Predation by the Barn Owl (Tyto alba) in Mediterranean Habitats of Chile, Spain and California: A Comparative Approach

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ABSTRACT: We show that the Mediterranean habitats of Chile, Spain and California are characterized by similar size distributions of small mammal species available to raptors, and that these prey resources are exploited by taxonomically related assemblages of owl species that exhibit similar distributions of body size. Barn owls *(Tyto alba)* in the three mediterranean areas are similar in that they take almost every small mammal species present. However, Spanish barn owls differ from those in Chile and California in that they take significant amounts of insects, amphibians and reptiles, and also in that the mean size of mammalian prey in their diet is considerably smaller than that for Chilean and California barn owls. These features are attributed to the reduced abundance of larger-sized small mammals in Spain, which presumably forces the barn owls to prey more heavily on the smallest mammals available and also on low-reward non-mammalian prey. The trophic parameters of barn owls in a Colorado grassland fall well within the range of variation exhibited by mediterranean barn owls and this is associated with size distributions of mammalian prey and of syntopic owls which are similar between the two habitat types. The essential features determining the predation pattern of the barn owl in different parts of its range seem to be the statistical distribution of mammalian prey sizes available, the relative abundance of these prey and the configuration of the assemblage of syntopic owls.

INTRODUCTION

The barn owl (*Tyto alba* Scopoli) is probably the most widespread Strigiform species in the world, occurring in a great diversity of habitats (Grossman and Hamlet, 1964; Burton, 1973). The food habits of this species have been examined in a number of mediterranean-type ecosystems (*see* di Castri and Mooney, 1973), especially southwestern Australia (Morton, 1975; Morton and Martin, 1979), central Chile (summarized by Jaksić and Yáñez, 1979; Herrera and Jaksić, 1980), southern Spain (summarized by Herrera, 1973a; Herrera and Jaksić, 1980) and California (*see* Clark *et al.*, 1978, for an entry to this literature). The approach of these studies was mainly descriptive or autoecological until Herrera and Jaksić (1980) attempted the first comparative analysis of the food habits of the barn owl in Chile and Spain. Because of the limited scope of that study, we here extend the analysis to California and document more thoroughly the trophic ecology of the barn owl in the mediterranean habitats of all three countries. By comparing the predation pattern of this single species in three widely separated areas of very similar climate, physiognomy and resources (di Castri and Mooney, 1973; Mooney, 1977; Thrower and Bradbury, 1977; Cody and Mooney, 1978), we hope to clarify how certain environmental variables are related to the trophic ecology of the barn owl in mediterranean ecosystems. We assess the degree of similarity in the taxonomic composition and morphological configuration of the owl and prey assemblages in each of the three regions and test some hypotheses on predator/prey size relationships. Also, in order to determine if the predation pattern exhibited by barn owls in mediterranean areas can be regarded as characteristic of this kind of habitat, we compare it with that of barn owls living in a grassland habitat of N-central Colorado (Marti, 1974). Our approach is similar to that used to test ecological convergence between taxonomic assemblages (Cody and Mooney, 1978) and aims at identifying the main ecological factors associated with predation by the barn owl in different parts of its geographic range.

MATERIALS AND METHODS

Sites and data sources.—General descriptions of the mediterranean habitats of Chile, Spain and California were given by di Castri and Mooney (1973), Mooney (1977) and Thrower and Bradbury (1977). These habitats are characterized by the presence of an assemblage of evergreen shrubby species called matorral in Chile, chaparral in California and maquis in Spain (Cody and Mooney, 1978). Detailed descriptions of Chilean and Spanish localities were reported by Herrera and Jaksić (1980); information on California habitats may be obtained from Bakker (1971). Marti (1974) described the climate, vegetation and physiognomy of the grassland where he worked in N-central Colorado.

Sources for food habits of barn owls in central Chile were Johnson (1965), Reise (1970), Schamberger and Fulk (1974), Fulk (1976), Jaksić *et al.* (1977), Jaksić and Yáñez (1979) and Jaksić (1979). In these studies a total of 3594 prey items were identified in 2545 pellets collected at 18 sites located between lat 30°30′ - 34°36′S and long 70°31′ - 71°40′W. Food data for Spain were obtained from Nos (1961), Vericad (1965), Nadal and Palaus (1967), Valverde (1967), Herrera (1973a), Vericad *et al.* (1976) (*see also* Herrera, 1974; Herrera and Hiraldo, 1976; Valverde, 1960). These sources reported a total of 14,407 prey items identified in nearly 3500 pellets obtained at 26 sites located between lat 36°30′ - 38°30′N and long 4° - 7°W. Based on the sources listed above, Herrera and Jaksić (1980) gave a detailed account of the prey of barn owls in both Chile and Spain. Sources used for the evaluation of food habits of the barn owl in California were Foster (1926, 1927), Hall (1927), Grinnell *et al.* (1930), Bolander (1939), Selleck and Glading (1943), Hawbecker (1945), Evans and Emlen (1947), Fitch (1947), Cunningham (1960) and Clark and Wise (1974). Also, Dixon (1922), McLean (1928), Dixon and Bond (1937), von Bloeker (1937), Bond (1939), Glading *et al.* (1943), Banks (1965) and Earhart and Johnson (1970) reported on the prey of the barn owl in California, but these sources were disregarded because either the prey items were not quantified or not clearly identified, barn owl pellets were mixed with those of other raptors, or the habitat sampled was not typically mediterranean. The usable food data collected from the above studies totalled 8236 prey items from an undetermined number of pellets collected in the Sierran foothills, central valley and coastal localities of California between lat 33°58′ - 40°28′N and long 118°25′-122°30′W. All the information collected in California is presented in condensed form in the Appendix 1. Because food data for the three mediterranean areas have been gathered over an ample time span and in all seasons of the year, we feel confident that they adequately reflect the food habits of the barn owl. Marti (1974) identified 4366 prey items from a sample of pellets collected over 4 years, mainly in a 200-km^2 area in the northeastern part of Larimer Co., Colorado.

Weights of adult mammalian prey identified in the Chilean samples were obtained from Glanz (1977) and from the mammal collection of Museo Nacional de Historia Natural (Santiago, Chile). Weights for small mammals from southern Spain were obtained from van der Brink (1968) and from the mammal collection of Estación Biológica de Doñana (Sevilla, Spain), as detailed in Herrera (1973a). Weights of small mammal prey of barn owls in California were obtained mainly from Glanz (1977), arbitrarily estimated to be the midpoint of the weight range reported by Burt and Grossenheider (1976), or from the mammal collection of the Museum of Vertebrate Zoology (University of California at Berkeley, USA). Two types of exceptions to these procedures are pointed out in Appendix 1. Weight data for Colorado small mammals were reported by Marti (1974). Mammal nomenclature used in this paper follows Osgood (1943) for Chile, Corbet (1978) for Spain and Burt and Grossenheider (1976) for California and Colorado.

The potentially syntopic owl species inhabiting the mediterranean habitats of Chile and Spain were reported by Herrera and Jaksić (1980). Weight data for Chilean owl species were taken from field tags of specimens deposited in the ornithological collections of Museo Nacional de Historia Natural, Instituto Central de Biología de la Universidad de Concepción, Museo de Historia Natural de Valparaíso and Instituto de Zoología de la Universidad Austral. All data from southern Spain were based on specimens preserved in the ornithological collection of Estación Biológica de Doñana, unless otherwise stated (Table 3). Potentially syntopic owl species in California mediterranean habitats were determined on the basis of descriptions of habitat selection, abundance, residence status and geographic distribution (Grinnell and Wythe, 1927; Grinnell and Miller, 1944; Small, 1974; McCaskie *et al.*, 1979). Weights of these species were obtained from field tags of specimens deposited in the ornithological collection of the Museum of Vertebrate Zoology. The syntopic owl species in Colorado grasslands and their weights were reported by Marti (1974). Nomenclature of owls follows Clark *et al.* (1978).

Quantitative and statistical methods.—In addition to computing the percentage contributed by the various prey categories to the diet for each geographical area, the trophic ecology of barn owls in each region was characterized by the following parameters: (1) H'NGG = trophic diversity (as defined by Hurtubia, 1973) in relation to the number of individuals contributed by each higher taxonomic category (mammals, birds, reptiles, amphibians, insects). Low values indicate that the predator has a narrow trophic niche (is relatively stenophagous), concentrating its predation on one or a few prey categories (classes in this case); high values denote a broader trophic niche, the predator consuming more equal amounts of the available prey categories (relatively euryphagous). (2) H'NM = trophic diversity in relation to the small mammal categories in the diet (rodents, lagomorphs, insectivores, marsupials and chiropterans). As above, low values suggest a narrow diet while high values indicate a relatively broad 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). We used this quantitative description of the barn owl diet to make our results comparable with those reported for the same species in western Europe (Herrera, 1974). (3) MWSM = mean weight of small mammal prey, which is the grand mean obtained by summing the products of the number of individual prey times their average weight (as reported by Herrera and Jaksić, 1980; Marti, 1974; Appendix 1), and dividing by the total number of mammalian prey in the sample of pellets.

Although MWSM is a convenient estimate of the mean size of prey consumed by the owls, the frequency distribution of prey weights in the diet of barn owls cannot be assumed to be normally distributed because it is based on averages, not on actual measurements. Hence, the significance of the difference between the statistical distributions observed in the study areas (excluding Colorado; *see below*) was evaluated with the Kruskal-Wallis test, a nonparametric test equivalent to the single-classification analysis of variance (Sokal and Rohlf, 1969:388). Subsequently, the Mann-Whitney *U*-test, a nonparametric method equivalent to the Student's *t*-test (Sokal and Rohlf, 1969:391), was used to determine which distribution differed from the others. Statistical differences in the frequency distribution of prey-weight ranges available to barn owls in Chile, Spain and California (using 10-g intervals and regarding each prey species as a single observation) were tested with pairwise Kolmogorov-Smirnov tests with chi-square approximation (Siegel, 1956:131). Because barn owl weights in the three mediterranean areas can be assumed to be normally distributed, the significance of the differences between continents was evaluated with a one-way analysis of variance and associated Student's *t*-test of the differences between two means (Sokal and Rohlf, 1969:220). The significance of the differences among Chile, Spain and California in the distribution of owl sizes within each assemblage was determined with the Kruskal-Wallis test. Quantitative data from Colorado were compared only with those from California, regarding them as control for results obtained in the comparison between California and the other two mediterranean habitats. Statistical differences in the frequency distribution of prey weights actually taken by barn owls in California and Colorado were tested with the Mann-Whitney *U*-test. The significance of the differences in the frequency distribution of prey weight ranges available for barn owls in the two areas (using 10-g intervals, as above) was determined with the Kolmogorov-Smirnov test with chi-square approximation. This same test was used to determine statistical differences in the distribution of owl weights within the assemblages in California and Colorado. The rationale underlying this set of comparisons is that if California data are more similar to those from Chile and Spain than to those from Colorado, then the hypothesis that barn owls exhibit a characteristic trophic ecology in mediterranean habitats can be supported.

RESULTS AND DISCUSSION

General trends of predation.—Mammals are clearly the most important prey of the barn owl in the mediterranean habitats of Chile, Spain and California (Table 1). The percent abundance of various prey taxa in Chile and California is strikingly similar, while Spain differs from both areas in the greater importance of reptiles, amphibians and insects. In a comparison of the diet of central European and Spanish barn owls, Herrera (1974) noted the inclusion of nonmammalian prey in the latter and attributed this to an observed decrease in small mammal abundance in the mediterranean area. Reptiles, amphibians and insects seem, therefore, to represent an alternative food resource for Spanish barn owls which may compensate for low densities of mammalian prey. Preliminary data obtained by Jaksić and Yáñez (1978) for Chile and by R. C. Soriguer (pers. comm.) for Spain reaffirm the comparatively low mammal densities in the latter area. Schamberger and Fulk (1974) obtained figures of 0.06, 0.13 and 0.34 individuals per trap night in three habitat types in central Chile, and year-round trapping by Jaksić and Yáñez (1978) in a matorral habitat gave a monthly average of 0.03 individuals per trap night (ranging as high as 0.07). In southern Spain, trapping success ranged between 0.00 and 0.04 individuals per trap night (with figures strongly skewed toward large values) in several habitat types in nearly 20 localities (R. C. Soriguer, pers. comm.). Small mammal densities are even higher in California than Chile (Glanz, 1977), and consequently reptiles, amphibians and insects are of only minor importance in the diet of the California barn owls. The percent importance of small mammals in the diet of Colorado barn owls is very similar to that for California (*see* Table 1).

Twelve species of terrestrial small mammals are taken by the barn owl in central Chile (Herrera and Jaksić, 1980). These include all mammalian species available in the area (which excludes both Andean and Coastal ranges), except for the European hare *Lepus capensis* (*see* Jaksić and Yáñez, 1979), which is relatively scarce and probably too large to be handled by the barn owl. In southern Spain, 10 of the 15 species of terrestrial small mammals (van der Brink, 1968) are found in barn owl pellets (Herrera and Jaksić, 1980). *Erinaceus europaeus* is present in the area but is likely too large to be taken. However, the larger syntopic *Bubo bubo* includes this prey in noticeable amounts (Hiraldo *et al.*, 1975; Vericad *et al.*, 1976). *Neomys anomalus* has been recorded in southern Spain, but only from a single locality (Herrera, 1973b). *Talpa caeca* is a strictly fossorial insectivore which explains its absence in the diet of the barn owl. *Lepus capensis* is probably too large to be handled and *Sciurus vulgaris* is both arboreal and diurnal, hardly available as prey to this nocturnal predator. Moreover, in southern Spain *Sciurus vulgaris* is known to be present in a single locality, the Sierras de Cazorla y Segura, where *Tyto alba* seemingly does not occur (R. C. Soriguer, pers. comm.).

In the mediterranean habitats of California, the barn owl takes 30 (Appendix 1) of the 37 terrestrial small mammals present in the area (presence based on geographic range, habitat selection, relative abundance and habits of the species, as described in Burt and Grossenheider, 1976). All species of marsupials, insectivores and lagomorphs known to be present in mediterranean California are taken by the barn owl. The greatest discrepancy is between the rodent composition in the field and in the diet. None of the three species of *Eutamias (E. amoenus, E. merriami, E. sonomae)* are identified in barn owl pellets. However, these species tend to be diurnal (Burt and Grossenheider, 1976). *Citellus lateralis* occurs in the area, but it is not taken by barn owls, probably because of its relatively large size (ca. 223 g). *Dipodomys agilis* and *Dipodomys venustus* are common in California and it is likely that they are included in the diet of the barn owl, but may be among the relatively numerous *Dipodomys* sp. reported in Appendix 1. *Sciurus griseus* is arboreal and more active in the morning, hardly available for a nocturnal predator. In Colorado, barn owls prey on all the available species of terrestrial small mammals, except those too large to be handled: *Cynomys ludovicianus* (1200 g), *Marmota flaviventris* (3000 g), *Rattus norvegicus* (221 g), *Lepus* spp. (2800 g). (*See* Marti, 1974, for further discussion of this topic.)

The unmistakable impression from this analysis is that the barn owl preys on almost all the available small mammals present in mediterranean habitats. (This also holds true in the grassland habitat in Colorado.) A few potential prey species are absent in pellets because they are either too large, or arboreal, or fossorial or diurnal. However, even though the barn owl preys on almost every species in the study areas, this does not mean that it is a nonselective predator. The way to determine the degree of selectivity is to evaluate prey abundance in hunting sites and contrast the estimate with the actual prey consumption (*see* Fulk, 1976; Jaksić and Yáñez, 1979). However, as we have lumped data for many localities, we cannot assess prey selection by the barn owl at this level.

Quantitative parameters of the diet. — A more quantitative view of the above results can be obtained from the analysis of trophic diversity. H′NGG, the diversity of the higher taxonomic units (classes) in the diet of the barn owl, is greatest in Spain and relatively small and similar in both Chile and California (Table 2). This is clearly associated with the greater representation of reptiles, amphibians and insects in the Spanish sample. The figure for Colorado is extremely low, about one third of that computed for California and Chile, and even less in comparison with Spain. This is related to the high importance of small mammals and the complete absence of reptiles, amphibians and insects in the diet of barn owls in Colorado. Consequently, Spanish barn owls can be characterized as the most euryphagous and Colorado barn owls as the most stenophagous of the four populations analyzed. On the other hand, the diversity of species taken within the small mammal sample (H′NM) is low in Spain as compared with both Chile and California (Table 2). Diversity of prey for Colorado is quite similar to that for California and Chile and consequently greater than in Spain. This is associated with the very high importance of only four small mammal species in the diet of Spanish barn owls (*Apodemus sylvaticus, Mus musculus, Pitymys duodecimcostatus,*

TABLE 1. — Prey of the barn owl (by classes) in the four study areas. N = sample size

	Chile		California		Spain		Colorado	
	N	%	N	%	N	%	N	%
Mammals	3417	95.1	7832	95.1	12,492	86.7	4305	98.6
Birds	130	3.6	258	3.1	590	4.1	61	1.4
Reptiles	..	0.0	5	<0.1	121	0.8	..	0.0
Amphibians	..	0.0	3	<0.1	539	3.8	..	0.0
Insects	47	1.3	138	1.7	665	4.6	..	0.0
Total prey	3594	100.0	8236	100.0	14,407	100.0	4366	100.0

Crocidura russula; see Herrera and Jaksić, 1980), which account for more than 94% of their mammalian prey.

The frequency distribution of weights of prey actually consumed by the barn owl in central Chile tends to be log-normal, while that in Spain is more strongly skewed to the right (with higher representation of small-sized prey; *see also* Herrera and Jaksić, 1980). The curve for California is the least smoothly shaped, exhibiting peaks at 20 g (mainly due to *Peromyscus* spp.), 50 g (due to *Microtus californicus*) and 160 g (due to *Thomomys bottae*) (Fig. 1). As expected from this description, there are significant differences among the mammalian prey-weight distributions in the diet of barn owls from the three mediterranean habitats analyzed ($P < 0.005$ overall; $P < 0.001$ for all pairwise comparisons). The same result is obtained in the comparison between California and Colorado ($P < 0.01$).

Mean weight of small mammals (MWSM) in the diet of barn owls is largest in Chile, similar in California, and smallest in Spain (Table 2). The figure for Colorado is intermediate between California and Spain. It is interesting to note that the weight-range distributions of small mammal species available for the barn owl do not differ among the three mediterranean areas ($P > 0.30$ in all three cases); the same holds true in the comparison between California and Colorado ($P > 0.98$). This suggests that the observed differences in MWSM for barn owls in these four areas are not owing to the absence of particular prey sizes, but rather to differential consumption of certain ranges of the available prey-weight distributions. Whether this is related to active selection by the owls, or to the relative proportions in which prey are encountered, the fact is that the barn owl in mediterranean Spain consumes proportionately more smaller-sized mammals than in Chile, California or Colorado. Herrera (1974) found the same when comparing the MWSM of Spain with central Europe. He attributed this to "the reduced diversity of small mammal populations in the Mediterranean region" (*see* also van der Brink, 1968), which "is accompanied by a pronounced decrease of the total densities in the field of all species combined" (Herrera, 1974:187). Whatever the cause is for the reduced density of small mammals in mediterranean Spain, it would be expected that the large species become comparatively rarer than the small since the first are at the right tail of the log-normal distribution of abundance according to size (Hutchinson and MacArthur, 1959). The Spanish barn owl, therefore, would be compelled to feed on relatively smaller prey items, thus rendering a low MWSM. A different explanation, not necessarily exclusive of the one above, is that the Spanish barn owls may experience stronger diffuse competition from owl species that are larger than those found in Chile, California or Colorado (*see* MacArthur, 1972). We examine this hypothesis in the next section.

Configuration of the owl assemblages and size relationships.—The owl assemblages in the three mediterranean areas are remarkably similar in both taxonomic composition and body size configuration (Table 3). Three genera (*Tyto, Bubo, Athene*) are found in all three areas; two others (*Glaucidium* and *Asio*) are shared between Chile and California, and *Otus* is shared between California and Spain. The only genus with no counterpart in other mediterranean habitats is *Strix* (in Spain). Although species of *Strix* are certain-

TABLE 2.—Quantitative parameters used to characterize the trophic ecology of the barn owl in the four study areas. H'NGG = trophic diversity at the class level of prey; H'NM = trophic diversity at the species level of mammalian prey; MWSM = mean weight of small mammal prey; MWBO = mean weight of barn owls. Figures are mean ± twice SE in the case of MWSM and MWBO; sample sizes are in parentheses

	Chile		California		Spain		Colorado	
H'NGG	0.225	(3594)	0.232	(8236)	0.560	(14407)	0.074	(4366)
H'NM	1.932	(3417)	1.988	(7832)	1.409	(12492)	1.856	(4305)
MWSM (g)	70.7 ± 1.8	(3391)	68.2 ± 1.3	(7827)	21.2 ± 0.4	(12351)	45.9 ± 1.7	(4305)
MWBO (g)	306.5 ± 21.6	(8)	442.1 ± 28.3	(15)	280.6 ± 18.8	(20)	479 ± . .	(. .)

ly found in both Chile (*S. rufipes*) and California (*S. nebulosa* and *S. occidentalis*), they are not considered ecological counterparts of the Spanish *S. aluco* because they are forest-dwellers, thus seldom syntopic with the barn owl. Even though *Asio flammeus* is present in both California and Spain, it is not considered an ecological counterpart of the Chilean *A. flammeus* (syntopic with *T. alba*), because in the first area it is very scarce and in the second it is only a winter resident. The assemblage of owl species in Colorado is similar, but less diverse than that in California: *T. alba, B. virginianus, A. otus* and *A. cunicularia* are found in the two areas, but *G. gnoma* and *O. asio* are not present in the grasslands of Colorado.

The distributions of body weights of owl species in the three mediterranean areas are not significantly different ($P > 0.75$), which further stresses the similarity of the owl assemblages in Chile, Spain and California. This is also the case in the comparison between California and Colorado ($P > 0.90$). Therefore, the low MWSM consumed by the Spanish barn owls does not appear to be associated with clear differences in the distribution of sizes of syntopic owl species. Rather, the reduced density of small mammals in the area seems a better explanation of the phenomenon (*see also* Herrera, 1974; Herrera and Hiraldo, 1976; Herrera and Jaksić, 1980), and this is also consistent with our results on trophic diversity of Spanish barn owls.

On the other hand, it is interesting to note that barn owls have different body sizes in the four areas compared. Even though mean body weight does not differ between Chile and Spain ($P > 0.12$), it is certainly larger in California ($P < 0.001$ in both pairwise comparisons). Barn owls in Colorado appear to be even larger than in California (*see* Table 2), but we could not test the significance of this difference because we lack statistical information from Colorado.

In contrast to the well-known correlations between predator and prey sizes (Rosenzweig, 1966; Schoener, 1967; Hespenheide, 1973; Wilson, 1975), the mean size

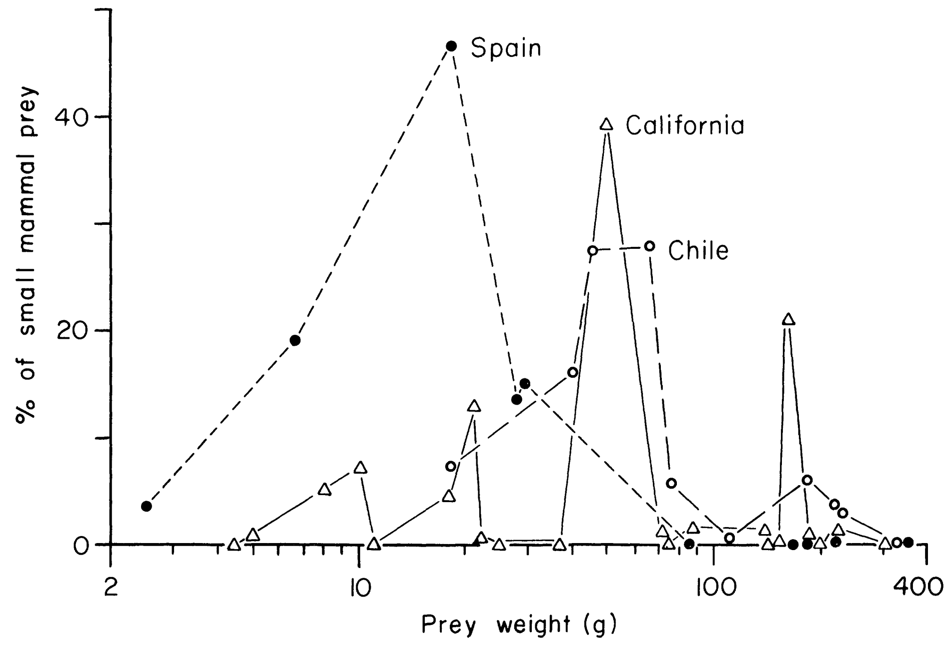

Fig. 1.—Small mammal prey (excluding bats) of barn owls in the mediterranean habitats of Chile, Spain and California. Body weights of small mammal species in the diet of the owls are ordered along a logarithmic axis; the sum of all points for each area equals 100 percent

TABLE 3. — Owl assemblages in the four study areas. Owl species are matched by genus. Average weights (g) and sample sizes (in parentheses) are shown

Chile		California		Spain		Colorado	
Tyto alba	307 (8)	*T. alba*	442 (15)	*T. alba*	281 (20)	*T. alba*	479 [(b)]
Bubo virginianus	1500 (2)	*B. virginianus*	1155 (32)	*B. bubo*	1886 (8)	*B. virginianus*	1553 [(b)]
Asio flammeus	350 (2)	*A. otus*	253 (19)	.....	.....	*A. otus*	270 [(b)]
Athene cunicularia	247 (3)	*A. cunicularia*	154 (19)	*A. noctua*	148 (30)	*A. cunicularia*	158 [(b)]
Glaucidium brasilianum	74 (4)	*G. gnoma*	67 (27)	.....	.....	.....	.....
......	.....	*Otus asio*	147 (60)	*O. scops*	69 (2)[a]	.....	.....
.....	.....	.....	.....	*Strix aluco*	426 (10)	.....	.....

[a]Average of male and female means; *see* Herrera and Jaksić (1980) for details
[b]Sample sizes not given by Marti (1974)

of the barn owl is not closely related to its mean prey size (*see* Table 2). In fact, the almost equal-sized Chilean and Spanish barn owls differ in MWSM by a factor of three, and the nearly similar MWSM taken by Chilean and Californian barn owls is associated with a 40% larger body size of the latter (Table 2). Also, the larger Colorado barn owls exhibit a MWSM which is one-third smaller than that in California. These anomalies could have two explanations: (1) The statistic mean weight of small mammal prey (MWSM) is very sensitive to disparately large—or small—weights of prey, even when they are represented in small frequencies in the diet of barn owls. Also, this statistic is meaningful only if the normal distribution of prey sizes in the diet of the predator is verified. This requirement is not fulfilled by data from the three mediterranean areas (*see* Herrera and Jaksić, 1980, and Appendix 1) nor by those of Marti (1974) for Colorado. In this case, a more appropriate statistic is the median (*see* Sokal and Rohlf, 1969:45), which is 49.8 g, 15.8 g, 44.5 g and 41.8 g for Chile, Spain, California and Colorado, respectively. However, these values are not well-correlated with the body size of barn owls in the four areas (*cf.* Table 2). The discrepancy, then, seems not to be a statistical one. (2) It is possible that a close relationship between predator and prey sizes can be found only within sets of predators hunting in the same area and with similar techniques (the hunting sets of Rosenzweig, 1966), rather than in comparisons between predator and prey of different hunting sets, despite their profound taxonomic and ecological similarities. A study of the trophic ecology of all the members of these hunting sets in the four areas could shed some light on the validity of this explanation. Herrera and Hiraldo (1976) have documented the food-niche relationships among owls of the Spanish assemblage and Marti (1974) has thoroughly studied food-niche segregation among owls in the grasslands of Colorado, but this kind of analysis has not been made in the mediterranean habitats of Chile or California (but *see* Jaksić *et al.*, 1977, for a preliminary attempt).

Grassland vs. mediterranean habitats.—Are barn owls in mediterranean habitats more similar in their feeding ecology than barn owls in a grassland habitat? We have shown that, in comparison to Chile, Spain, and California, the trophic ecology of the barn owl in Colorado is characterized by values of H'NM and MWSM that fall well within the range of values encompassed by the same species in mediterranean habitats. This could be due to the insignificant differences found in the distribution of prey-weight ranges available in the four areas, coupled with the similarities in taxonomic composition and body size relationships among the owl assemblages in those areas. The only parameter that contrasts strongly in Colorado is the low value of H'NGG, the diversity of higher taxonomic units in the diet of barn owls in that region. This means that barn owls in the grassland of Colorado are extremely stenophagous, concentrating their predation efforts almost exclusively on small mammals. Whether this phenomenon is associated with marked prey preference, or with low abundance of alternative prey like amphibians, reptiles, birds or invertebrates, is not known. At any rate, it seems that the trophic ecology of barn owls in mediterranean habitats is not very different from that observed in a temperate grassland. This strongly suggests that given certain conditions in the spectrum of prey sizes available in an area, and in the configuration of the owl assemblage exploiting it, barn owls tend to maintain the same kind of relationships with their prey, at least regarding the quantitative parameters analyzed.

CONCLUSIONS

Barn owls in mediterranean habitats of Chile, Spain and California are similar in that they prey on almost every small mammal species present in the respective areas. Otherwise, Spanish owls diverge from those in Chile and California in that they take significant amounts of prey other than mammals, such prey being smaller in size than that in the diet of Chilean and California barn owls. Mean size of mammalian prey does not appear to be correlated with barn owl size, which is different in the three study areas. The statistical distribution of mammalian sizes available as prey to barn owls, as well as that of syntopic owl species, is similar in Chile, Spain and California. Therefore, the small mean prey size taken by Spanish barn owls can be attributed to a reduced abundance of larger mammalian prey in that area (there are data that support this contention), which in turn seems to force the barn owls to prey heavily on the smallest mammals and on low-rewarding prey such as insects, amphibians and reptiles. The trophic parameters of barn owls in a Colorado grassland fall well within the range of variation demonstrated by barn owls in mediterranean habitats; this is attributable to the essentially similar size distribution of mammalian prey and of syntopic owls present in Colorado. We conclude that the most important features determining the trophic ecology of the barn owl in different parts of its range are the statistical distribution of mammalian prey sizes available in a given area, the relative abundance of those prey, and the configuration of the assemblage of syntopic owl species. In our analysis we documented the presumptive effect of differences in prey abundance, the size-related variables being similar everywhere. Studies conducted in areas where the size-distribution of available prey, of the syntopic owls, or of both differ, could greatly aid our understanding of predation by barn owls.

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Appendix 1.—Number of small mammal prey documented for California barn owls; prey weight (g) in parentheses; juvenile weight is based on Grinnell *et al.* (1930), Orr (1940), Evans and Emlen (1947) and Fitch (1947); expected weight is the statistical expectation based on the weight of congeneric species actually taken by barn owls.

Rodents: 1 juvenile *Citellus beecheyi* (200), 91 *Dipodomys heermanni* (72), 21 *D. ingens* (153), 125 *Dipodomys* sp. (87.2; expected), 3096 *Microtus californicus* (49), 359 *Mus musculus* (18), 105 *Neotoma fuscipes* (221), 4 *Ondatra zibethica* (weight unknown), 4 *Onychomys torridus* (22), 48 *Perognathus californicus* (22), 564 *P. inornatus* (10), 27 *Perognathus* sp. (10.9; expected), 1 *Peromyscus boylei* (21), 1 *P. californicus* (37), 405 *P. maniculatus* (21), 4 *P. truei* (25), 609 *Peromyscus* sp. (21.1; expected), 2 *Rattus norvegicus* (317), 59 *R. rattus* (183.5), 406 *Reithrodontomys megalotis* (8), 1654 *Thomomys bottae* (160.5).

Lagomorphs: 6 juvenile *Lepus californicus* (75), 5 juvenile *Sylvilagus auduboni* (200), 79 juvenile *S. bachmani* (144).

Insectivores: 8 *Neurotrichus gibbsi* (11), 2 *Notiosorex crawfordi* (4.5), 67 *Scapanus latimanus* (140), 47 *Sorex ornatus* (5), 31 *Sorex* sp. (5; expected).

Marsupials: 1 *Didelphis marsupialis* (weight unknown).