

COMPARATIVE FOOD HABITS OF *BUBO* OWLS IN MEDITERRANEAN-TYPE ECOSYSTEMS

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ABSTRACT.—We tested whether food habits of *Bubo* owls were more similar among mediterranean-type ecosystems (shrublands in Chile, Spain, and California) as compared to those in a different ecosystem (a grassland in Colorado). To do this, we estimated the diet diversity at both the class and species level of mammalian prey, and the mean weight of mammalian prey in the diet. These owls in all four areas did not differ markedly in their diet composition; they all preyed heavily on rabbits, little on mammals weighing less than 20 g, and somewhat on other vertebrates as well as large invertebrates. They did, however, differ in their diet diversity. At the class level of prey selection, Spanish *Bubo* were most diverse and Colorado *Bubo* the least (a three-fold difference). At the mammalian species level, Spanish *Bubo* were the least diverse and both Chilean and Californian *Bubo* the most diverse (about 2.6 times higher). These owls also differed markedly in the mean weight of mammal prey in their diet. Spanish *Bubo* had the highest mean value, whereas California *Bubo* took mammals on average almost six times smaller. Weights of available categories of mammal prey did not differ among regions. Differences in the weights of prey taken by owls apparently reflect differential abundance of local mammals. The owl assemblages in the four regions are similar in both taxonomic composition and configuration of owl sizes. Sympatric *Athene* and *Tyto* owls do not closely parallel the dietary trends seen in *Bubo*.

Owls of the genus *Bubo* are nearly cosmopolitan, being found everywhere except in the Australian region and on southwest Pacific islands, where they are replaced by *Ninox* owls, and in the arctic, where their place is taken by *Nyctea scandiaca* (Grossman and Hamlet 1964, Burton 1973). In North and South America the genus *Bubo* is represented by the Great Horned Owl (*B. virginianus*), whose distribution ranges from central Canada and Alaska to Tierra del Fuego. This owl occurs in boreal forests, deciduous woodlands, shrublands, deserts, rainforests, and mountainous regions (Humphrey et al. 1970, Burton 1973). The Eagle Owl (*B. bubo*), the Old World equivalent of the Great Horned Owl, is widely distributed throughout most of Eurasia, south to the southern edge of the Sahara, to Arabia, Iran, India and southern China. The Eagle Owl occupies a variety of environments similar to its New World congener (Grossman and Hamlet 1964, Burton 1973).

Of the ecosystems where *Bubo* owls occur, few (if any) have been subjected to closer scrutiny than the mediterranean-type shrublands of Chile, California, and the Mediterranean Basin (di Castri and Mooney 1973, Mooney 1977, Thrower and Bradbury 1977, Cody and Mooney 1978). The resulting studies have

shown convergence in many ecological attributes of these ecosystems, ranging from vegetational physiognomy to structure of different plant and animal communities. Herrera and Jaksić (1980), Jaksić and Marti (1981), and Jaksić et al. (1982) showed that size configuration and taxonomic composition of owl assemblages are closely parallel in Chile, Spain, and California, thus providing a framework for comparative studies of the ecology of owl species in these mediterranean-type regions. Three owl genera are present in all three regions: *Athene*, *Tyto*, and *Bubo*. Jaksić and Marti (1981) compared the food habits of Burrowing Owls (*A. cunicularia*) in Chile and California with those of Little Owls (*A. noctua*) in Spain, and Jaksić et al. (1982) made a similar study of Barn Owls (*T. alba*) in these three countries. We here complete our ecological survey by analyzing the food habits of *Bubo* owls in the mediterranean-type shrublands of Chile, Spain, and California.

We synthesized and quantified data from many sources on the food habits of the Pacific Great Horned Owl (*B. virginianus pacificus*), and the European Eagle Owl (*B. bubo bubo*) in Spain. Also, we gathered more dietary information (additional to that reported by Jaksić and Yáñez 1980) for Tucúquere Great Horned

Owls (*B. virginianus magellanicus*) in central Chile. To determine whether the food habits of *Bubo* owls in mediterranean-type shrublands can be regarded as characteristic of this kind of ecosystem, we compared them with those of a western population of Great Horned Owls (*B. virginianus occidentalis*), studied by Marti (1974) in a grassland of Colorado. We refer to this subspecies as "Colorado Horned Owl" to avoid confusion. The rationale for this comparison is the same as that for studies of ecological convergence (see Mooney 1977). We asked whether similar environments (mediterranean-type) acting on organisms differentiated at the species level (*B. virginianus* in Chile and California; *B. bubo* in Spain) result in food habits significantly more similar than those of a congeneric species living in a different environment (*B. virginianus* in Colorado grassland).

To assess what is a "significant" similarity or difference, we used two types of quantitative estimators of the diet. As an estimate of dietary diversity we used the trophic diversity measurements of Hurtubia (1973, see also Levins 1968), which have been widely applied to other owl studies (Herrera 1974, Herrera and Hiraldo 1976, Herrera and Jaksic 1980, Jaksic and Marti 1981, Jaksic et al. 1982). We considered trophic diversity measurements to be adequate for evaluating similarity among species because they focus on the general patterns of prey consumption, with the taxonomic component held constant at a chosen level (see Jaksic and Marti 1981 for further discussion). We also characterized the food habits of owls by the mean weight of prey in their diet. Predators discriminate, under certain conditions, by size rather than by kind of prey (Rosenzweig 1966, Schoener 1968, Hespeneide 1975). Therefore, mean weight of prey consumed by an owl can be considered an estimator complementary to diet diversity measures; the former considers only prey size, the latter taxonomic diversity.

MATERIALS AND METHODS

SITES AND DATA SOURCES

The mediterranean-type ecosystems of Chile, Spain, and California are characterized by the presence of shrublands called "chaparral" in California and "matorral" in both Chile and Spain (di Castri and Mooney 1973, Mooney 1977, Thrower and Bradbury 1977). They have hot-dry summers and rainy-mild winters. Chilean and Spanish localities were described further by Herrera and Jaksic (1980) and Jaksic et al. (1981); California localities were described by Bakker (1971). Climate, vegetation,

and physiognomy of the grassland localities in Colorado were described by Marti (1974).

We obtained information on food habits of Great Horned Owls in central Chile from Housse (1938), Greer and Bullock (1966), Yáñez et al. (1978), Jaksic and Yáñez (1980), and from an uncounted but substantial number of pellets from localities around Santiago (33°26'S, 70°39'W); the pellets were analyzed by J. L. Yáñez and H. Núñez (Museo Nacional de Historia Natural, Santiago, Chile). Data on food of Eagle Owls in Spain were obtained from Pérez (1973), Hiraldo et al. (1975a), and Vericad et al. (1976), who reported prey from an uncounted number of pellets and a few nest remains. Dietary data for Great Horned Owls in California were obtained from Carpenter (1907), Bryant (1913), Dixon (1914), Hunt (1918, see also Bryant 1918), Stoner (1931a,b, 1932, 1936), Sampson (1932), Dixon and Bond (1937), Fitch (1940, 1947), Fox (1948), Vaughan (1954), Cunningham (1960), Peeters (1963), Wiley (1975), Page and Whitacre (1975), and Rudolph (1978). These authors documented food data mostly from pellets (sample sizes not reported) with minor inclusions of stomachs and nest remains. Because food data for Chile, Spain, and California were gathered over long periods, in many localities, and in all seasons of the year, we feel that they adequately reflect the food habits of *Bubo* owls. Marti (1974) reported the prey of Great Horned Owls in Colorado from an uncounted number of pellets collected over three years mainly in a 200-km² area in the northeastern part of Larimer County. Arguably, in comparison to the samples from the mediterranean-type localities, those from Colorado are too restricted in both space and time. This fact, however, does not seem to affect the quantitative diet estimators presented below. Similar studies of *Athene* and *Tyto* owls conducted in the same regions (including Colorado) support this contention (Jaksic and Marti 1981, Jaksic et al. 1982). Overall, taxonomic resolution of prey categories for all four regions ranged from species and genus level for vertebrates to the ordinal level for invertebrates. Shortcomings in the use of pellets to assess food habits of raptors have been discussed among others, by Errington (1930, 1932), and Glading et al. (1943).

Weights of adult mammalian prey identified in the Chilean samples were obtained from Herrera and Jaksic (1980), Jaksic and Marti (1981), Jaksic et al. (1982), and from the mammal collection of Museo Nacional de Historia Natural (Santiago, Chile). Weights of adult mammals from southern Spain came from the above-mentioned literature sources, plus Hir-

aldo et al. (1975b), Jaksic and Soriguer (1981), and from the mammal collection of Estación Biológica de Doñana (Seville, Spain), as detailed in Herrera (1973a). Weights of adult mammalian prey taken by the owls in California were obtained either from Fitch et al. (1946), Fitch (1947, 1949), Jaksic and Marti (1981), Jaksic et al. (1982) or from the mammal collection of the Museum of Vertebrate Zoology (Berkeley, California), or were arbitrarily estimated to be the midpoint of the weight range reported by Burt and Grossenheider (1976). Weight data for Colorado mammals were reported by Marti (1974). Nomenclature of mammals follows Osgood (1943) for Chile, Corbet (1978) for Spain, and Burt and Grossenheider (1976) for California and Colorado.

Weights of mature owls in Chile were supplied by J. L. Yáñez (Museo Nacional de Historia Natural). Weights for Spanish Eagle Owls were based on mature specimens in the ornithological collection of Estación Biológica de Doñana (see Herrera and Jaksic 1980). Weights of mature owls in California were obtained from specimen records in the Museum of Vertebrate Zoology. Weights for Colorado owls were taken from Imler (1937) and unpublished records of C. D. Marti. Nomenclature of owls follows Clark et al. (1978).

QUANTITATIVE AND STATISTICAL METHODS

In addition to computing the percentages of various prey categories in the diet, we characterized the food habits of the owls by three additional estimators: 1) H'_{NGG} is the diet diversity in relation to the number of individuals contributed by each higher taxonomic category, i.e., classes (mammals, birds, reptiles, amphibians, bony fishes, crustaceans, insects, arachnids, and chilopods). 2) H'_{NM} is the diet diversity in relation to the number of mammal species in the diet. Both H'_{NGG} and H'_{NM} were computed by means of the Shannon information function as described in Herrera (1974, see also Pielou 1969). Low values of these estimators indicate that a population has a narrow diet (is relatively specialized), while high values denote a broader diet, with the population exhibiting a more varied or even consumption of the available prey categories (relatively generalized in food habits). Feinsinger et al. (1981) discussed the relationship among diet diversity, food availability, and specialized/generalized food habits. Hurtubia (1973), Hurlbert (1971), and Routledge (1980) presented some pros and cons regarding the use of diversity indices. We feel justified in using them because we dealt with closely re-

lated birds in similar environments, and because these same indices were used in previous studies (Jaksic and Marti 1981, Jaksic et al. 1982), thus allowing direct comparison of results. 3) MWM is the mean weight of mammal prey in the diet, i.e., the grand mean obtained by summing the products of the number of individual prey items times their mean weight and dividing by the total number of prey. Individuals of a given prey species were assumed to be adult-sized because no data were available on either size-classes (and frequencies) represented in the owls' diets, or on the weight of juvenile prey individuals. We assumed that the resulting overestimation of MWM was evenly distributed among the four regions considered, thus cancelling out spurious differences. Other measures of central tendency could have been used (e.g., median), but we chose MWM so as to render our results directly comparable to previous studies (Jaksic and Marti 1981, Jaksic et al. 1982).

Although MWM is a convenient estimate of the mean size of mammal prey consumed by the owls, the frequency distribution of prey weights in the diet cannot be assumed to be normal because it is based on averages (not on actual measurements) and because of the log-normal distribution of body sizes in nature (see Hutchinson and MacArthur 1959). Hence, we evaluated the significance of the differences in MWM among the four regions with the Kruskal-Wallis single factor ANOVA by ranks (Siegel 1956, Sokal and Rohlf 1969). With the same test we also evaluated the significance of differences in the frequency distribution of prey weights used by *Bubo* owls among the four regions. In this latter case, each prey species provided a single weight datum, regardless of its numerical contribution to the bulk of the diet. We used this procedure to assess whether categories of prey weight were similarly available in all regions.

RESULTS AND DISCUSSION

TAXONOMIC COMPOSITION OF THE DIET

Mammals were numerically the most important prey of *Bubo* owls in all four regions, followed by arachnids in Chile, insects in California, and birds in both Spain and Colorado (Table 1). The arachnid prey of Great Horned Owls in Chile were almost exclusively large spiders of the genus *Grammostola*. Insect prey of Great Horned Owls in California were mostly large Jerusalem crickets (*Stenopelmatus* sp.). Birds consumed by Spanish Eagle Owls represented at least 46 species in 12 orders, the most common of which were the Woodpigeon (*Columba palumbus*), and the Red-legged Par-

tridge (*Alectoris rufa*). In Colorado, few birds, mostly passerines, were consumed by Great Horned Owls.

Because mammals seemed to be the staple prey, we present detailed taxonomic information on them (Table 2). Twelve species of small terrestrial mammals were taken by owls in Chile. These included all species known to occur in the region (which excludes both Andean and Coastal ranges), except for the European hare (*Lepus capensis*), which is relatively scarce, and the rodents (*Spalacopus cyanus* [fossorial]), and *Mus musculus* (the smallest mammal in central Chile = 17 g). The most common prey species in the diet of these owls was the native rodent *Phyllotis darwini*, followed by the introduced *Rattus rattus*, *R. norvegicus* and *Oryctolagus cuniculus* (Table 2). Because the three latter species are progressively larger, their biomass contribution to the owls' diet goes in the reverse order. Introduction of these relatively large mammals to Chile has probably increased the mean size of prey taken by these Great Horned Owls.

In Spain, 11 of the 15 species of small terrestrial mammals known to occur in the region were eaten by Eagle Owls. Exceptions were the rodents *Neomys anomalus*, known only from a few localities (Herrera 1973b), and *Sciurus vulgaris*, which is diurnal, arboreal, and present at only one locality where Eagle Owl diet data were collected (R. C. Soriguer, pers. comm.). The other two exceptions were the insectivores *Talpa caeca* (fossorial), and *Suncus etruscus* (the smallest Spanish mammal = 2.5 g). Two other mammals weighing less than 20 g (*Crociodura russula* and *Mus musculus*) were taken in negligible amounts by Spanish Eagle Owls (0.6% of the mammal sample). The native European rabbit (*Oryctolagus cuniculus*) was by far the most important prey of Eagle Owls in Spain, being not only the numerically most common mammal in the diet (81% of the sample), but also fairly large (Table 2).

In mediterranean-type shrublands of California, Great Horned Owls took 29 of the 37 terrestrial small mammals occurring in the region. Neither *Citellus lateralis* nor any of the three species of *Eutamias* (*E. amoenus*, *E. merriami*, *E. sonomae*) were found as prey, probably owing to their diurnal habits. Several species weighing less than 20 g (*M. musculus*, *Perognathus* spp., *Reithrodontomys megalotis*, *Notiosorex crawfordi*, and *Sorex ornatus*) form part of the diet of these owls, representing 12.4% of the mammal sample by number. The most abundant mammalian prey in the diet were voles (*Microtus* spp.), woodrats (*Neotoma fuscipes*), and pocket gophers (*Thomomys*

TABLE 1. Percent by number of prey categories at the class level in the diet of *Bubo* owls in the four regions studied (*tr* = traces [$<0.01\%$]).

Prey categories	Chile	Spain	California	Colorado
Mammals	74.9	65.3	76.6	93.6
Birds	9.8	25.1	4.2	4.5
Reptiles	0.3	0.8	1.6	—
Amphibians	—	0.3	0.8	—
Fishes	—	2.6	—	0.3
Subtotal vertebrates	85.0	94.1	83.2	98.4
Insects	2.8	5.5	15.0	1.3
Arachnids	12.2	0.4	1.8	—
Chilopods	—	<i>tr</i>	—	—
Crustaceans	—	—	—	0.3
Subtotal invertebrates	15.0	5.9	16.8	1.6
Total by number	982	3,506	2,913	2,288

bottae), followed by cottontails (*Sylvilagus audubonii*). Their biomass contribution to the owls' diet was approximately the reverse order (Table 2).

In the Colorado study area, most small terrestrial mammals were eaten except for primarily diurnal species. Species weighing less than 20 g (*M. musculus*, *Perognathus* spp., and *Reithrodontomys* spp.) constituted 5.6% of the mammals in the diet. The numerically most important prey of these owls were deer mice (*Peromyscus* spp.) followed by prairie voles (*Microtus ochrogaster*). Both species contributed similar biomass to the owls' diet because of the smaller size of *Peromyscus*. Cottontails (*Sylvilagus* spp.) ranked third in numerical occurrence as prey, but probably contributed more biomass than the two rodent species combined owing to their larger size.

Bubo owls preyed on almost all available small mammals present in the four regions. A few potential prey species were either absent or poorly represented in the diet because they are diurnal, fossorial, or arboreal. Species weighing less than 20 g were seldom preyed upon by these owls, never exceeding 13% of the mammal prey by numbers, hence accounting for very little biomass in the owls' diet. In contrast, sympatric *Athene* and *Tyto* owls ate many mammals weighing less than 20 g (Jaksić and Marti 1981, Jaksić et al. 1982), indicating that the abundance of these prey was not the factor preventing their consumption by *Bubo* owls. Perhaps such prey are too small to be worth the energetic costs of capture, or else, a rich supply of larger prey enabled *Bubo* owls to ignore small prey. Lagomorphs appear to be important food (both in number and biomass) for all *Bubo* populations. In fact, Span-

TABLE 2. Percent by number of mammal prey categories in the diet of *Bubo* owls in the four regions studied (*tr* = traces [$<0.01\%$]). Subtotals are in parentheses. Species typical of, or endemic to, each region are denoted as Ch (Chile), Sp (Spain), Ca (California), Co (Colorado), Cn (cosmopolitan).

Prey categories	Weight (g)	Chile	Spain	California	Colorado
Rodents	—	(.828)	(.107)	(.881)	(.849)
<i>Abrocoma bennetti</i> (Ch)	219	.086	—	—	—
<i>Akodon longipilis</i> (Ch)	76	.082	—	—	—
<i>A. olivaceus</i> (Ch)	40	.020	—	—	—
<i>Apodemus sylvaticus</i> (Sp)	27.3	—	.024	—	—
<i>Arvicola sapidus</i> (Sp)	216	—	.029	—	—
<i>Citellus beecheyi</i> (Ca)	500	—	—	.001	—
<i>Cynomys ludovicianus</i> (Co)	1,200	—	—	—	<i>tr</i>
<i>Dipodomys agilis</i> (Ca)	58	—	—	.014	—
<i>D. heermanni</i> (Ca)	72	—	—	.098	—
<i>D. merriami</i> (Ca)	42	—	—	<i>tr</i>	—
<i>D. ordii</i> (Co)	68	—	—	—	.023
<i>Dipodomys</i> sp. (Ca)	57.3 ^a	—	—	.003	—
<i>Eliomys quercinus</i> (Sp)	82.5	—	.022	—	—
<i>Marmota flaviventris</i> (Ca, Co)	3,000	—	—	—	.001
<i>Microtus californicus</i> (Ca)	49	—	—	.058	—
<i>M. montanus</i> (Ca)	56.5	—	—	<i>tr</i>	—
<i>M. ochrogaster</i> (Co)	40	—	—	—	.206
<i>M. pennsylvanicus</i> (Co)	45	—	—	—	.043
<i>Microtus</i> spp. (Ca)	52.8 ^b	—	—	.181	—
<i>Mus musculus</i> (Cn)	^c	—	<i>tr</i>	.078	.003
<i>Neotoma fuscipes</i> (Ca)	221	—	—	.149	—
<i>N. lepida</i> (Ca)	181	—	—	<i>tr</i>	—
<i>Neotoma</i> spp. (Ca, Co)	217 ^d	—	—	.001	.004
<i>Notiomys megalonyx</i> (Ch)	68	.004	—	—	—
<i>Octodon degus</i> (Ch)	230	.016	—	—	—
<i>Ondatra zibethica</i> (Co)	700	—	—	—	.006
<i>Onychomys leucogaster</i> (Co)	38	—	—	—	.008
<i>Oryzomys longicaudatus</i> (Ch)	45	.061	—	—	—
<i>Perognathus cal. & ino.</i> (Ca)	16 ^e	—	—	.009	—
<i>P. formosus</i> (Ca)	19	—	—	<i>tr</i>	—
<i>P. hispidus</i> (Co)	39	—	—	—	.007
<i>Perognathus</i> sp. (Ca, Co)	8 ^d	—	—	.019	.013
<i>Peromyscus boy. & man. & tru.</i> (Ca, Co)	22 ^f	—	—	.015	—
<i>Peromyscus</i> spp. (Ca, Co)	21 ^d	—	—	.088	.405
<i>Phyllotis darwini</i> (Ch)	66	.200	—	—	—
<i>P. micropus</i> (Ch)	75	.024	—	—	—
<i>Pitimys duodecimcostatus</i> (Sp)	27.5	—	.002	—	—
<i>Rattus norvegicus</i> (Cn)	^g	.131	.017	—	.001
<i>R. rattus</i> (Cn)	^h	.106	.013	—	—
<i>Reithrodontomys megalotis</i> (Ca, Co)	8	—	—	.015	—
<i>Reithrodontomys</i> spp. (Ca, Co)	12 ^d	—	—	—	.040
<i>Sciurus griseus</i> (Ca)	500	—	—	<i>tr</i>	—
<i>Thomomys bottae</i> (Ca)	160.5	—	—	.148	—
<i>T. talpoides</i> (Co)	132	—	—	—	.089
Unidentified	—	.098	—	.004	—
Lagomorphs	—	(.127)	(.845)	(.109)	(.150)
<i>Lepus californicus</i> (Ca, Co)	2,300	—	—	.005	—
<i>L. capensis</i> (Ch, Sp)	2,000	—	.037	—	—
<i>Lepus</i> spp. (Co)	2,800 ^d	—	—	—	.008
<i>Oryctolagus cuniculus</i> (Ch, Sp)	ⁱ	.127	.808	—	—
<i>Sylvilagus audubonii</i> (Ca, Co)	800	—	—	.103	—
<i>S. bachmani</i> (Ca)	700	—	—	.001	—
<i>S. nuttalli</i> (Co)	1,000	—	—	<i>tr</i>	—
<i>Sylvilagus</i> spp. (Co)	1,000 ^{dj}	—	—	—	.142
Insectivores	—	(.000)	(.042)	(.005)	(.000)
<i>Crocidura russula</i> (Sp)	6.6	—	.006	—	—
<i>Erinaceus europaeus</i> (Sp)	850	—	.036	—	—
<i>Notiosorex crawfordi</i> (Ca, Co)	4.5	—	—	.002	—
<i>Scapanus latimanus</i> (Ca)	140	—	—	.002	—
<i>Sorex ornatus</i> (Ca)	5	—	—	.001	—
Chiropterans	—	(.004)	(.000)	(.002)	(.000)
<i>Antrozous pallidus</i> (Ca, Co)	32.5	—	—	.001	—
<i>Lasiurus borealis</i> (Ca, Co)	11	—	—	<i>tr</i>	—

TABLE 2. Continued.

Prey categories	Weight (g)	Chile	Spain	California	Colorado
<i>Tadarida brasiliensis</i> (Ch, Ca, Co)	10.5	—	—	<i>tr</i>	—
Unidentified	—	.004	—	—	—
Carnivores	—	(.000)	(.004)	(.001)	(.001)
<i>Felis cf. silvestris</i> (Sp)	7,500	—	<i>tr</i>	—	—
<i>Mustela frenata</i> (Ca, Co)	178	—	—	.001	.001
<i>M. nivalis</i> (Sp)	100	—	.001	—	—
<i>Spilogale putorius</i> (Ca, Co)	727	—	—	<i>tr</i>	—
<i>Vulpes vulpes</i> (Sp, Ca, Co)	8,000	—	.003	—	—
Marsupials	—	(.041)	(.000)	(<i>tr</i>)	(.000)
<i>Didelphis marsupialis</i> (Ca, Co)	4,950	—	—	<i>tr</i>	—
<i>Marmosa elegans</i> (Ch)	40	.041	—	—	—
Artiodactyls	—	(.000)	(.002)	(.000)	(.000)
Unidentified	—	—	.002	—	—
Unidentified mammals	—	(.000)	(.000)	(.002)	(.000)
Total by number	—	735	2,281	2,235	2,141

* Unweighted mean for *D. agilis*, *D. heermanni*, and *D. merriami*.

† Unweighted mean for *M. californicus* and *M. montanus*.

‡ 18 g in Ca and Co, 20 g in Sp.

§ See Marti (1974).

¶ Unweighted mean for *P. californicus* and *P. inornatus*.

‡ Unweighted mean for *P. boylei*, *P. maniculatus*, and *P. truei*.

• 320 g in Ch, 390 g in Sp, 221 g in Co.

• 158 g in Ch, 180 g in Sp.

• 1,300 g in Ch, 1,100 g in Sp.

• Probably involving *S. audubonii*, *S. floridanus*, and *S. nuttalli*.

ish Eagle Owls depended heavily on such prey (see Hiraldo et al. 1975a, 1976; Herrera and Hiraldo 1976).

QUANTITATIVE DESCRIPTION OF THE DIETS

A detailed picture emerges from the analysis of the quantitative diet estimators (Table 3). The diversity of prey categories at the class level (H'NGG) was highest in Spain, high and similar between Chile and California, and very low in Colorado. This reflects the greater representation of mammals in the diet of the Colorado owls, and the more diverse prey in the diet of owls in the three other regions. Diversity of mammal prey taken (H'NM) was highest and similar between Chile and California, intermediate in Colorado, and lowest in Spain. Chilean and Californian owls had relatively broad diets, with a more even incidence of mammal prey species as compared to Spanish owls, which seemingly hunted mostly rabbits.

The mean weight of mammal prey in the diet (MWM) was greatest for Spanish Eagle Owls and decreased in the order Chile, Colorado, and California for Great Horned Owls (Table 3).

The Kruskal-Wallis ANOVA detected a highly significant difference among regions in the frequency distribution of prey weights taken by the owls ($H = 3873.3$; $P < 0.001$). This was not due to a heterogeneous representation of prey weight categories because they were

similarly available in all four regions ($H = 2.929$; $P > 0.30$). Consequently, the owls differed in MWM in their diet because they disproportionately consumed some of the available species. Considering the diversity of prey taken by *Bubo* owls throughout their range (see, for example, Errington et al. 1940, Craighead and Craighead 1969, Herrera and Hiraldo 1976, Olsson 1979), differences in relative prey abundance/vulnerability among regions may have accounted for the observed variation in MWM.

Eagle Owls are substantially heavier than Great Horned Owls, while three subspecies of Great Horned Owls have similar mean weights (Table 3). The ratios of MWM to owl mean weight were 24.7%, 55.0%, 15.4%, and 14.2% in Chile, Spain, California, and Colorado, respectively. These disparate figures suggest, again, that *Bubo* owls take prey of different sizes according to their regional availability. Eagle Owls, for example, are known to exploit smaller prey in central and northern Europe in association with the northward decrease in rabbit numbers and concurrent increase in vole and lemming populations (Herrera and Hiraldo 1976, Hiraldo et al. 1976).

OWL ASSEMBLAGES AND THEIR PREY

The assemblages of owls in the four regions are taxonomically similar (Jaksić and Marti 1981, Jaksić et al. 1982). Three genera are common to Chile, Spain, California and Col-

TABLE 3. Trophic statistics used to characterize the feeding ecology of *Bubo* owls in the four regions studied. H'NGG = trophic diversity at the class level of prey; H'NM = trophic diversity at the species level of mammalian prey; MWM = mean weight of mammal prey in the diet; MWB = mean weight of *Bubo* owls. Figures are mean \pm twice SE; sample sizes are in parentheses.

Statistics	Chile <i>B. v. magellanicus</i>	Spain <i>B. b. bubo</i>	California <i>B. v. pacificus</i>	Colorado <i>B. v. occidentalis</i>
H'NGG*	0.820 (982)	0.967 (3,506)	0.796 (2,913)	0.295 (2,288)
H'NM**	2.314 (735)	0.897 (2,281)	2.396 (2,235)	1.803 (2,141)
MWM (g)	303.3 \pm 32.2 (660)	1,037.9 \pm 22.0 (2,277)	179.7 \pm 12.2 (2,222)	207.1 \pm 18.3 (2,141)
MWB (g)	1,227.2 \pm 196.5 (6)	1,885.5 \pm 268.0 (8)	1,166.1 \pm 82.5 (30)	1,460.3 \pm 78.4 (14)

* All pairwise comparisons, using Hutcheson's (1970) test, are significantly different ($P < 0.001$) except for the pair Chile-California.

** All pairwise comparisons (Hutcheson's test) are significantly different ($P < 0.01$).

orado (*Athene*, *Tyto*, and *Bubo*); *Asio* is resident in all regions except Spain; *Glaucidium* and *Otus* are common to two regions each. Only the Spanish *Strix aluco* lacks counterparts in the shrublands of Chile and California, although congeners live in nearby woodlands (*S. rufipes* in Chile, *S. occidentalis* and *S. nebulosa* in California). *Strix occidentalis* occurs in Colorado, but not in the grasslands where Marti (1974) worked. In addition, the frequency distribution of owl species weights does not differ among the four regions (Jaksić and Marti 1981, Jaksić et al. 1982). In spite of this relative constancy across regions, the quantitative estimators of diet do not closely covary in *Athene*, *Tyto*, and *Bubo* owls.

Values of H'NGG and H'NM for *Tyto* owls in Chile, Spain, California and Colorado, closely follow the pattern described here for *Bubo* owls (cf. Jaksić et al. 1982 and Table 3), but this is not so in the case of *Athene* owls (cf. Jaksić and Marti 1981). Trends in MWM for these three genera differ among regions. For example, in Spain, *Bubo* owls had the highest MWM, *Tyto* the lowest and *Athene* intermediate values in comparison to congeners in the other regions. In contrast, both *Tyto* and *Athene* owls in Chile showed larger MWM compared to congeners in the other regions whereas Chilean *Bubo* did not (cf. Jaksić and Marti 1981, Jaksić et al. 1982; Table 3). It seems, then, that each owl species responds to regional prey levels independently of the rest of the assemblage. These trends in H'NGG, H'NM, and MWM are not clearly correlated with concomitant differences in the body sizes of the regional owls. In fact, Jaksić and Marti (1981) and Jaksić et al. (1982) found that variations in these three diet estimators better reflected differences in the regional abundance of prey.

CONCLUSIONS

Bubo owls in mediterranean-type shrublands of Chile, Spain and California were more similar to each other only in H'NGG values than to those in Colorado. Colorado Great Horned

Owls have a relatively narrow diet, preying mostly on mammals, whereas mediterranean Great Horned and Eagle owls eat more diverse prey at the class level. The quantitative estimators used to characterize the mammal component of the diet (H'NM and MWM), however, do not clearly separate the Colorado owls from the others. In general, the food habits of *Bubo* owls in mediterranean-type ecosystems did not differ markedly from those in a grassland ecosystem. This occurs because the size configuration of both mammal prey and owl assemblages is nearly alike among the four regions. The food habits of *Bubo* owls (as well as those of *Athene* and *Tyto*) seem to be mainly related to the availability of different prey. Obviously, this "availability" must be scaled to the size of the owls considered. For *Athene* owls, for example, arthropods constitute abundant prey that is profitably exploitable, whereas rabbits are unavailable prey. Conversely, to the *Bubo* owls, mammals weighing less than 20 g seem not to be very profitable (i.e., the energetic costs of capturing them may exceed the actual gains). Such small prey and some arthropods are perhaps included in the diet when they become exceedingly abundant or vulnerable (e.g., during eruptions).

Our findings suggest that owls are fairly opportunistic hunters and that the trophic structure of their assemblages is strongly affected by the size and abundance distributions of prey in a given region. Because *Bubo* are the largest species in most owl assemblages, they have a greater range of prey sizes available relative to sympatric owls.

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