new buffer systems, or better staining regimes may reveal the expression of enzymes not seen in our study. Rather, the total score for each tissue over all the taxa we examined is more informative. Therefore, a quantitative comparison was made by assigning a 1 to all tissues with faint expression and a 2 to those with good expression and then totalling these numbers for all enzymes in each tissue (see bottom of Table 1). Again, feather pulp was more informative than blood but less informative than internal organs.

There are only two serious limitations to using feather pulp for electrophoretic analysis. First, the birds must either be molting when sampled or be subjected to plucking to stimulate feather regrowth and then recaptured at a later date. Second, in small birds such as Bobolinks, warblers (Parulidae), or chickadees (*Parus* spp.), only tiny amounts of tissue can be obtained from the flight and tail feathers, necessitating the use of two or more feathers. Mengden and Stock (1976) point out, however, that small quantities of tissue may be put into cell culture to increase the amount available; such tissue cultures may also be stored for indefinite periods of time. Alternatively, other forms of electrophoresis that require smaller quantities of tissue (e.g. cellulose acetate) may be performed when only a few loci need to be examined.

Especially useful to field workers, the tissue is conveniently "pre-packaged," and may be placed, whole or with the upper shaft removed, directly onto dry ice or into a portable liquid nitrogen flask. In terms of ease of sample collection and minimization of stress to birds, we suggest that feather pulp is a viable alternative tissue for non-destructive sampling in avian electrophoretic studies.

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Food-niche Relationships Between Great Horned Owls and Common Barn-Owls in Eastern Washington

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Great Horned Owls (*Bubo virginianus*) and Common Barn-Owls (*Tyto alba*) have recently become sympatric in the Pacific Northwest (Stewart 1980, Smith and Knight 1981) and provide an opportunity for examining resource partitioning between two members of the same feeding guild. We quantified diet relationships from our analysis of 622 Common Barn-Owl pellets, from 6 nesting and 2 roosting sites, and 234 Great Horned Owl pellets, from 4 nesting and 3 roosting sites, collected between October 1977–June 1979 in Esquatzel Coulee, Franklin County, Washington. The study area and its raptor populations are

described in Knight and Smith (1982). Fitch (1947), Rudolph (1978), and Jaksić and Yáñez (1980) have examined food-niche relationships between these two species when sympatric in California and Chile, providing the opportunity for comparisons.

Prey remains in pellets were identified to species level, and mean fresh weights were obtained from the Bureau of Land Management (1979). The following parameters for each owl species were calculated: (1) mean prey size (MPS) (Herrera and Jaksić 1980), (2) food-niche breadth (Levins 1968: 43), and (3) food-niche overlap (Pianka 1974: 2142). The numbers of prey species in each owl species' diet were used as entries for computation of niche breadths and overlaps.

Small mammals were the major prey of Great Horned Owls and Common Barn-Owls at the Esquatzel Coulee study area, both in percentage of total prey items (91.1% and 97.8%, respectively) and in percentage of total prey biomass (77.9% and 98.3%) (Table 1). Mammals comprised a lower percentage of total prey biomass in the diet of Great Horned Owls than of Common Barn-Owls ($\chi^2 = 162.34$, $P < 0.001$). Two species of mammals, northern pocket gopher (scientific names given in Table 1) and Great Basin pocket mouse, comprised over half of the total prey items in the diets of both owl species (50.1% for Great Horned Owl and 69.3% for Common Barn-Owl), as well as a major portion of total prey biomass (42.2% and 73.9%). Rabbits were the third most important prey species, in terms of biomass, in the diet of Great Horned Owls, although they were not found in Common Barn-Owl pellets. Because Common Barn-Owls are smaller than Great Horned Owls (Marti 1974), they may have difficulty in capturing rabbits (Jaksić and Yáñez 1980). Common Barn-Owls do occasionally eat rabbits (Fitch 1947, Marti 1974); therefore, an alternative explanation for the absence of rabbits as a Common Barn-Owl prey item in our study may be that the largely crepuscular Nuttall cottontail

(Kritzman 1977: 107) is temporally unavailable for the strictly nocturnal Common Barn-Owl (Marti 1974, Rudolph 1978). Common Barn-Owls are the fourth most important prey item, in terms of total prey biomass, in the diet of Great Horned Owls.

MPS of Great Horned Owls ($\bar{x} \pm 2$ SE $= 55.24 \pm 9.31$ g, $n = 872$) was significantly greater ($P < 0.001$) than MPS of Common Barn-Owls (27.44 ± 1.70 g, $n = 2628$). This was the result of Great Horned Owls preying on larger prey items such as rabbits and Common Barn-Owls. The food-niche breadth of Great Horned Owls was 4.12, considerably greater than the 2.28 of Common Barn-Owls, suggesting that Great Horned Owls apply a more uniform predation pressure over a wider range of animals. Food-niche overlap was 0.97 (of a maximum of 1.00). This is largely due to the importance of northern pocket gophers and Great Basin pocket mice in both owl species' diets.

On our study area, these two species show a high degree of ecological overlap in several traits other than diet. Strongest evidence of habitat overlap is the presence of Common Barn-Owls in the diet of Great Horned Owls (Herrera and Hiraldo 1976). Additionally, Common Barn-Owls and Great Horned Owls showed few or no differences in nest-site structure, mean nest height, mean nest-structure height, land-use patterns near nesting sites, and distances of nest sites to human activity (Knight and Smith 1982). Nesting Great Horned Owls exhibited regular and Common Barn-Owls random intraspecific distributions. Their interspecific pattern was random, however, indicating no interspecific territoriality. There were indications of ecological differences between the two species. Common Barn-Owls may utilize habitats not frequented by Great Horned Owls, as evidenced by differences in prey species (e.g. house mouse). Common Barn-Owls are strictly nocturnal and hunt mainly on the wing, whereas Great Horned Owls are more crepuscular and hunt primarily by flights from perches (Marti 1974, Rudolph 1978). Fi-

TABLE 1. Prey items from 234 pellets of Great Horned Owls and from 622 pellets of Common Barn-Owls in Esquatzel Coulee, eastern Washington. Common names are in parentheses.

Prey	Weight (g)	Great Horned Owl		Common Barn-Owl	
		Number of prey (%)	Total prey biomass (%)	Number of prey (%)	Total prey biomass (%)
Mammals					
Sylvilagus nuttallii (Nuttall cottontail)	514	1.3	12.4	—	—
Spermophilus washingtoni (Washington ground squirrel)	172	0.1	0.4	—	—
Thomomys talpoides (northern pocket gopher)	200	7.7	29.7	5.44	39.3

TABLE 1. Continued.

Prey	Weight (g)	Great Horned Owl		Common Barn-Owl	
		Number of prey (%)	Total prey biomass (%)	Number of prey (%)	Total prey biomass (%)
Perognathus parvus (Great Basin pocket mouse)	15	43.1	12.5	63.85	34.6
Dipodomys ordii (Ord's kangaroo rat)	53	1.4	1.4	0.53	1.0
Reithrodontomys megalotis (western harvest mouse)	11	1.5	0.3	3.39	1.3
Peromyscus maniculatus (deer mouse)	19	16.9	6.2	13.77	9.5
Neotoma cinerea (bushy-tailed wood rat)	310	0.3	2.1	0.04	0.4
Microtus montanus (montane meadow mouse)	30	13.3	7.7	8.11	8.8
Rattus sp. (rat)	300	—	—	0.08	0.8
Mus musculus (house mouse)	17	0.7	0.2	1.75	1.1
Unidentified Microtinae	50	4.7	4.5	0.84	1.5
Mustela frenata (long-tailed weasel)	178	0.1	0.4	—	—
Birds					
Anas platyrhynchos (Mallard)	1,185	0.1	2.6	—	—
Phasianus colchicus (Ring-necked Pheasant)	1,138	0.1	2.5	—	—
Fulica americana (American Coot)	654	0.1	1.5	—	—
Charadrius vociferus (Killdeer)	104	0.1	0.2	—	—
Columba livia (Rock Dove)	332	—	—	0.04	0.5
Tyto alba[a] (Common Barn-Owl)	603	0.9	10.7	—	—
Sturnus vulgaris (European Starling)	79	—	—	0.08	0.2
Sturnella neglecta (Western Meadowlark)	96	0.1	0.2	0.04	0.1
Unidentified Fringillidae	26	0.3	0.2	0.23	0.2
Unidentified Passeriformes	56	1.1	1.2	0.27	0.5
Other					
Unidentified snake	207	0.3	1.4	—	—
Cyprinus carpio (carp)	583	0.1	1.3	—	—
Unidentified Scorpionidae	1	0.3	tr[b]	—	—
Stenopelmatus sp. (Jerusalem cricket)	2	4.0	0.2	1.45	0.1
Unidentified Scarabaeidae	1	0.9	tr[b]	0.11	tr[b]
Unidentified Locustidae	1	0.2	tr[b]	—	—
Total		872	99.9	2,628	99.9

[a] Remains found beneath Great Horned Owl nesting and roosting sites; not found in pellets.
[b] tr = trace amount; 0.01 g.

TABLE 2. Comparison of three trophic statistics for the Great Horned Owl and Common Barn-Owl.

Geographic area and latitude	Mean prey size (g)		Food-niche breadth		Food-niche overlap	Study
	Com-mon Barn-Owl	Great Horned Owl	Com-mon Barn-Owl	Great Horned Owl		
Central Washington, USA, 46°N	27	55	2.28	4.12	0.97	This study
Northern California, USA, 41°N	30	28	1.98	1.92	0.99	Rudolph (1978)[a]
Central California, USA, 37°N	52	98	2.95	8.17	0.24	Fitch (1947)[a]
Central Chile, 33°S	123	266	3.98	6.90	0.48	Jaksić and Yáñez (1980)

[a] We calculated trophic statistics using Table 1 in Rudolph (1978) and Tables 2 and 7 in Fitch (1947). Weights of prey items were obtained from both papers and the Bureau of Land Management (1979).

nally, Great Horned Owls, because of their greater size and strength, are able to utilize a wider variety of potential prey.

The almost complete food-niche overlap between the two species in our study and the low level of spatial and temporal segregation may be the result of their recent sympatry, which probably has been caused by the expansion of irrigated farming in the region (Smith and Knight 1981: 24). Alternatively, it may reflect the normal situation wherever the two species overlap. A comparison of trophic parameters between these two species where they have coexisted for differing periods of time is revealing. In areas of recent sympatry, such as northern California and Washington (Stewart 1980), there is almost complete food-niche overlap, whereas in areas where both species have coexisted longer, such as central California and central Chile, overlap values are one-half to one-quarter as great (Table 2). Thus, high food-niche overlap values are not always characteristic of associations between Great Horned Owls and Common Barn-Owls, lending support to the recent sympatry explanation. Perhaps the high diet overlap detected in northern California and Washington is not the result of recent sympatry but is instead a characteristic of *Bubo-Tyto* pairs in temperate shrub-steppe areas. Likewise, low diet overlap may be characteristic of owls in mediterranean ecosystems. Central California is the climatic/physiognomic analog of central Chile, both of which are mediterranean-type ecosystems (Thrower and Bradbury 1977). Herrera and Hiraldo (1976) found high dietary overlap in owl communities in middle and northern Europe and minimal overlap in a mediterranean owl community. These differences were associated with a tight clustering of owl species feeding on microtines with high population levels in middle and northern Europe and fewer owl species with wider niche breadths depending on less abundant small mammals in the mediterranean community.

Evidence presented in Table 2 for coexisting Great Horned Owls and Common Barn-Owls in North and

South America is in agreement with the findings of Herrera and Hiraldo. MPS and food-niche breadth for both owl species increase from Washington to Chile, suggesting that owls in temperate shrub-steppe areas prey on smaller more numerous prey than do owls in mediterranean habitats. For both owl species there are increases of over four-fold in MPS between Washington and Chile. Indeed, the MPS of Common Barn-Owls in Chile is over twice as large as the MPS of Great Horned Owls in Washington. This is all the more surprising as the adult body weight of Common Barn-Owls decreases from north to south (Jaksić et al. 1982). This is in sharp contrast to the usual relationships between predator and prey sizes (Wilson 1975). In conclusion, we are unable to attribute the high dietary overlap between the Great Horned Owl and the Common Barn-Owl in our study solely to recent sympatry. Further studies of trophic relationships among New World owl species communities and prey populations are needed to clarify our understanding of the coexistence mechanisms of owls.

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Broodedness in Bobolinks

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Extensive quantitative information on the number of broods raised per female bird per season is scarce (Cody 1971). This knowledge is necessary for an accurate analysis (or modelling) of population dynamics or reproductive "strategies" of individuals. In particular, a comparison of the reproductive fitness of monogamous males with that of polygynous males depends on knowing the reproductive success of paired females, which is pertinent also to questions dealing with sexual selection, female choice, and polygyny threshold models. To obtain complete data on reproduction, it is necessary that individual females be marked and monitored throughout the breeding season.

Replacement of lost clutches of eggs is common in birds (Lack 1968), but Lack (1968: 302) generalized that "most species of birds raise only one brood in a year, because the time required for courtship, nest-building, incubation and raising the young to independence is so long that a second brood could not normally be completed before the ecological conditions which permit breeding have ended for the year." Great Tits (*Parus major*), however, were found to raise two broods per year more frequently in habitat where food was more abundant (Perrins 1965), and older females were more likely to be double-brooded than younger females in this species (Kluijver 1951). The latitude at which a bird breeds apparently is related to broodedness in two opposing ways. Lack (1968: 196) stated that ". . . most passerine birds of high latitudes raise more than one brood each year . . . ," presumably because the longer daylength reduces the time to fledging relative to that at lower latitudes. Ecological conditions, however, may be suitable for nesting for a longer period of time at lower latitudes, and, therefore, more broods per female may be raised in a year than at higher latitudes (e.g. doves, many passerines).

The Bobolink (*Dolichonyx oryzivorus*) is a polygynous, ground-nesting icterid that winters from November to March in South America between latitudes 8°S and 32°S (Engels 1969) and breeds in North American hayfields and meadows from May to July between latitudes 40°N and 50°N. Recent studies of populations of marked birds in Wisconsin (Martin 1971), Oregon (Wittenberger 1978), and New York (R. L. Kalinoski pers. comm.) reaffirmed the earlier conclusion of Bent (1958) that Bobolinks can renest after nest failure but do not attempt a second nesting after fledging young from the first nest. An un-