and overlap, we grouped some prey taxa because of the large number of prey that could not be identified to species. Woodrats (*Neotoma* spp.), kangaroo rats (*Dipodomys* spp.), and dabbling ducks (*Anas* spp.) were grouped by genus; three species of small mice were treated as a single taxon; snakes and lizards were grouped by suborder; and rabbits, small passerines, and invertebrates were grouped by order. Prey items that could only be identified as “rodents” or “reptiles” were excluded from overlap and breadth calculations. Greene and Jaksic (1983) demonstrated problems associated with grouping prey at the ordinal level, so we examined the two hawks' diets for possible differences in relative frequencies of identified prey within the lumped taxa.

Interspecific overlap along the prey size axis was evaluated using interspecific normalized distances (Jaksic and Braker 1983). Normalized distances were calculated by dividing the distance (d) between the geometric mean prey weights in the two hawks' diets by the average of their standard deviations (w). All prey types were pooled in the analysis, and prey weights were log-transformed because, as in Jaksic and Braker's (1983) analysis, weights of prey taken by raptors were usually skewed to the right.

Statistical tests were evaluated at the 0.05 level of significance. G-tests contrasting prey frequencies in the diets were evaluated at adjusted α levels for simultaneous test procedures to achieve an experimentwise α of 0.05 (Sokal and Rohlf 1981: 728–729).

Results

Composition of the diet

Prior to the drought, Townsend ground squirrels were the most common prey in both hawks' diets, comprising 42.3% of the *B. regalis* prey and 27.7% of the *B. jamaicensis* food items (Appendix). Townsend pocket gophers (*Thomomys townsendii*) were the second most common prey of *B. regalis*, and snakes were the second most common prey of *B. jamaicensis*. *B. regalis* took significantly more pocket gophers before the drought than did *B. jamaicensis* ($G=21.94$), and *B. jamaicensis* took significantly more snakes ($G=28.84$). Pocket gophers occurred in the *B. jamaicensis* diet only in unshared ranges. Otherwise, no differences in relative frequencies of taxa could be detected between shared and unshared ranges for either hawk species.

The frequencies of ground squirrels in *B. regalis* diets decreased significantly ($G=13.51$) from normal to low prey years (Appendix). Relative frequencies of pocket gophers, snakes, and rabbits in *B. regalis* diets did not change significantly. In contrast, *B. jamaicensis* diets showed significant increases in the frequencies of rabbits ($G=18.96$) and pocket gophers ($G=11.85$), while the relative number of snakes in *B. jamaicensis* diets was unchanged ($G=0.68$). The decrease in frequencies of ground squirrels in *B. jamaicensis* diets was not significant ($G=6.54$) at the adjusted α level.

During low prey years, *B. regalis* pairs continued to take significantly more pocket gophers than did *B. jamaicensis* ($G=110.91$), and *B. jamaicensis* continued to take more snakes ($G=11.16$). The higher proportion of rabbits in *B. jamaicensis* diets also became significant ($G=20.21$) during low prey years. After the drought, no differences in relative frequencies of taxa could be detected between shared and unshared ranges for either species.

An examination of the relative frequencies of identified prey within the lumped taxa provided no evidence that the two hawk species partitioned prey resources within the groups that were lumped. Gopher snakes were the most common snakes identified in both species' diets, and Western Meadowlarks (*Sturnella neglecta*) were the most commonly taken passerines. Black-tailed jack rabbits and mountain cottontails (*Sylvilagus nuttallii*) were common in both diets, and the relative frequencies of the two lagomorph species with respect to each other did not differ in the two predators' diets ($G=0.28$, $P=0.60$). Nor did the relative frequencies differ between year types (G 's = 1.92, 2.69; P 's = 0.16, 0.10) or range types (G 's = 0.06, 1.46; P 's =

Table 3. Estimates of diet overlap, diet breadth, and habitat similarity for hawks in southwestern Idaho

	Diet overlap	Diet breadth	Habitat similarity ^a
Normal years (1975–76)			
Shared ranges			
<i>B. jamaicensis</i>	0.553	6.459	0.839
<i>B. regalis</i>		2.497	
Unshared ranges			
<i>B. jamaicensis</i>	0.770	5.227	0.283
<i>B. regalis</i>		5.268	
Low prey years (1977–78)			
Shared ranges			
<i>B. jamaicensis</i>	0.493	5.688	0.566
<i>B. regalis</i>		5.494	
Unshared ranges			
<i>B. jamaicensis</i>	0.353	5.594	0.596
<i>B. regalis</i>		3.342	

^a Included only as a gauge by which to evaluate differences in diet. Because habitat similarity was a function of our annual selection of sampling sites, it should not be interpreted as a measure of hawk use or preference

Table 4. Intraspecific diet similarities for two species of *Buteo* in southwestern Idaho

	Normal vs. low prey years		Shared vs. unshared ranges	
	Shared ranges	Unshared ranges	Normal years	Low years
<i>B. jamaicensis</i>	0.812	0.703	0.903	0.970
<i>B. regalis</i>	0.842	0.660	0.836	0.969

0.81, 0.23) in either of the two species. The 3 species of mice and 5 species of lizards were taken too infrequently to detect any differences among subsamples.

Pooled interspecific dietary overlap in years when prey were normal was 0.731. During normal years (Table 3), hawks with unshared ranges exhibited higher interspecific dietary overlap (0.770) than hawks with shared ranges (0.553). According to conventional interpretations, these patterns might support the prediction of increased resource partitioning in the face of competition pressure.

After the ground squirrel decline, when competition and resource partitioning should have been most pronounced, diets of the two species diverged sharply. Diet overlap based on all pairs dropped from 0.731 to 0.430 (Table 3). Again, the patterns appeared to support predictions of competition theory.

The dietary patterns in shared and unshared ranges during the low years, however, were contrary to predictions. The overall decrease in overlap was caused primarily by a sharp decrease in overlap between pairs with unshared ranges (from 0.770 to 0.353), where competition should not have occurred. Overlap in shared ranges declined only slightly during the prey shortage, from 0.553 to 0.493.

Intraspecific diet similarities (Table 4) indicated consistently greater overlap within species than between species

(cf Table 3). Intraspecific similarity tended to be lower between year types than between shared and unshared ranges. Within year types, intraspecific dietary similarity between shared and unshared ranges was high for both species. The trends suggest that neither species' diet was strongly affected by the presence of an interspecific and that geographic differences between foraging ranges apparently did not play a large role in determining the relative proportions of prey consumed (see below).

Diet breadths of some hawks decreased after the drought, while others increased (Table 3). Neither predator retreated to a more specialized food-niche in the face of interspecific competition and reduced food resources. Our observations on changes in diet breadth may be ambiguous with respect to the question of interspecific competition (Wiens and Rotenberry 1979). Optimal foraging theory predicts that diets should be broader at lower resource levels (Schoener 1971; Pyke et al. 1977). Under pressure from competition, however, diets should become more narrow as species retreat to more restricted, specialized niches (Smith et al. 1978). Reduced diet breadth in the presence of potential competitors has been considered circumstantial evidence for interspecific competition (Schmitt and Coyer 1983). Other studies, however, have shown that reduced diet overlap can be associated with either increased (Werner 1977; Horn 1983) or unchanged (Dunham 1983) diet breadths. Diet breadths of *B. jamaicensis* ranged from 5.227 to 6.459, whereas *B. regalis* diet breadths ranged from 2.497 to 5.494 (Table 3). Both the widest and narrowest diets were observed in shared ranges during normal prey years: *B. regalis* pairs had the more specialized diets, and *B. jamaicensis* pairs had the more general. As prey abundance decreased, *B. jamaicensis* diet breadths decreased slightly in shared ranges and increased slightly in unshared ranges. In contrast, *B. regalis* diet breadths increased sharply in shared ranges and decreased sharply in unshared ranges. During low prey years, both species had broader diets in shared than in unshared ranges.

Weights of prey taken by *B. jamaicensis* ranged from 1 to 2114 g, and prey taken by *B. regalis* weighed between 1 and 1808 g. The two hawk species did not differ significantly ($F=0.71$, $P=0.40$) in mean sizes of prey taken (Table 5). Sizes of *B. jamaicensis* prey varied significantly between normal and low years ($F=8.73$, $P=0.003$) but not between shared and unshared ranges ($F=1.14$, $P=0.29$). Year type and range type had no significant independent effects on *B. regalis* prey weights (F 's=3.69, 2.90; P 's=0.06, 0.09), but the interaction between year type and range type was significant ($F=19.30$, $P<0.001$). At normal prey levels, *B. regalis* took larger prey in shared ranges than in unshared ranges, but at low prey levels, prey taken in unshared ranges were larger.

Normalized distances, expressed as d/w ratios (Table 5), indicate the degree of separation between predators on the prey size axis and are inversely related to measures of overlap. May and MacArthur (1972) predicted that at least one standard deviation should separate resource utilization curves of sympatric species and that d/w ratios should be greater than or equal to 1. More recent work (Turelli 1981; Abrams 1983) suggests that values of limiting similarity are not constant for all species and situations. In this study, all d/w values were far below 1.0, and values for these buteos were lower than those reported for other groups of sympatric species (reviewed in May and MacArthur 1972),

Table 5. Sizes of prey taken by *B. regalis* and *B. jamaicensis* and interspecific normalized distances

	Mean Prey Weight (g)	Geom Mean Prey Wt	Geom Prey Wt SD	d	w	d/w
Normal years (1975-76)						
Shared ranges						
<i>B. jamaicensis</i>	91.4	4.52	1.246	0.56	0.936	0.599
<i>B. regalis</i>	161.2	5.08	0.625			
Unshared ranges						
<i>B. jamaicensis</i>	112.7	4.72	1.639	0.68	1.709	0.398
<i>B. regalis</i>	56.8	4.04	1.780			
Low prey years (1977-78)						
Shared ranges						
<i>B. jamaicensis</i>	148.2	5.00	1.391	0.24	1.338	0.179
<i>B. regalis</i>	116.7	4.76	1.285			
Unshared ranges						
<i>B. jamaicensis</i>	166.4	5.11	1.289	0.01	0.972	0.010
<i>B. regalis</i>	164.9	5.11	0.654			

most notably accipiter hawks (Reynolds and Meslow 1984). Relative differences between d/w ratios of sympatric buteos in Idaho were inconsistent with competition theory. Although sizes of prey taken by the two hawk species were more similar in unshared than in shared ranges, d/w ratios in both shared and unshared ranges decreased sharply during the prey shortage as the two hawk species converged on similar-sized prey.

Habitat variability

One factor that may have obscured any competition-induced patterns is geographic variability in habitat composition and prey availability. High diet overlaps might have been associated with similar habitats in the groups that were compared, and low diet overlaps may have resulted from samples from dissimilar habitats. To examine this possibility, we compared indexes of habitat similarity with diet overlap measures for the same groups. Percentages of habitat types in the subsamples were compared using the same measure of similarity used to describe diet overlap. The degree of diet overlap did not reflect the habitat similarities in the groups that were compared (Table 3). The unexpected high diet overlap between pairs with unshared ranges in low prey years was based on pairs in territories with less similar habitats than those of groups with unexpectedly low diet overlap.

PAE's were available for rabbits, lizards, passerines, ground squirrels, and small rodents other than ground squirrels. PAE's did not differ significantly among the eight subsamples of hawks for any of the five prey groups tested (Kruskal-Wallis tests; P 's>0.05). To determine if differences in PAE's at individual foraging ranges within subsamples were responsible for individual variation in frequencies of major prey taken, we ran Spearman rank correlation tests, treating each sample nest as a separate data point. Within year type, PAE's for rabbits and ground squirrels were not correlated (P 's>0.05) with the proportions of

Table 6. Characteristics of *Buteo* nesting populations in the southwestern Idaho study area, 1975–78. Sample sizes in parentheses

	\bar{x} number of nesting pairs	\bar{x} number of young fledged per attempt ^a	\bar{x} number of young fledged per attempt ^b
<i>B. jamaicensis</i>			
Normal years			
Shared ranges	6	3.0(3)	2.0(5)
Unshared ranges	26	2.0(2)	1.9(15)
Low prey years			
Shared ranges	10	3.0(2)	1.5(8)
Unshared ranges	24	3.0(1)	1.0(15)
<i>B. regalis</i>			
Normal years			
Shared ranges	5	3.0(2)	2.2(4)
Unshared ranges	3	3.0(1)	3.3(3)
Low prey years			
Shared ranges	8	1.5(4)	1.0(10)
Unshared ranges	4	3.0(1)	0.8(4)

^a Based only on pairs sampled for diet

^b Based on all pairs in the study area

those respective taxa in the diets of either *B. regalis* (r 's = 0.10 for ground squirrels in normal years; -0.22 and 0.31 for jack rabbits and ground squirrels, respectively in low years) or *B. jamaicensis* (r 's = 0.05 and 0.65 for normal years; -0.34 and 0.04 for low years). Not only did the eight subsamples come from a relatively homogeneous environment, but minor differences in habitat composition and prey availability at sampling sites were insufficient to explain deviations from the predicted response.

Raptor population levels

Population levels were assessed in conjunction with dietary shifts to determine whether food may have been limiting during the study, and whether certain dietary patterns were associated with reduced fitness.

Numbers of *B. jamaicensis* pairs nesting in the study area each year ranged from 31 to 34, while numbers of *B. regalis* pairs varied from 6 to 12 and increased steadily during the study. Both species of hawks nested throughout the area; interspecifics nested as close as 200 m to one another. The frequency of foraging ranges that were shared with interspecifics did not differ between normal and low prey years for either species ($G=0.01$, $P=0.93$; $G=1.69$, $P=0.19$).

All except one of the nesting pairs used in the diet analysis raised young that successfully fledged. The exception was a *B. jamaicensis* pair during one of the normal prey years. Productivity of pairs sampled for diet did not differ significantly between normal and low prey years (Mann-Whitney; U 's = 3.5, 4.5; P 's = 0.22, 0.33) or between shared and unshared ranges (Mann-Whitney; U 's = 3.0, 3.5; P 's = 0.30, 0.19) in either species (Table 6). However, data from all pairs in the study area suggested that low prey numbers in 1977–78 had a negative effect on the reproduction of *B. regalis*. Number of *B. regalis* fledged per nesting attempt, based on all pairs in the study area, was significantly lower (Mann-Whitney; $U=21$, $P=0.03$) during the years when

prey were scarce (Table 6). Similar reproductive responses of *B. regalis* to prey changes have also been observed in other areas (Howard and Wolfe 1976; Woffinden and Murphy 1977; Smith and Murphy 1978, 1979; Thurow et al. 1980; Smith et al. 1981). Reproductive rates of all *B. regalis* pairs in the study area, however, did not differ between shared and unshared ranges (Mann-Whitney; $U=4.25$, $P=0.61$), even during low prey years (Mann-Whitney; $U=1.75$, $P=0.68$). Numbers of *B. jamaicensis* fledged per nesting attempt did not differ significantly between either normal and low prey years (Mann-Whitney; $U=1.68$, $P=0.12$) or shared and unshared ranges (Mann-Whitney; $U=172.5$, $P=0.54$). If food was limiting reproduction in either species after the drought, the effect apparently was not magnified by the presence of a potential competitor. The pairs with high interspecific diet overlap did as well as or better than those with low overlaps.

Discussion

Several findings of this study were consistent with predictions of competition theory. During normal prey years, pairs that shared foraging ranges with interspecifics showed less diet overlap, both in species and size composition, than pairs with unshared ranges. In addition, species composition of the pooled diets of the two species diverged considerably after a prey decline. The most critical prediction of this analysis, however, was not realized. During a prey shortage in which food may have been limiting, hawks that shared foraging ranges had higher diet overlaps than pairs with unshared ranges. The two hawk species also converged on similar-sized prey during the prey shortage, contrary to predictions. Available data on differences in habitat composition and prey availabilities could not support the contention that geographic variability may have confounded the predicted response. The results suggest, therefore, that diet divergence was not proximally associated with the presence or absence of a potential congeneric competitor. Pácala and Roughgarden (1982) showed that present competition was weak among species that had already partitioned resources but strong among species with high niche overlaps. In this study, dietary overlap was consistently high, but evidence for present competition was weak.

Several assumptions should be considered when interpreting the results. The first assumption is that geographic variations in prey availability did not mask the patterns induced by interspecific competition. Our approach should have minimized the effects of geographic variations in food availability, and the differences we were able to detect did not explain the directions of the deviations from the predicted response. Microgeographic variations in prey availability that we were unable to measure, however, may have influenced prey choice.

A second assumption is that the sample pairs were representative of the populations in the area. Although sample sizes in this analysis were necessarily small, we have no evidence that the pairs we studied were unusual in any respect.

A third assumption is that the patterns we observed were unaffected by the activities of other predators in the area. Our analysis did not consider the potential effects of diffuse competition. Dense populations of other diurnal raptors including Golden Eagles (*Aquila chrysaetos*), Prairie Falcons (*Falco mexicanus*), and Northern Harriers (*Circus*

cyaneus) also breed in the area, as do six species of owls and a number of carnivorous mammals. The diets of these species overlap with those of buteos to varying degrees. We have assumed that any influence these other predators had on the buteo diets affected all sample pairs similarly.

Finally, we have no data on how the sample pairs used the space within their foraging ranges. It is possible that they segregated spatially either through interspecific aggression or differential habitat selection. These results would be consistent with the "compression hypothesis" (MacArthur and Pianka 1966; MacArthur and Wilson 1967; Schoener 1974), which predicts that increased competition and/or decreased resource abundance will result in a restriction of the habitats used rather than a decrease in the range of prey types captured. Differences in foraging mode (e.g. time spent hovering versus perched) might also have given the two species access to different groups of prey animals. If the hawks in our study did segregate behaviorally or spatially, it apparently did not result in a divergence of diets as it has in studies of other vertebrates (Werner 1977; Dunham 1983).

The patterns exhibited by buteos in this study contrast sharply with those observed in accipiters (Lack 1946; Storer 1966; van Beusekom 1972; Opdam 1975; Reynolds and Meslow 1984; Schoener 1984) but are similar to those of other raptor assemblages that feed principally on mammals (Craighead and Craighead 1969; Schmutz et al. 1980; Jaksić and Braker 1983). In these latter studies as well as the present one, raptors concentrated predation on one or two "superabundant" (Schoener 1971, 1982) prey species. Our observations of changes in diet breadths, high intraspecific similarity, and low correlations between PAE's and prey in the diet support predictions of optimal foraging theory (Schoener 1971; Pyke et al. 1977), and our findings of intermediate to high interspecific diet overlaps, wide diet breadths, and d/w ratios less than 1 are consistent with predictions for opportunistic foragers outlined by Wiens and Rotenberry (1979: Table 10). It seems that the diet shifts in our study can be explained adequately in the context of simple foraging theory, without implicating interspecific competition as a mediating factor.

Only three of 30 studies reviewed by Schoener (1982) found increased overlap during lean periods, and most investigations of spatial differences in niches have shown reduced overlap in sympatric and/or syntopic situations (Schoener 1975; Diamond 1978; Alatalo 1981; Schmitt and Coyer 1983). This study differs from previous nonexperimental studies of niche shifts in that we have assessed shifts in space and time simultaneously. Instead of comparing geographically disjunct populations, we have restricted our analysis to a continuous geographic area where the responses of individuals could be evaluated in local situations. Our approach provides insights on the role of present competition in affecting niche shifts in ecological time but not on how evolutionary shifts have been influenced by past competition. Our accompanying data on breeding densities and reproductive rates provide little evidence for differential selection pressure during a severe prey shortage. One wonders how many of the studies cited by Schoener (1982) would have affirmed proximate, instantaneous effects of competition if spatial and temporal relationships had been analyzed simultaneously. As it is, they provide only indirect evidence for possible evolutionary shifts.

Our investigation does not provide definitive answers

about the foraging ecology of buteos or about the role of interspecific competition in regulating hawk populations, but our results reinforce the notion that competition is only one of many factors that may lead to dietary divergence. Caution should be used when making inferences from dietary shifts; broad generalizations may be misleading if they do not take into account the processes involved. Future investigations will reveal more about the role of interspecific competition in shaping niches if they focus on mechanisms that cause diets to change.

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Appendix. Frequencies and proportions of prey items in the diets of nesting *Buteo* hawks, 1975-78

	Normal Prey Years						Low Prey Years					
	<i>Buteo regalis</i>			<i>Buteo jamaicensis</i>			<i>Buteo regalis</i>			<i>Buteo jamaicensis</i>		
	Shared ranges	Unshared ranges	All pairs	Shared ranges	Unshared ranges	All pairs	Shared ranges	Unshared ranges	All pairs	Shared ranges	Unshared ranges	All pairs
<i>Mammals</i>												
Shrew (<i>Sorex</i> spp.)	-	-	-	1(1.4%)	-	1(0.7%)	-	-	-	-	-	-
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	-	-	-	-	-	-	1(1.5%)	-	1(0.8%)	-	-	-
Townsend ground squirrel (<i>Spermophilus townsendii</i>)	26(49.1%)	15(34.1%)	41(42.3%)	18(26.1%)	23(29.1%)	41(27.7%)	11(16.2%)	13(23.6%)	24(19.5%)	20(20.0%)	19(14.2%)	39(16.7%)
White-tailed antelope squirrel (<i>Ammospermophilus leucurus</i>)	-	-	-	-	-	-	2(2.9%)	-	2(1.6%)	-	-	-
Least chipmunk (<i>Eutamias minimus</i>)	-	-	-	1(1.4%)	-	1(0.7%)	-	-	-	-	-	-
Townsend pocket gopher (<i>Thomomys townsendii</i>)	21(39.6%)	6(13.6%)	27(27.8%)	-	9(11.4%)	9(6.1%)	23(33.8%)	26(47.3%)	49(39.8%)	-	1(0.7%)	1(0.4%)
Great Basin pocket mouse (<i>Perognathus parvus</i>)	-	-	-	-	-	-	-	-	-	1(1.0%)	-	1(0.4%)
Kangaroo rat (<i>Dipodomys</i> spp.)	2(3.8%)	-	2(2.1%)	3(4.3%)	1(1.3%)	4(2.7%)	4(5.9%)	6(10.9%)	10(8.1%)	19(19.0%)	23(17.2%)	42(17.9%)
Western harvest mouse (<i>Reithrodontomys megalotis</i>)	-	-	-	-	-	-	-	-	-	1(1.0%)	2(1.5%)	3(1.3%)
Deer mouse (<i>Peromyscus maniculatus</i>)	-	-	-	3(4.3%)	1(1.3%)	4(2.7%)	-	-	-	-	2(1.5%)	2(0.9%)
Mouse-unidentified	1(1.9%)	1(2.3%)	2(2.1%)	-	-	-	1(1.5%)	-	1(0.8%)	-	1(0.7%)	1(0.4%)
Desert woodrat (<i>Neotoma lepida</i>)	-	-	-	-	-	-	-	1(1.8%)	1(0.8%)	1(1.0%)	-	1(0.4%)
Bushy-tailed woodrat (<i>Neotoma chereza</i>)	-	-	-	-	-	-	-	-	-	1(1.0%)	-	1(0.4%)
Woodrat (<i>Neotoma</i> spp.)	-	1(2.3%)	1(1.0%)	3(4.3%)	1(1.3%)	4(2.7%)	1(1.5%)	-	1(0.8%)	-	1(0.7%)	1(0.4%)
Montane vole (<i>Microtus montanus</i>)	-	1(2.3%)	1(1.0%)	3(4.3%)	-	3(2.0%)	3(4.4%)	-	3(2.4%)	-	1(0.7%)	1(0.4%)
Rodent-unidentified	-	-	-	1(1.4%)	-	1(0.7%)	1(1.5%)	-	1(0.8%)	-	-	-
Black-tailed jackrabbit (<i>Lepus californicus</i>)	-	-	-	2(2.9%)	-	2(1.4%)	3(4.4%)	1(1.8%)	4(3.3%)	11(11.0%)	15(11.2%)	26(11.1%)
Mountain cottontail (<i>Sybilagus nuttalli</i>)	1(1.9%)	-	1(1.0%)	2(2.9%)	5(6.3%)	7(4.7%)	1(1.5%)	1(1.8%)	2(1.6%)	8(8.0%)	17(12.7%)	25(10.7%)
Rabbit-unidentified	-	1(2.3%)	1(1.0%)	-	-	-	-	-	-	2(2.0%)	4(3.0%)	6(2.6%)
Long-tailed weasel (<i>Mustela frenata</i>)	-	-	-	1(1.4%)	-	1(0.7%)	-	-	-	-	-	-

Appendix (continued)

	Normal Prey Years				Low Prey Years				All pairs	All ranges	All pairs	All ranges	All pairs	All ranges
	<i>Buteo regalis</i>		<i>Buteo jamaicensis</i>		<i>Buteo regalis</i>		<i>Buteo jamaicensis</i>							
	Shared ranges	Unshared ranges	Shared ranges	Unshared ranges	Shared ranges	Unshared ranges	Shared ranges	Unshared ranges						
<i>Reptiles</i> (continued)														
Western whiptail (<i>Cnemidophorus tigris</i>)	–	1(2.3%)	1(1.0%)	3(4.3%)	2(2.5%)	5(3.4%)	–	–	–	–	–	–	1(0.7%)	1(0.4%)
Lizard-identified	1(1.9%)	4(9.1%)	5(5.2%)	3(4.3%)	–	3(2.0%)	–	–	–	–	–	–	–	1(0.4%)
Racer (<i>Coluber constrictor</i>)	–	–	–	1(1.4%)	–	1(0.7%)	–	–	–	–	–	–	–	–
Striped whipsnake (<i>Masticophis taeniatus</i>)	–	–	–	–	–	–	1(1.5%)	–	–	–	–	–	1(0.7%)	5(2.1%)
Gopher snake (<i>Pituophis melanoleucus</i>)	–	–	–	10(14.5%)	21(26.6%)	31(20.9%)	3(4.4%)	3(5.5%)	6(4.9%)	11(11.0%)	20(14.9%)	31(13.2%)	–	–
Long-nosed snake (<i>Rhinocheilus lecontei</i>)	–	–	–	–	–	–	–	–	–	–	–	–	–	1(0.4%)
Night snake (<i>Hypsiglena torquata</i>)	–	–	–	–	–	–	–	–	–	–	–	–	–	1(0.4%)
Western rattlesnake (<i>Crotalus viridis</i>)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Snake-identified	–	2(4.5%)	2(2.1%)	4(5.8%)	–	4(2.7%)	2(2.9%)	–	–	–	–	–	–	–
Reptile-identified	–	1(2.3%)	1(1.0%)	1(1.4%)	1(1.3%)	2(1.4%)	2(2.9%)	–	–	–	–	–	–	–
<i>Invertebrates</i>														
Scorpionida	–	–	–	1(1.4%)	3(3.8%)	4(2.7%)	–	–	–	–	–	–	–	2(0.9%)
Araneida	–	–	–	–	1(1.3%)	1(0.7%)	–	–	–	–	–	–	–	–
Orthoptera	–	4(9.1%)	4(4.1%)	–	3(3.8%)	3(2.0%)	2(2.9%)	–	–	–	–	–	–	–
Homoptera	–	1(2.3%)	1(1.0%)	–	–	–	–	–	–	–	–	–	–	–
<i>Total</i>	53	44	97	69	79	148	69	55	123	100	134	234		