

Numerical and behavioral estimates of predation upon rabbits in mediterranean-type shrublands: a paradoxical case

Estimadores numéricos y conductuales de depredación sobre conejos en matorrales de tipo mediterráneo: Un caso paradójico

FABIAN M. JAKSIC* and RICHARD S. OSTFELD

Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA.

ABSTRACT

Rabbits are present in mediterranean-type shrublands of Chile (Oryctolagus cuniculus, introduced), Spain (O. cuniculus), and California (Sylvilagus audubonii and S. bachmani). The incidence of rabbits in the diets of local predators is lower in Chile than in Spain, and rabbits in Chile behave as if they are predator-free whereas those in Spain exhibit marked refuging behavior. Jaksic & Soriguer (1981; J. Anim. Ecol. 50: 269-281) advanced the explanation that lack of long-term association between Chilean predators and the recently introduced rabbits results in inefficient exploitation of this prey. Two assumptions are implicit in this contention: 1) that predation pressure upon rabbits can be estimated from the average contribution of rabbits as prey to all the local predator species, and 2) that if co-adaptation in ecological time influences predation levels on rabbits, their importance as prey should be similar in regions where they have a long-term association with the local predators. We test both assumptions by examining the importance of rabbits as prey in California, where long-term association with local predators has occurred and rabbits exhibit a refuging behavior similar to that in Spain. Our results show that the incidence of California rabbits in the diets of local predators is closer to Chilean than Spanish figures. Consequently, the second assumption of Jaksic & Soriguer is not verified. We also argue that their first assumption is most likely incorrect. We conclude that lack of long-term association between rabbits and predators still is the best explanation available for the behavioral differences between rabbits in Chile and Spain (and perhaps also for California). Jaksic & Soriguer reached the right conclusion but for the wrong reason.

Keywords: Rabbits – Oryctolagus and Sylvilagus – Refuging behavior – Mediterranean shrublands – Chile – Spain – California – Predators – Diets – Co-adaptation.

RESUMEN

Existen conejos en matorrales de tipo mediterráneo en Chile (Oryctolagus cuniculus, introducido), España (O. cuniculus) y California (Sylvilagus audubonii y S. bachmani). Jaksic y Soriguer (1981, J. Anim. Ecol. 50: 269-281) mostraron que la incidencia de conejos en la dieta de depredadores locales es menor en Chile que en España. Los conejos chilenos se comportan como si no fueran depredados, en tanto que los españoles presentan una marcada conducta de refugio. Jaksic y Soriguer propusieron que la falta de suficiente asociación temporal (coadaptación en tiempo ecológico) entre depredadores chilenos y los recientemente introducidos conejos resulta en explotación ineficiente de esta presa. Dos suposiciones están implícitas en su hipótesis: 1) que la presión de depredación sobre conejos puede estimarse por la incidencia promedio de ellos en la dieta de los depredadores locales y 2) que si la coadaptación en tiempo ecológico influye en los niveles de depredación sobre conejos, su incidencia como presa debiera ser similar entre regiones en que ellos han estado asociados con depredadores locales por tiempos ecológicamente extensos. Nosotros ponemos a prueba ambas suposiciones examinando la incidencia de conejos en la dieta de depredadores en California, región en que conejos y depredadores han estado asociados por largo tiempo y donde aquéllos presentan una conducta de refugio similar a la observada en España. Nuestros resultados muestran que la incidencia de conejos californianos en la dieta de depreda-

* Present address: Departamento de Biología Ambiental, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.

Offprint requests to: F.M. Jaksic.

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dores locales es más similar a la observada en Chile que a la observada en España. En consecuencia, la suposición 2) de Jaksic y Soriguer no se verifica. También discutimos que la suposición 1) es probablemente incorrecta. Concluimos que la falta de suficiente asociación temporal entre conejos y depredadores aún es la mejor explicación disponible para las diferencias conductuales observadas en conejos de Chile y España (y quizás también de aquellas observadas en California). Es decir, Jaksic y Soriguer llegaron a la conclusión correcta, pero por razones equivocadas.

Palabras claves: Conejos – Oryctolagus y Sylvilagus – Conducta de refugio – Matorrales mediterráneos – Chile – España – California – Depredadores – Dietas – Coadaptación.

INTRODUCTION

The European rabbit (*Oryctolagus cuniculus* Linnaeus 1758) is a native of the evergreen sclerophyllous scrub (= matorral) of the Iberian Peninsula (Zeuner 1963). It was introduced to similar scrub areas of central Chile in the mid-eighteenth century (Housse 1953) but it did not become abundant until about 1960 (Greer 1965). Since its introduction to central Chile the European rabbit has produced a pronounced change in the spatial distribution of some native herbs (Jaksic & Fuentes 1980), and has caused considerable mortality among seedlings of introduced pines and native shrubs (Pine et al. 1979, Fuentes et al. in press). These deleterious effects seem to be directly related to the foraging behavior of the European rabbit in central Chile. In Spain rabbits restrict their foraging activities to areas beneath or near the shelter of shrubs (Rogers 1978, Rogers & Myers 1979, 1980), but in central Chile they feed in open spaces between shrubs—at least the adult ones— (Jaksic et al. 1979a, 1979b, Simonetti & Fuentes 1982). In addition, rabbits in Chile and Spain differ in their use of the available shrub cover when considered on a macroscopic scale. According to Jaksic & Soriguer (1981) the greatest activity (or abundance) of rabbits in Chile is observed in habitat patches with 20-30% shrub cover (open matorral), whereas in Spain they are most active (or abundant) in patches with 70-80% shrub cover (dense matorral). It has been suggested that foraging under or close to cover is a result of strong predation pressure upon rabbits in Spain (Soriguer 1979, Delibes 1980), whereas foraging in the open may be a consequence of weaker predation pressure. Reduced predation might thus allow rabbits in central Chile to forage safely in the open spaces, where their food supply

(herbs) appears to be most abundant, rather than closer to shrubs where the numerous native rodents concentrate their foraging activities (Jaksic et al. 1979a, 1979b). The food supply for rabbits in Spain probably is more plentiful in open areas away from shrubs, and so their microhabitat preference is apparently based on shelter rather than food (Rogers & Myers 1979).

Jaksic et al. (1979a, 1979b), based on semiquantitative information suggested that the tendency of rabbits in central Chile to forage far from refuges (as if they were predator-free) is related to the ineffectiveness of local predators in hunting for a recently introduced prey. Jaksic & Soriguer (1981) surveyed the food habits of potential rabbit predators in Chile and Spain and found that predation upon rabbits appears negligible in Chile compared to Spain. Predation levels were estimated by the overall contribution of rabbits to the diets of all predator species occurring in the two regions. Jaksic & Soriguer (1981) also found that this result is not attributable to differences in the statistical location of predator body sizes in Chile and Spain, but more likely is related to the higher densities of alternative prey (rodents) and the lack of long-term association (co-adaptation) between predators and rabbits in Chile.

Implicit in the statements of Jaksic & Soriguer (1981) are two assumptions; 1) that predation pressure upon rabbits can be estimated from the average contribution of rabbits as prey to all the predator species present in a given region, and 2) that if co-adaptation in ecological time is the main agent in determining levels of predation on rabbits, the importance of rabbits as prey should be similar in areas where local predators have a long-term association with native rabbits. We test both assumptions using California rabbits as models.

California rabbits (*Sylvilagus audubonii* Baird 1857 and *Sylvilagus bachmani* Waterhouse 1838) appear to be adequate subjects for the proposed comparative study. They inhabit scrub areas (= chaparral) that have been shown to be ecologically similar to those in Chile and Spain (they are called "mediterranean-type" shrublands; see di Castri and Mooney 1973, Cody and Mooney 1978). Also, their habitat use patterns are quite similar to those of Spanish rabbits. Unlike rabbits in Chile, California rabbits restrict their habitat use to the vicinity of potential shrub refuges (Bartholomew 1970), and they are found almost exclusively in dense chaparral areas (Orr 1940, Ingles 1941, Fitch 1947b, Biswell et al. 1952, Connell 1954, Chapman 1974, Chapman & Willner 1978). Indeed, the common name of *S. bachmani* is "brush rabbit". Judging from observations by Orr (1940), Bartholomew (1970), Chapman (1974), and Chapman and Willner (1978), the "preference" of California rabbits for heavy brush is more likely to be related to predator avoidance than to other factors. Supporting evidence comes from the fact that on Año Nuevo Island (off the California coast) *S. bachmani* (introduced from the mainland in 1949) extends its habitat use to include areas far from the brush (Zoloth 1969), just as rabbits do in central Chile. Chapman (1974) attributes this phenomenon to the smaller number of predators on the island as compared to the California mainland.

All of these accounts suggest that the patterns of habitat use by rabbits in physiognomically similar regions of Chile, Spain, and California are affected by local predation pressures. Rabbits presumably subjected to high predation pressure (Spanish *O. cuniculus*, California mainland *Sylvilagus* spp.) are found in dense shrub patches and restrict their foraging activities to the vicinity of protective shrubs. Rabbit populations that supposedly experience low or mild predation pressure (Chilean *O. cuniculus*, California insular *S. bachmani*), are found in open scrub patches and forage in areas away from shrubs. It is significant that populations that exhibit expansion of habitat use are recent colonizers and have

conspecific counterparts with restricted habitat use. These behavioral changes are consequently more likely related to proximal ecological factors such as predation pressure than to ultimate factors such as genetic differentiation of populations.

Here we compare the incidence of rabbits as prey in the mediterranean-type shrublands of Chile, Spain, and California in order to assess whether consumption of rabbits is more similar between regions where this prey has a long-term association with its predators (Spain and California mainland), than either is with an area where it has recently been introduced (Chile). In order to minimize the sources of variation, we scrutinize only one locality in each of the three regions instead of pooling data from many places (as Jaksic & Sorriquer 1981, did). With this procedure we eliminate the problem of giving equal weight to information obtained in localities where rabbit abundance may differ markedly, and gain the advantage of knowing the food habits of predators in sites where all of them are of known occurrence and residence status, and presumably exploit the same rabbit populations. In fact, the only study sites with the characteristics stated are: La Dehesa-Los Dominicos (Santiago Province, central Chile; described in Jaksic et al. 1981); Marismas del Guadalquivir (Huelva Province, southern Spain; described in Valverde 1967); and San Joaquin Experimental Range (Madera County, central California; described in Talbot et al. 1942).

Other lagomorphs present in these localities are *Lepus capensis* Linnaeus 1758 in both Chile (introduced) and Spain (native), and *Lepus californicus* Gray 1837 in California. We do not include these species in the analysis because: 1) *L. capensis* is very rare in La Dehesa-Los Dominicos and apparently is not preyed upon at all there (Jaksic et al. 1981); *L. capensis* is somewhat uncommon in Marismas del Guadalquivir and significantly preyed upon only by Imperial Eagles (5.3% of their diet is made of *L. capensis*; see Valverde 1967); *L. californicus* "...is rare on the Range" (Horn & Fitch 1942: 104), and its only potential predator in this locality are Golden Eagles,

which "occasionally occur on the area, but are not known to nest there" (Horn & Fitch 1942: 99). 2) The pattern of habitat use and escape response of these *Lepus* spp. is markedly different from that of rabbits (both *Oryctolagus* and *Sylvilagus*). *Lepus* spp. forage in the open and do not run for cover when threatened by predators (see Housse 1953, Valverde 1960, Lechleitner 1958, for behavioral observations in Chile, Spain, and California, respectively). This behavior does not allow an independent assessment of the efficacy of predation upon *Lepus* spp. (as is the case for rabbits), because they are found in the open whatever the intensity of predation.

MATERIAL AND METHODS

Nomenclature of predators follows Brown & Amadon (1968) for falconiforms; Clark et al. (1978) for strigiforms; Osgood (1943) and Peters & Orejas-Miranda (1970, as modified by Thomas 1977) for Chilean carnivores and snakes, respectively; Corbet (1978) and Arnold & Burton (1978) for Spanish carnivores and snakes, respectively; Burt & Grossenheider (1976) and Stebbins (1966) for Californian carnivores and snakes, respectively.

Food habits of most of the resident predatory species in La Dehesa-Los Dominicos (central Chile) are documented by Jaksic et al. (1981). The diets of *Felis guigna* and *Milvago chimango* in the locality are here assumed not to be different from those reported by Jaksic & Soriguer (1981) and Yáñez et al. (1982) for nearby areas. No dietary information is available for the carnivore *Grison cuja* (which is of rare occurrence in the locality). Mean weights of adult-sized predators are taken from Jaksic & Soriguer (1981), Jaksic et al. (1981), Yáñez et al. (1982), and Greene & Jaksic (unpublished). Food habits and occurrence of resident predatory species in Marismas del Guadalquivir (southern Spain) are reported by Valverde (1967). Complementary information on diets is taken from Jaksic & Soriguer (1981). No food data are available for the carnivore *Mustela nivalis* (which is very scarce in the locality), or for

the falconiform carrion-eater *Gyps fulvus*. Mean weights of adult-sized predators are taken from Hiraldo et al. (1975) and Jaksic & Soriguer (1981). Occurrence of predator species in San Joaquín Experimental Range (central California) is taken mainly from Horn & Fitch (1942). Food habits of resident predatory species are documented by Fitch (1941, 1947a, 1947b, 1948, 1949), Fitch & Twining (1946), and Fitch et al. (1946a, 1946b). The diets of *Taxidea taxus*, *Lynx rufus*, *Otus asio*, and *Falco sparverius* are here assumed not to differ from those reported by Leach & Frazier (1953), Ross (1969), and Balgooyen (1976) from other nearby chaparral localities where rabbits are present. No food information is available for the strigiform *Asio otus*. Although the carnivores *Mephitis mephitis*, *Mustela frenata*, and *Procyon lotor* are also recorded from the area, they are very scarce (Horn & Fitch 1942), casting doubt about their status as residents. The Golden Eagle, *Aquila chrysaetos* occasionally occurs in the area but is not a resident either (Horn & Fitch 1942). The snakes *Diadophis punctatus* and *Thamnophis sirtalis* are also very scarce in the locality (Fitch 1949) and are not included in the analysis. Weight data are taken mainly from Fitch's papers cited above, complemented with information reported by Balgooyen (1976), Burt & Grossenheider (1976), and Jaksic et al. (1982), or recorded from specimens preserved in the Museum of Vertebrate Zoology. Only one species of rabbit is present in San Joaquín Experimental Range, *Sylvilagus audubonii* (Fitch 1947b).

Because vertebrates are the staple prey for the majority of the predators in the three localities surveyed, we compute the incidence of rabbits as prey as percentage of the number of vertebrates in the diet of each predator species. In this way we estimate the importance of different predators as consumers of rabbits and, summing up over all species, the contribution of rabbits as prey to the complete predator assemblages. The Kruskal-Wallis one-way analysis of variance (Siegel 1956: 185) is used to test for differences in the statistical location of predator weights in the three me-

diterranean areas. Correlation analyses are performed with the Spearman rank correlation coefficient, and their significance evaluated through *t*-transformation of the coefficients using two-tailed tests (Siegel 1956: 204, 212). Linear regressions were performed between the angular-transformed proportions of rabbits in the predators' diets and natural logarithms of their body weights (independent variable), for each of the areas.

RESULTS

Chile-Spain comparisons

The qualitative and natural history aspects of predation upon rabbits in the matorral areas of Chile and Spain are discussed by Jaksic & Soriguer (1981). Here we concentrate on the quantitative aspects of the comparison. Based on their regional survey, Jaksic & Soriguer (1981) show that the role of rabbits as prey is less important in Chile than in Spain, despite the fact that the median size of predator species in the two regions is statistically identical. Both claims are supported by our higher resolution analysis: percent dietary composition of rabbits per predator species is smaller in the Chilean locality (*z*-transformed $U = 1.817$; $P < 0.04$, 1-tailed test), but the median predator size is not significantly different between the localities in Chile and Spain (*z*-transformed $U = 0.685$; $P > 0.49$, 2-tailed test). Thus, the contention of Jaksic et al (1979a, 1979b) and Jaksic & Soriguer (1981) that the low importance of rabbits as prey in Chile is related to the lack of long-term association between predators and this prey is not falsified by analysis at the local level of resolution.

Qualitative comparisons among Chile-Spain-California

Mean proportion of the diet represented by rabbits, averaged over all predator species, is lowest in Chile, intermediate in California, and highest in Spain (Table 1). The same tendency is observed at the level of the falconiform subsets. This might be considered a result of the presence in Spain

of two very large raptors (*Aegypius monachus* and *Aquila heliaca*) that include a large proportion of rabbits in their diet and lack size-counterparts in both Chile and California. However, this explanation is not verified in other cases. Congeneric counterparts of similar size are present in Chile (*Buteo polyosoma*), Spain (*B. buteo*), and California (*B. jamaicensis*), and still rabbit consumption is greater for the Spanish raptor (22.0% of its diet), than for its Chilean (6.1% rabbit) or Californian (9.3% rabbit) congeners. Moreover, the imperial eagle (*A. heliaca*) is an endangered species represented by only a few individuals in the Spanish locality (Rogers & Myers 1980), and consequently its overall effect on rabbit populations should be relatively small. In sum, size per se does not completely explain the greater average consumption of rabbits by the Spanish falconiforms. Rabbit predation by carnivores shows the same trend with Spain, California, and Chile ranking from highest to lowest. Although it is tempting to speculate that the Chilean carnivore assemblage uses rabbits in low proportion because it lacks adequate size-counterparts for Spanish and Californian canids, felids, and mustelids, the reason appears not to be that simple. In fact, the Chilean red fox (*Dusicyon culpaeus*), whose weight is about half that of the Californian coyote (*Canis latrans*), preys on rabbits in very similar proportion (19.7% versus 19.3%). On the other hand, the similar-sized Spanish red fox (*Vulpes vulpes*) includes rabbits in its diet in about double (37.0%) the proportion reported for *D. culpaeus*. Also, the Spanish lynx (*Felis lynx*) consumes 60.7% rabbit prey, whereas the similar-sized Californian counterpart (*Lynx rufus*) totals only 27.8% rabbits in its diet. With respect to mustelids, the small Spanish polecat (*Mustela putorius*) includes more than twice as many rabbits in its diet as the large Californian badger (*Taxidea taxus*)—30.0% versus 12.5%. A partial reversal of the overall trend is observed in the strigiform subsets, which in Chile and California have similar rabbit consumption levels, both being higher than Spain. This is clearly related to the absence of the eagle owl (*Bubo bubo*) from the Spanish locality, which is a vor-

TABLE 1

Percent representation of rabbits (by number) in the vertebrate prey of different predator species in mediterranean habitats of Chile, Spain, and California. WT = mean weight of adult-sized predators; % RABB = percent of the total number of vertebrate prey (= VERT) that are rabbits. Partial means and sample sizes (n) in parentheses; N = total sample size.

Representación porcentual numérica de conejos entre las presas vertebradas de diferentes especies de depredadores en hábitats mediterráneos de Chile, España y California. WT = Peso promedio de depredadores al tamaño adulto. % RABB = Porcentaje del número total de presas vertebradas (= VERT) que está constituido por conejos. Promedios parciales y tamaños muestrales parciales (n) entre paréntesis N = tamaño muestral total.

PREDATORS	WT (g)	CHILE		SPAIN		CALIFORNIA	
		% RABB	VERT	% RABB	VERT	% RABB	VERT
Falconiformes	—	(4.4; n=6)		(23.8; n=11)		(4.7; n=3)	
<i>Accipiter cooperii</i>	332	—	—	—	—	4.8	42
<i>Aegypius monachus</i>	10000	—	—	40.3	1191	—	—
<i>Aquila heliaca</i>	3000	—	—	64.8	375	—	—
<i>Buteo buteo</i>	950	—	—	22.0	59	—	—
<i>Buteo jamaicensis</i>	1092	—	—	—	—	9.3	4148
<i>Buteo polyosoma</i>	960	6.1	391	—	—	—	—
<i>Circaetus gallicus</i>	2000	—	—	8.3	12	—	—
<i>Elanus leucurus</i>	300	0.0	151	—	—	—	—
<i>Falco peregrinus</i>	816	—	—	0.0	81	—	—
<i>Falco sparverius</i>	a	0.0	125	—	—	0.0	b
<i>Falco subbuteo</i>	208	—	—	0.0	19	—	—
<i>Falco tinnunculus</i>	200	—	—	0.0	72	—	—
<i>Geranoaetus melanoleucus</i>	2000	18.8	170	—	—	—	—
<i>Hieraaetus pennatus</i>	800	—	—	33.3	12	—	—
<i>Milvago chimango</i>	294	0.0	43	—	—	—	—
<i>Milvus migrans</i>	1000	—	—	42.9	366	—	—
<i>Milvus milvus</i>	1000	—	—	32.3	99	—	—
<i>Neophron percnopterus</i>	2000	—	—	18.1	249	—	—
<i>Parabuteo unicinctus</i>	890	1.2	172	—	—	—	—
Strigiformes	—	(5.4; n=3)		(1.5; n=3)		(7.3; n=3)	
<i>Athene cucularia</i>	250	0.5	633	—	—	—	—
<i>Athene noctua</i>	150	—	—	4.3	23	—	—
<i>Bubo virginianus</i>	c	15.8	114	—	—	21.0	1039
<i>Otus asio</i>	147	—	—	—	—	0.0	29
<i>Otus scops</i>	69	—	—	0.0	d	—	—
<i>Tyto alba</i>	e	0.0	599	0.2	1342	0.8	513
Carnivora	—	(9.9; n=2)		(25.3; n=7)		(17.7; n=4)	
<i>Canis latrans</i>	15500	—	—	—	—	19.3	1954
<i>Dusicyon culpaeus</i>	8600	19.7	319	—	—	—	—
<i>Felis guigna</i>	2230	0.0	4	—	—	—	—
<i>Felis lynx</i>	11000	—	—	60.7	28	—	—
<i>Felis silvestris</i>	7500	—	—	22.0	b	—	—
<i>Genetta genetta</i>	1600	—	—	0.0	10	—	—
<i>Herpestes ichneumon</i>	7500	—	—	22.0	50	—	—
<i>Lynx rufus</i>	11200	—	—	—	—	27.8 ^f	90
<i>Meles meles</i>	16000	—	—	5.1	811	—	—
<i>Mustela putorius</i>	850	—	—	30.0	b	—	—
<i>Taxidea taxus</i>	8500	—	—	—	—	12.5 ^f	8
<i>Urocyon cinereoargenteus</i>	4500	—	—	—	—	11.2	98
<i>Vulpes vulpes</i>	8000	—	—	37.0	273	—	—

PREDATORS	WT (g)	CHILE		SPAIN		CALIFORNIA	
		% RABB	VERT	% RABB	VERT	% RABB	VERT
Serpentes	—	(1.4; n=2)		(1.5; n=5)		(2.9; n=5)	
<i>Coronella girondica</i>	30	—	—	0.0	6	—	—
<i>Crotalus viridis</i>	300	—	—	—	—	10.2	285
<i>Elaphe scalaris</i>	196	—	—	5.3	19	—	—
<i>Lampropeltis getulus</i>	280	—	—	—	—	0.0	14
<i>Malpolon monspessulanus</i>	445	—	—	2.4	82	—	—
<i>Masticophis lateralis</i>	150	—	—	—	—	0.0	7
<i>Natrix maura</i>	50	—	—	0.0	60	—	—
<i>Philodryas chamissonis</i>	96	2.7	37	—	—	—	—
<i>Pituophis melanoleucus</i>	500	—	—	—	—	4.2	72
<i>Tachymenis peruviana</i>	22	0.0	46	—	—	—	—
<i>Thamnophis couchi</i>	92	—	—	—	—	0.0	85
<i>Vipera Jatasti</i>	40	—	—	0.0	15	—	—
Mean Consumption/ Predator		5.0 (N=13)		17.4 (N=26)		8.1 (N=15)	

- a Chile = 120g; California = 111g
- b Sample size not reported, but substantial
- c Chile = 1500g; California = 1155g
- d Preys only on invertebrates
- e Chile = 310g; Spain = 280 g; California = 442 g
- f Some *Lepus californicus* are included in this figure.

cious consumer of rabbits elsewhere in Spain (Jaksić & Soriguer 1981, and references therein). Finally, snake predation upon rabbits appears more similar between Chile and Spain, and greater in California. This does not seem related to the presence of any particularly large species in the California locality, but to the fact that the only large venomous species is found here (*Crotalus viridis*). It is likely that this snake is more effective in preying on rabbits because the injection of venom allows it to subdue relatively large prey (Fitch & Twining 1946).

Quantitative comparisons among Chile-Spain-California

The mean incidence of rabbits as prey is not associated with corresponding differences in the configuration of predator sizes present in the three mediterranean localities. No statistically significant difference is detected in the median predator weights (on a species basis) in the study areas ($H = 0.377$; $df = 2$; $P > 0.82$). Statistically sig-

nificant coefficients are obtained between the predators' size and percent representation of rabbits in their diet in Chile ($r_s = 0.559$; $df = 11$; $P < 0.05$), Spain ($r_s = 0.699$; $df = 24$; $P < 0.001$), and California ($r_s = 0.907$; $df = 13$; $P < 0.001$). Because all the coefficients are positive, this indicates that larger predators are heavier consumers of rabbits than are smaller predators. Because adult rabbits are relatively large prey (*O. cuniculus* = 1300 g in Chile, 1100 g in Spain; *S. auduboni* = 800 g), it is likely that small predators are not as capable as larger ones in handling this prey and therefore have access to only a fraction of the total rabbit populations (i.e., juveniles). In fact, Simonetti & Fuentes (1982) have shown that juvenile rabbits in Chile are preyed upon to a larger extent than are adults. However, predation upon juvenile rabbits in Chile is still very low in comparison to similar-sized native rodents (Simonetti & Fuentes 1982). This gives further support to the contention that size per se does not prevent Chilean predators from preying on rabbits of whichever age, but something else.

Although positively correlated, the relative importance of rabbits as prey according to predators' size differs among sites. In Spain, the equation describing the angular-transformed representation of rabbits (dependent variable) in relation to the natural logarithm of body weight of local predators is $y = -24.95 + 6.60x$ ($r^2 = 0.472$), whereas in Chile $y = -19.20 + 4.47x$ ($r^2 = 0.450$), and in California $y = -24.20 + 5.59x$ ($r^2 = 0.735$). A gradient is observed in both intercept and slope of the three regression lines, with Spain exhibiting the greatest, California intermediate, and Chile the smallest figures. This means that, for a given size, predators include relatively high, intermediate, or low proportions of rabbits in their diet in Spain, California, and Chile, respectively. Whether this trend represents a gradient of coadaptive adjustment between predators and rabbits is an interesting question that we cannot presently answer.

The mean incidence of rabbits as prey, averaged over all predator species in California (8.1%) falls closer to that in Chile, considering that the midpoint between Chile and Spain is 11.2% (see Table 1). Owing to its rather intermediate status, California data on predation levels do not differ significantly from either Chilean or Spanish figures. Consequently, the expectation that the importance of rabbits as prey should be more similar between Spain and California than with Chile is not met.

DISCUSSION

Rabbits in Chile behave as if they are predator-free, but rabbits in both Spain and California do not. Whereas rabbits in Chile forage far from protective shrubs and choose very sparse habitat patches, in both Spain and California they restrict their activities to the vicinity of protective vegetation and select habitat patches of greater cover. The restricted habitat use of Spain and California rabbits does not coincide with food abundance, and does not appear to be a result of competition (see Bartholomew 1970, Rogers & Myers 1979). The most likely explanation for the difference in habitat use between native and intro-

duced rabbit populations is the different predation pressure to which those populations are subject. Jaksic & Soriguer (1981) attempted to test the hypothesis that predation pressure on rabbits in Chile is weaker than it is on rabbits in Spain by calculating the mean proportion of predator diets represented by rabbits and averaging over all predator species. They found that predators in Spain include a higher proportion of rabbits in their diets than do predators in Chile, and concluded that this supports their hypothesis. They further asserted that the lack of long-term association between rabbits and predators in Chile is responsible for these results. We decided that this assertion could be tested by examining predation levels upon rabbits in California. These animals have had a long-term association with the local predator assemblage and their refuging behavior is similar to rabbits in Spain. For consistency we followed the methods of Jaksic & Soriguer (1981) in determining predation levels. Consequently, our results would indicate that rabbits in California sustain a low level of predation, similar to that on rabbits in Chile. This would appear to reject the hypothesis of Jaksic & Soriguer, and creates an apparent paradox between low predation as measured and the refuging behavior observed in *Sylvilagus*. We believe, however, that Jaksic & Soriguer's hypothesis should not be rejected because it still is the best one available, and that no paradox really exists, due to the inadequacy of the methods proposed by Jaksic & Soriguer (1981) to examine predation pressure.

The unweighted mean incidence of rabbits in the diets of local predator assemblages does not necessarily measure predation pressure, which is the proportion of a rabbit population that is taken by the set of local predators. The densities of predators or rabbits within the localities examined have not been compared and consequently the relative predation pressure upon rabbits in any of the three areas cannot be assessed. On the one hand, if densities of predators in California are high, then predation pressure may be high despite the fact that each predator species includes

a small number of rabbits in its diet. Unfortunately, the densities of predators in these localities are not known. On the other hand, if the density of rabbits in the California locality is low, and given the proportion of it represented in our calculations, predation pressure may actually be high. In fact, yearly mean densities of rabbits range between 1.0 and 36.6 rabbits/hectare in different parts of Huelva Province in Spain (R.C. Soriguer, personal communication), whereas densities in San Joaquín Experimental Range, in California, range between 1.0 and 2.1 rabbits/hectare (Fitch 1947b). No quantitative estimates are available for the abundance of rabbits in the Chilean site, but judging from reports about their agricultural-pest status (Greer 1965, Pine et al. 1979, Jaksić & Soriguer 1981), their density probably exceeds that of the Spanish locality. Thus, although the calculated value of "predation pressure" in California is low, it may indeed indicate that a large proportion of the rabbit population is preyed upon in comparison to Spain or, especially, to Chile.

In order to explain the paradox of California rabbits in light of Jaksić & Soriguer's (1981) hypothesis it could be advanced that the low incidence of California rabbits in predator diets is due to the greater availability of alternative prey. In fact, Jaksić & Soriguer (1981) produced quantitative information supporting the claim that the availability of alternative prey (rodents) is greater in Chile than in Spain, thus explaining the expanded habitat use by Chilean rabbits. This explanation, however, is inconsistent with the observations made by Glanz (1977) showing that alternative (rodent) prey is more abundant in California than in Chile. Thus, the incidence of California rabbits in predator diets should be lower than that of Chilean rabbits, but this is not the case.

Another possible explanation for the observed results is that, although rabbits in California and Spain both have conservative refuging behavior, different escape thresholds may affect the ease with which the two species are caught by predators. Rabbits of the genus *Sylvilagus* are far less social than *Oryctolagus* (see Orr 1940,

Lockley 1964, respectively). Also, both *Sylvilagus* species are smaller than *Oryctolagus*, and are consequently exposed to a broader spectrum of predators capable of killing and handling them (provided that the statistical differences in predator body sizes are not significant among the three regions). In consequence, the apparent lack of social aggregation in *Sylvilagus* spp., as well as their smaller size, may render these rabbits more susceptible to close approach by predators of a wider array of body sizes. These two factors could have favored a more conservative refuging behavior of *Sylvilagus*, thus resulting in strong escape responses even under light predation pressure. By this argument, the low incidence of California rabbits as prey is due to the more timid and secretive behavior of *Sylvilagus*, as compared to *Oryctolagus*. However, these differences in sociality have not been studied in reference to the escape response of either rabbit genus. Hence, the hypothesis of differential threshold in escape response between these rabbits remains little more than a plausible but untested story.

We conclude that Jaksić & Soriguer (1981) reached the right conclusion about relative predation pressure on rabbits in Chile and Spain, but for the wrong reasons. The inclusion of California rabbits in the comparison illustrates the shortcomings of their approach. Using their methods we have achieved results that must be explained by reference to either inconsistent or untested scenarios. It seems to us far more parsimonious and realistic to reject the idea that predation pressure can be measured by the mean incidence of rabbits in predator diets averaged over an assemblage of unknown density.

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