

## Predation upon Reptiles in Mediterranean Habitats of Chile, Spain and California: A Comparative Analysis

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**Summary.** Predation on reptiles at three Mediterranean-type habitat sites was assessed by computing the incidence of reptiles as a percentage of vertebrates in the diet of each predator species and the incidence of each reptile species as prey for the entire assemblage of predators at each locality. The overall importance of reptiles is lowest in Chile, intermediate in California, and highest in Spain. These differences do not appear to result from interlocality variation in the size distributions of predators or of prey. The incidence of particular reptile species as prey is correlated with their relative abundances in Spain and California, but not in Chile. Behavioral and morphological attributes evidently make some species more vulnerable to predation and others less so than their abundances would predict. Predation on the speciose lizard genus *Liolaemus* in Chile is sufficient to promote behavioral responses but not major morphological divergence.

### Introduction

It is widely recognized that predation can have important effects on local communities (Paine 1966; Connell 1975; Sousa 1979; Sousa et al. 1981), and perhaps on entire faunas (Moynihan 1971; Janzen 1976). Efforts to study these phenomena by global comparisons are severely hampered by our meager knowledge of diet in entire predator assemblages (Barbehenn 1973). Unfortunately, attempts to estimate comparative predation levels based on injury frequencies are subject to potential errors of interpretation (Greene 1973; Schoener 1979; Jaksic and Fuentes 1980; Schoener and Schoener 1980). These problems are circumvented to the extent that actual predation can be assessed in all (or at least most) of the predators at a site. When several such studies are comparable the search for repeated patterns can begin. Here we examine the utilization of reptiles as prey by predators in comparable mediterranean habitats of Chile, Spain, and California. We chose reptiles as the focus of this analysis because their role as food resources for predators is less well understood than that of small mammals and birds (Andersson and Erlinge 1977; Calderón 1977; Glue and Morgan 1977; Jaksic and Soriguer 1981; but see Wunderle 1981), and also because by restricting our study to reptiles we can concentrate on finer details of taxonomic resolution. In addition, Chilean reptiles provide an intriguing case when compared to the two other mediterranean areas. In Chile, lizard species diversity is the greatest (but almost all belong to the single genus *Liolaemus*; see Jaksic et al.

1980 for a synopsis of the literature), and snake diversity is the lowest, with only two species in most of the country (Greene and Jaksic, ms.). At least in this sense, Spain and California appear more similar to each other than to Chile and it seems interesting to assess the degree to which this situation affects overall predation levels, and viceversa.

Mediterranean-type ecosystems converge in a number of ecological attributes, ranging from vegetational physiognomy to community structure of birds, small mammals, lizards, and other groups (di Castri and Mooney 1973; Mooney 1977; Thrower and Bradbury 1977; Cody and Mooney 1978). However, in a comparative analysis of the predator assemblages present in the mediterranean habitats of Chile and Spain (which included diurnal and nocturnal birds of prey, carnivores, and snakes), some marked differences were demonstrated at this trophic level (Jaksic and Soriguer 1981). They mainly involved the species richness and diversity of predators, which affected dramatically the use of rabbits (*Oryctolagus cuniculus*) as prey. This suggests that the composition of predatory assemblages – in both number and type of species – may be an important factor affecting the levels of consumption of different prey resources. In order to minimize the sources of variation, we analyze only one locality of each mediterranean area instead of pooling data from many places, as Jaksic and Soriguer (1981) did in the case of the rabbits. This procedure eliminates the problem of giving equal weight to information obtained in sites where reptile abundance is different, and gains the advantage of studying trophic relationships in localities where all the predators exploit prey populations of known occurrence.

### Material and Methods

**Predator/Prey Assemblages, Predation, and Species Weights.** The only sites with appropriate quantitative information on both predators and reptile prey species are: La Dehesa-Los Dominicos (central Chile), described in Jaksic et al. (1981a); Marismas del Guadalquivir (southern Spain), described in Valverde (1967); and San Joaquin Experimental Range (central California), described in Talbot et al. (1942). Occurrence of predators with known food habits in these three mediterranean localities, and the corresponding reptile species available are reported in Tables 1 and 2, respectively. Snakes are considered both as predators and as prey. Food habits of most of the resident predatory species in La Dehesa-Los Dominicos were documented by Jaksic et al. (1981a). No dietary information was available for the carnivores *Felis guigna* and *Grison cuja* (it is unclear if they were actually present in this locality), or for the carrion-eating falconi-

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form *Milvago chimango*. Occurrence of reptile prey species in the area is based on Sage (1973) and personal observations of FM Jaksic and HW Greene. Mean weights of adult-sized predators were taken from Jaksic et al. (1981a) and Greene and Jaksic (ms.), and weights of lizards were recorded from fresh adult specimens collected in the general area. Food habits and occurrence of resident predator and reptile prey species in Marismas del Guadalquivir were reported by Valverde (1967). Quantitative dietary information was not available for the carnivores *Felis silvestris*, *Herpestes ichneumon*, *Meles meles*, *Mustela nivalis*, *Mustela putorius*, or *Vulpes vulpes* (most of which were apparently very scarce in the locality), nor for the falconiform carrion-eaters *Aegypius monachus*, *Gyps fulvus*, or *Neophron percnopterus*. Mean weight of adult-sized predators and reptile prey were taken from Jaksic and Soriguer (1981) and Hiraldo et al. (1975). In contrast to Chile and California, squamates alone do not constitute all the reptile prey available in southern Spain. The chelonians *Emys orbicularis*, *Mauremys leprosa*, and *Testudo graeca* are present but apparently not consumed by local predators, and therefore are not included in Table 2. Occurrence of predators and reptile species in San Joaquin Experimental Range was taken mainly from Horn and Fitch (1942). Food habits of resident predatory species were obtained from Fitch (1941, 1947a, b, 1948, 1949), Fitch and Twining (1946), and Fitch et al. (1946a, b). Resident predators for which no food information was available were the carnivores *Taxidea taxus* and *Lynx rufus*, the falconiform *Falco sparverius*, and the strigiforms *Asio otus* and *Otus asio*. Although the carnivores *Mephitis mephitis*, *Mustela frenata*, and *Procyon lotor* were also recorded from the area, they were very scarce (Horn and Fitch 1942), which casts doubt about their status as residents. Also very rare were the ring-necked snake *Diadophis punctatus*, with only two specimens locally collected between 1938–1947 (Fitch 1949:514, 569), and the garter snake *Thamnophis sirtalis*, much scarcer than the congeneric *T. couchi*, (Fitch 1949:567). Weight data were taken mainly from Fitch's papers cited above, supplemented by information reported by Jaksic et al. (1981b) and Burt and Grossenheider (1976), or recorded from specimens preserved in the Museum of Vertebrate Zoology (University of California, Berkeley).

We computed the incidence of reptile prey (all species pooled) as a percentage of the number of vertebrates in the diet of each predator species, and also the incidence of each reptile species as prey of the entire predator assemblage in each locality. With the first type of information we estimate the importance of different predators as consumers of reptiles, and with the latter, the importance of specific reptile prey as food resources for the three predator assemblages.

The Kruskal-Wallis one-way analysis of variance (Siegel 1956:185) was used to test for differences in the statistical distribution of predator and reptile prey weights in the three mediterranean areas. Correlation analyses were 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).

**Relative Prey Abundances.** Qualitative assessments of relative abundances of reptile species have been made by Valverde (1967) for the Spanish site, and by Fitch (1949) for the California locality, thus permitting correlation analysis between amount of predation and prey abundance. Also, abundance estimates can be made for the reptiles in central Chile (FM Jaksic and HW Greene, personal observations), but we do not know how predation is distributed among the five local species of *Liolaemus*. We indirectly estimated predation levels upon these species based

on the population frequencies of tail breakage documented for *Liolaemus* spp. in central Chile (Jaksic and Fuentes 1980). We regard these figures as crude estimates of predation encounters (see Jaksic and Fuentes 1980 for a cautionary note), thus enabling the ranking of all reptile species in the study area according to both their estimated relative abundance and their contribution as prey to the local predator assemblage (see Table 2). Predation estimates were drawn from Table 2, partitioning the importance of *Liolaemus* species as prey according to the ranks indicated by data in Jaksic and Fuentes (1980). Spanish reptile species were given abundance ranks according to their description of very common, common, somewhat common, uncommon, or scarce, by Valverde (1967:23–57). These categories were ranked 1 through 5 and correlated with the amount of predation – ranked from highest to lowest – as reported in Table 2. California snakes were ranked in abundance following the ordinal scale reported by Fitch (1949:574). For lizards it was necessary to translate into ranks the categories most common, common, much less common given by Fitch and Twining (1946:64) and integrate them with other abundance specifications as reported by Fitch (1949:516). The abundance rankings of snakes and lizards were subsequently combined to render a single ordinal scale for reptiles as a whole in the California locality. Estimates of predation were drawn from Table 2.

Correlation analyses were performed with Spearman rank correlation coefficients, and their significance evaluated with *t*-transformation using two-tailed tests (Siegel 1956:204–212).

## Results and Discussion

### General Trends and Size Relationships.

The importance of reptiles as prey is lowest in Chile, intermediate in California, and highest in Spain (Table 1). The same tendency is observed at the level of the strigiform subset. A reversal of the trend is observed between California and Spanish data for the falconiform and carnivore subsets. The snakes also behave differently; their consumption of reptiles is similar in Chile and Spain, but remarkably low in California (Table 1). This fact is clearly associated with the much higher importance of mammalian prey for California snakes than for Chilean or Spanish ones (Fitch and Twining 1946; Fitch 1949; Valverde 1967; Jaksic et al. 1981a; Greene and Jaksic, ms.). In general, snakes are the chief predators of reptiles in both Chile and Spain, while in California it is the falconiforms that prey upon reptiles more heavily than any other predator subset (Table 1).

Overall levels of predation on reptiles are not associated with differences in the configuration of predator sizes present in the three mediterranean localities. No statistically significant difference was detected in the overall distribution of predator weights in the study areas ( $H=0.510$ ;  $df=2$ ;  $P>0.77$ ). Similarly, no statistically significant correlation coefficients were obtained between predator size and percent representation of reptiles in their diet for Chile ( $r_s=-0.427$ ;  $df=9$ ;  $P>0.19$ ), Spain ( $r_s=-0.159$ ;  $df=17$ ;  $P>0.51$ ), or California ( $r_s=-0.073$ ;  $df=9$ ;  $P>0.83$ ). Although it is suggestive that all the coefficients are negative, indicating that the importance of reptiles as prey varies inversely with predator size, the combined probabilities are still insignificant ( $\chi^2=5.041$ ;  $df=6$ ;  $P>0.26$ ; l-tailed test; see Sokal and Rohlf 1969:623). These results do not seem to be artifacts of combining into single samples predators of different morphology and, presumably, different hunting strategies. When correlation analyses were performed with predator orders having more than three component species (see Table 1), the same results

**Table 1.** Percent representation of reptiles (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; % REPT=percent of the total number of vertebrate prey (=VERT) that are reptiles. Partial means and sample sizes (*n*) in parentheses. *N*=total sample size

Predators	WT (g)	Chile		Spain		California	
		% REPT	VERT	% REPT	VERT	% REPT	VERT
Falconiformes	–	(3.8; <i>n</i> =5)		(20.1; <i>n</i> =9)		(43.0; <i>n</i> =2)	
<i>Accipiter cooperii</i>	332	–	–	–	–	64.3	42
<i>Aquila heliaca</i>	3,000	–	–	1.6	375	–	–
<i>Buteo buteo</i>	950	–	–	27.1	59	–	–
<i>Buteo jamaicensis</i>	1,092	–	–	–	–	21.6	4,148
<i>Buteo polyosoma</i>	960	0.3	391	–	–	–	–
<i>Circaetus gallicus</i>	2,000	–	–	83.4	12	–	–
<i>Elanus leucurus</i>	300	0.0	151	–	–	–	–
<i>Falco peregrinus</i>	816	–	–	0.0	81	–	–
<i>Falco sparverius</i>	120	9.3	125	–	–	–	–
<i>Falco subbuteo</i>	208	–	–	0.0	19	–	–
<i>Falco tinnunculus</i>	200	–	–	37.5	72	–	–
<i>Geranoaetus melanoleucus</i>	2,000	4.1	170	–	–	–	–
<i>Hieraaetus pennatus</i>	800	–	–	8.3	12	–	–
<i>Milvus migrans</i>	1,000	–	–	17.2	366	–	–
<i>Milvus milvus</i>	1,000	–	–	6.1	99	–	–
<i>Parabuteo unicinctus</i>	890	5.2	172	–	–	–	–
Strigiformes	–	(0.1; <i>n</i> =3)		(6.0; <i>n</i> =3)		(2.6; <i>n</i> =2)	
<i>Athene cunicularia</i>	250	0.2	633	–	–	–	–
<i>Athene noctua</i>	150	–	–	17.4	23	–	–
<i>Bubo virginianus</i>	<sup>a</sup>	0.0	114	–	–	4.2	1,039
<i>Otus scops</i>	69	–	–	0.0	<sup>b</sup>	–	–
<i>Tyto alba</i>	<sup>c</sup>	0.0	599	0.6	1,342	1.0	513
Carnivora	–	(4.7; <i>n</i> =1)		(5.0; <i>n</i> =2)		(12.0; <i>n</i> =2)	
<i>Canis latrans</i>	15,500	–	–	–	–	7.6	1,954
<i>Dusicyon culpaeus</i>	8,600	4.7	319	–	–	–	–
<i>Felis lynx</i>	11,000	–	–	0.0	28	–	–
<i>Genetta genetta</i>	1,600	–	–	10.0	10	–	–
<i>Urocyon cinereoargenteus</i>	4,500	–	–	–	–	16.3	98
Serpentes	–	(41.5; <i>n</i> =2)		(50.4; <i>n</i> =5)		(18.6; <i>n</i> =5)	
<i>Coronella girondica</i>	30	–	–	100.0	6	–	–
<i>Crotalus viridis</i>	300	–	–	–	–	9.2	285
<i>Elaphe scalaris</i>	196	–	–	10.5	19	–	–
<i>Lampropeltis getulus</i>	280	–	–	–	–	21.3	14
<i>Malpolon monspessulanus</i>	445	–	–	68.3	82	–	–
<i>Masticophis lateralis</i>	150	–	–	–	–	57.1	7
<i>Natrix maura</i>	50	–	–	0.0	60	–	–
<i>Philodryas chamissonis</i>	96	46.0	37	–	–	–	–
<i>Pituophis melanoleucus</i>	500	–	–	–	–	5.6	72
<i>Tachymenis peruviana</i>	22	37.0	46	–	–	–	–
<i>Thamnophis couchi</i>	92	–	–	–	–	0.0	85
<i>Vipera latasti</i>	40	–	–	73.3	15	–	–
Mean consumption/predator	–	9.7 ( <i>N</i> =11)		24.3 ( <i>N</i> =19)		18.9 ( <i>N</i> =11)	

<sup>a</sup> Chile=1,500 g; California=1,155 g

<sup>b</sup> Preys only on invertebrates

<sup>c</sup> Chile=310 g; Spain=280 g; California=442 g

prevailed. No significant correlations were demonstrated between predator size and reptile prey in the diet for either Chilean falconiforms ( $r_s = -0.300$ ;  $df=3$ ;  $P > 0.62$ ), Spanish falconiforms ( $r_s = 0.108$ ;  $df=7$ ;  $P > 0.78$ ), Spanish snakes ( $r_s = -0.600$ ;  $df=3$ ;  $P > 0.85$ ), or California snakes ( $r_s = 0.000$ ;  $df=3$ ;  $P > 0.99$ ). Note that by using *t*-transformed coefficients based on small sample size we are more likely to incur a type-I rather than type-II error; i.e., despite the power of the test used no significant figures are obtained. Taking into consideration this

information we can conclude that the size of the predator species and their size configuration in the three mediterranean localities do not directly determine levels of predation upon reptiles in the study areas. Consequently, if the predator-size factor can be considered constant in Chile, Spain, and California, it could be that differences of predation on the study sites are dependent on the statistical distribution of reptile prey sizes. If reptiles are larger on the average in any of the sites, they should appear more rewarding in energetic terms – all else being equal – to

**Table 2.** Percent representation (by number) of different reptile species in the combined diets of all predator species in mediterranean habitats of Chile, Spain and California. ABUND. RANK=rank given to each species within a given locality according to its relative abundance; higher ranks reflect greater abundance. WT=mean weight of reptilian species. Subtotals in parentheses

	ABUND. RANK	WT (g)	Chile % preyed	Spain % preyed	California % preyed
Amphisbaenia	–	–	(0.0)	(2.3)	(0.0)
<i>Blanus cinereus</i>	10	6	–	2.3	–
Sauria	–	–	(42.2)	(60.4)	(51.1)
<i>Acanthodactylus erythrurus</i>	3	6	–	11.5	–
<i>Callopistes maculatus</i>	6	82	0.0	–	–
<i>Chalcides bedriagai</i>	6.5	4	–	1.4	–
<i>Cnemidophorus tigris</i>	3.5	25	–	–	24.0
<i>Eumeces gilberti</i>	5.5	20	–	–	11.6
<i>Gerrhonotus multicarinatus</i>	11.5	38	–	–	0.8
<i>Lacerta lepida</i>	3	100	–	10.6	–
<i>Liolaemus chiliensis</i>	5	13	<sup>a</sup>	–	–
<i>Liolaemus fuscus</i>	3	2.5	<sup>a</sup>	–	–
<i>Liolaemus lemniscatus</i>	2	2.5	<sup>a</sup>	–	–
<i>Liolaemus monticola</i>	1	5.5	<sup>a</sup>	–	–
<i>Liolaemus tenuis</i>	4	4.5	<sup>a</sup>	–	–
<i>Liolaemus</i> sp. <sup>b</sup>	–	–	42.2	–	–
<i>Phrynosoma coronatum</i>	9.5	30	–	–	0.0
<i>Podarcis hispanica</i>	10	3	–	12.0	–
<i>Psammotromus algerius</i>	3	10	–	13.8	–
<i>Psammotromus hispanicus</i>	3	3	–	9.2	–
<i>Sceloporus occidentalis</i>	7.5	15	–	–	6.5
<i>Tarentola mauritanica</i>	12	8	–	0.5	–
<i>Uta stansburiana</i>	1.5	4	–	–	0.8
Unidentified Sauria	–	–	–	1.4	7.4
Serpentes	–	–	(57.8)	(37.3)	(48.9)
<i>Coronella girondica</i>	13	30	–	0.0	–
<i>Crotalus viridis</i>	1.5	300	–	–	8.2
<i>Elaphe scalaris</i>	10	196	–	0.5	–
<i>Hypsigena torquata</i>	5.5	13	–	–	0.1
<i>Lampropeltis getulus</i>	11.5	280	–	–	1.2
<i>Malpolon monspessulanus</i>	6.5	445	–	5.1	–
<i>Masticophis lateralis</i>	7.5	150	–	–	5.4
<i>Natrix maura</i>	3	50	–	8.3	–
<i>Philodryas chamissonis</i>	7	96	55.6	–	–
<i>Pituophis melanoleucus</i>	3.5	500	–	–	26.0
<i>Rhinocheilus lecontei</i>	13	91	–	–	0.1
<i>Tachymenis peruviana</i>	8	22	2.2	–	–
<i>Thamnophis couchi</i>	9.5	92	–	–	0.3
<i>Vipera latasti</i>	8	40	–	0.0	–
Unidentified Serpentes	–	–	–	23.4	7.6
Total reptilian prey	–	–	45	217	1,175

<sup>a</sup> Preyed upon in unknown proportion

<sup>b</sup> Either *L. chiliensis*, *L. fuscus*, *L. lemniscatus*, *L. monticola*, or *L. tenuis*

the “average” predator, thus contributing to higher consumption of reptilian prey in that locality. We explore this hypothesis with the same statistical tools used for the predator assemblages.

Using information in Table 2, no statistically significant difference is observed in the distributions of reptile weights – by species – among the three mediterranean areas ( $H=4.529$ ;  $df=2$ ;  $P>0.10$ ). Nor are significant correlations obtained between weight of reptile species and their respective contribution as prey in Chile ( $r_s=-0.196$ ;  $df=6$ ;  $P>0.64$ ), Spain ( $r_s=-0.288$ ;

$df=11$ ;  $P>0.34$ ), or California ( $r_s=0.283$ ;  $df=11$ ;  $P>0.34$ ). This lack of correlation suggests that reptile prey are not consumed by predators solely on the basis of their profitability as estimated by body weight. Separating lizards and snakes and performing new correlation analyses, the following results emerge (Chilean snakes are not included because  $df=0$ ; see Table 2): no significant correlation exists between lizard species weight and their incidence as prey in Chile ( $r_s=-0.671$ ;  $df=4$ ;  $P>0.14$ ), Spain ( $r_s=0.098$ ;  $df=5$ ;  $P>0.83$ ), or California ( $r_s=-0.214$ ;  $df=4$ ;  $P>0.68$ ). The results for snakes are not as consistent; while no significant correlation is obtained for Spain ( $r_s=0.675$ ;  $df=3$ ;  $P>0.60$ ), a highly significant one is observed in California ( $r_s=0.955$ ;  $df=5$ ;  $P<0.001$ ). This could result from predators in the California study site preying upon snakes in direct relation to their prey weight (i.e., according to the expected energetic reward). However, an alternative hypothesis is that larger snakes in the California site are more abundant (or catchable because of their greater visibility) than the smaller snakes. If this is the case, it would be more parsimonious to consider the correlation between snake weight and importance as prey, as a reflection of their relative abundance (or vulnerability) rather than a consequence of size selection by discriminative predators (see discussion in Jaksic et al. 1981a). This will be dealt with in the next section.

#### The Importance of Reptile Prey Abundance

The correlation between reptile species abundance in Chile, and their corresponding importance as prey to the local predator assemblage, is not significant ( $r_s=0.333$ ;  $df=6$ ;  $P>0.42$ ). The superabundant *Liolaemus* – which encompass the five highest ranks of abundance – appear neglected as prey when compared with the high proportion made by the scarce snake *Philodryas chamissonis* (abundance rank 7, where 8 is the lowest) in the diet of local predators.

Quite a different situation is observed in the two other mediterranean areas. A highly significant relationship is found between Spanish reptile prey abundance and their representation in the diet of local predators ( $r_s=0.683$ ;  $df=11$ ;  $P<0.01$ ). This indicates that the more abundant Spanish reptiles are preyed upon more heavily regardless of whether they are lizards or snakes. In the case of the California study site we also found a highly significant correlation between abundance of reptile species and their incidence as prey ( $r_s=0.779$ ;  $df=11$ ;  $P<0.002$ ). These results clearly suggest that reptiles in both the Spain and California study areas are represented in the diets of predator assemblages in much the same proportion as they are available.

#### Natural History Aspects of Predation upon Reptiles

Thus far, we have analyzed statistical patterns of predation. Here we discuss some ecological characteristics of the reptile prey that might render some species more vulnerable to predation.

Our information on Chilean reptiles is based on literature accounts and field observations by FM Jaksic and HW Greene. The lizards most preyed upon in the Chilean locality are the diurnal *Liolaemus*, which are the most abundant reptiles in the area. Based on population frequencies of tail breakage, Jaksic and Fuentes (1970) showed that predation levels were greater for species using elevated perches (either trees, shrubs, or rocks) than for ground-dwelling species. In the study area, Both *L.*

*fuscus* and *L. monticola* are strictly saxicolous lizard, *L. lemniscatus* is a grass-ground dweller, *L. chiliensis* is also a ground dweller but found in dense shrub patches and exhibiting some degree of arboreality, and *L. tenuis* is exclusively arboreal. Unfortunately, because *Liolaemus* prey were not identified to the species level in the predators' diets, we cannot assess how predation levels are partitioned among these five species.

The diurnally active teiid *Callopistes maculatus* is not preyed upon at all in the study site, and this is surprising for several reasons. This lizard is conspicuous because of its relatively large body size and gaudy coloration, and it moves extremely fast between shrubs in the sparsely vegetated stands it inhabits. Its activity temperature is high (40.2° C as compared to about 35° C for *Liolaemus* spp.; see Fuentes and Jaksić 1979b) and its minimum-distance escape response is elicited at about 15 m. Even though *C. maculatus* reaches high densities in some localities of central Chile (particularly in those with barren sandy soil and sparse shrub cover), it has never been reported in the diet of any predator in the region. A teiid in California, *Cnemidophorus tigris*, and a Spanish lacertid, *Lacerta lepida*, are ecological analogs of *C. maculatus* in terms of habitat preferences and escape behavior, but at least in some areas the former two lizards are heavily preyed upon (see Ohmart 1973 for *C. tigris*, and below for *L. lepida*).

The snake *Philodryas chamissonis* dwells in open vegetation patches, whereas the much less abundant *Tachymenis peruviana* is found associated with denser vegetation in the wettest areas of the locality; both species are presumably diurnal. The relative scarcity of *T. peruviana*, coupled with its rather restricted distribution, seems to render it less vulnerable to predation than *P. chamissonis*. However, the apparent high predation on this latter species is not directly related to its abundance, which is lower than that of *C. maculatus* and *Liolaemus* spp. in the study area. Perhaps the considerably larger body size of *P. chamissonis* (as compared to all *Liolaemus*), its selection of open habitat patches (as compared to *T. peruviana*), and its lower escape-agility (as compared to *C. maculatus*), render this species both a vulnerable and highly-rewarding prey for the local predators despite its relatively low abundance.

The following account of the ecological characteristics of reptile prey in the Spanish site is based mainly on Valverde (1967), and on field observations by HW Greene and SD Busack. The amphibaenian *Blanus cinereus* and the lizard *Chalcides bedriagai* share the lowest incidence in predators' diets as well as common habitat preferences (sandy soils) and fossorial habits. Their fossorial life, coupled with their reported low abundances, renders them relatively unavailable to predators. The rest of the lizards are subject to similar predation levels with the exception of the nocturnal *Tarentola mauritanica*, which is scarce and restricted to a single spot in the study area. All are apparently diurnal, but found in distinct habitats. *Acanthodactylus erythrus* chooses patches of sandy soil with little shrub cover and devoid of herbaceous vegetation. *Psammodromus algirus* (and presumably also *P. hispanicus*) is seemingly an ecological replacement of *A. erythrus* in that it also chooses sandy soils, but with dense shrub cover and a homogeneous herb layer. *Lacerta lepida* preferentially dwells in herbaceous patches with sparse shrub cover, and is also found under flat rocks, but rarely ventures into the open sand dunes where *A. erythrus* is found. *Podarcis hispanica* restricts its activities to trunks of *Quercus* sp. and surrounding areas, as well as on rock boulders. Despite their differential habitat selection, and judging from their similar representation in the diet of the local predator assemblage, none of these species seem to become especially vulnerable or safe

in any of these habitat patches. As documented above, it is their abundance that seems to be the proximate factor determining the predation levels upon these lizard species.

Two of the most preyed-upon snakes in the Spanish site, apart from their abundance, share little in common. *Malpolon monspessulanus* is strictly diurnal and found everywhere in the area, even hunting for *A. erythrus* in the open sand dunes. *Natrix maura* is of crepuscular habit and almost always found associated with ponds, lagoons, streams, and marshes. It seems to become especially vulnerable to predation when traversing land to reach other water bodies (Valverde 1967). The much less preyed-upon *Elaphe scalaris* shares some similarities in habitat use with *M. monspessulanus*, but it is found in areas of denser cover of shrubs and trees, frequently climbing up them, and is partially nocturnal. The two snake species that are seemingly not preyed upon also differ strikingly in habit. *Coronella girondica* is crepuscular and restricted to areas with dense shrub and herb cover. *Vipera latasti* is found everywhere in the locality, most frequently in the open sand dunes. It is nocturnal, climbing up trees and shrubs during the summer months. This is a venomous snake, which in part could explain its low representation in the diet of local predators. Apart from relative abundance, no single feature characterizes the snakes that are most or least preyed upon. Neither activity period, nor habitat selection seem to render these snakes particularly vulnerable to predators.

Information on the natural history of California reptiles is based on Fitch (1949), Stebbins (1954), and our field observations. *Cnemidophorus tigris* and *Phrynosoma coronatum* prefer open, sunny microhabitats, and depend on speed and crypticity plus spines, respectively, to escape predators. *Eumeces gilberti* and *Gerrhonotus multicarinatus* are much more secretive, and are capable of effectively biting and struggling free from predators. *Sceloporus occidentalis* and *Uta stansburiana* are relatively sedentary lizards that perch on ground objects in open areas. All of these species are diurnal, although *G. multicarinatus* is also sometimes active at night. It is noteworthy that the most important prey lizard, *C. tigris*, is the one that travels the greatest distance per activity period.

Of the snakes in the California study site, *Masticophis lateralis*, *Pituophis melanoleucus*, and *Thamnophis couchi*, are largely or completely diurnal. *Lampropeltis getulus* and *Crotalus viridis* are active both day and night, and *Hypsiglena torquata* and *Rhinocheilus lecontei* are normally nocturnal. Only *C. viridis* is venomous, but *P. melanoleucus* is perhaps a rattlesnake-mimic (Kardong 1980), *M. lateralis* bites readily, and both *L. getulus* and *R. lecontei* have offensive cloacal discharges (Lardie 1961; McCoy and Gehlbach 1967; Price and LaPointe 1981). Fitch (1949) noted that predators at the study site took *C. viridis* and *P. melanoleucus* in reverse order of their relative abundance, probably because of the venomous nature of the former and the size, visibility, and lack of speed of the latter. He also suggested that the relatively secretive habits of *L. getulus* might make it less vulnerable to predators.

#### *A Case Study of Predation upon Chilean Lizards*

Our results indicate that although the statistical distributions of body sizes are not different in either predator or prey assemblages of Chile, Spain, and California, the consumption of reptiles by predator species is comparatively very low in Chile. Moreover, while Spanish and Californian predators tend to include reptile prey in about the proportion of their abundance in the field, Chilean predators tend to neglect the superabundant *Liolaemus* lizards. Here we analyze the possible causes and effects of this phenomenon.

Jaksić et al. (1981a) examined the feeding ecology of predators in La Dehesa-Los Dominicos and found that they preyed upon small mammals in proportion to their abundance in the area, i.e., that they behave similarly to Spanish and Californian reptile-eaters. This suggests that Chilean predators respond “abnormally” to their reptile prey. A similar behavior was documented by Jaksić and Soriguer (1981) for Chilean predators when compared to their Spanish counterparts regarding consumption of rabbits. Jaksić and Soriguer (1981) showed that the predator assemblages in Chile and Spain do not differ in size configuration and concluded that the negligible predation upon rabbits by Chilean predators was related – among other things – to the greater abundance of alternative prey (mainly small mammals), which was shown to occur at higher densities in central Chile than in Spain. Interestingly, in comparative analyses of the feeding ecology of barn owls (*Tyto alba*) in Chile and Spain, Herrera and Jaksić (1980) and Jaksić et al. (1982) found that Spanish barn owls prey upon low-reward prey such as insects, amphibians and reptiles, probably because of the reduced densities of their preferred prey (small mammals). In contrast, Chilean barn owls prey almost exclusively on small mammals. These facts all seem to point to a single conclusion: Chilean predators can afford to ignore certain prey types (e.g., reptiles, rabbits) and rely on the great abundance of alternative prey (small mammals), at least in comparison to Spanish predators. This is not the whole story, however, as small mammal densities can also be high in California (see Glanz 1977) while reptile consumption remains relatively important. More research is needed to clarify the situation in California.

Whatever the cause for the low consumption that predators make of Chilean reptiles, the relatively well known central Chilean *Liolaemus* constitute a good subject from which to address the question of how predation may affect a particular reptile group. It has been claimed that predation is the main force driving the microhabitat segregation of *L. nigromaculatus* and *L. platei* (Fuentes and Cancino 1979), the contrasting escape responses of *L. fuscus* and *L. lemniscatus* (Jaksić and Núñez 1979), the replacement of *L. platei* by *L. lemniscatus* along a habitat gradient (Fuentes and Jaksić 1980), and the short-limbedness of *L. lemniscatus* in comparison to eleven other *Liolaemus* (Jaksić et al. 1980). A combined role of predation, microhabitat selection, and geologic events has been postulated by Fuentes and Jaksić (1979a) to explain the impressive species richness of the genus *Liolaemus* in Chile.

On the other hand, predation has been considered as playing but a minor role in the expression of sexual dimorphism in *Liolaemus* (Jaksić and Fuentes 1980). Also, the generalized morphology of central Chilean *Liolaemus* (excluding *L. lemniscatus*), despite broad differences in their microhabitat selection (open ground, rocks, shrubs, trees, etc.), could be interpreted as a relaxation of selective forces, particularly of predation. In this case, reduced predation pressure would impose little selection for “optimal” phenotypes, each specialized in the utilization of particular microhabitat categories. Finally, the intriguing problem posed by the ant-specialist *L. monticola* (see Fuentes and Ipinza 1979) could also be interpreted from the scope of reduced predation. Some other strictly myrmecophilous lizards (*Phrynosoma* and *Moloch*) share a bizarre phenotype (spiny body form, cryptic coloration and behavior), which has been assumed to be an antipredator adaptation (Pianka and Pianka 1970; Pianka and Parker 1975). Consequently, the generalized morphology of *L. monticola* could exemplify the situation of a myrmecophage subjected to negligible predation pressure (see Jaksić et al. 1979 and Greene 1981 for further discussion).

In summary, predation seemingly has an observable effect on *Liolaemus* in regard to behavioral patterns such as microhabitat selection and escape response, but it seems ineffective in promoting morphological divergence. This suggests that although predation pressure upon a certain group of organisms might be low, it still may be capable of shaping some of their phenotypic characteristics. As seen in *Liolaemus*, the phenotypic component that responds with greater plasticity (and perhaps more rapidly in evolutionary time) is behavior, very distantly followed by morphology. In the other two regions examined (Spain and California), predation is apparently greater in importance and the reptile fauna more diversified in both phylogenetic and morphological aspects. Whether predators influence diversity or diversity enhances predation is something that we cannot answer at this time.

### Concluding Remarks

The main weakness of our study is the absence of information on absolute densities of predator and prey species (see Case 1979). This is because predators are typically secretive (except for falconiforms) and reptiles are not customarily censused (see Turner 1977 for exceptions). However, we have credible estimates of the relative abundance of reptile prey species at the study sites and believe that the assessment of reptile predation in convergent ecosystems is sufficiently interesting to merit this approach. Two further problems warrant mention. First, there might be substantial mortality of reptiles that is not evident in our analysis. For example, Fitch (1949) reported that ground squirrels (*Spermophilus beecheyi*) killed – but did not eat – large numbers of young gopher snakes (*P. melanoleucus*). He also suggested that roadrunners (*Geococcyx californianus*, present but not studied at the California site) were important predators of *C. viridis* (but see Bryant 1916; Ohmart 1973). Second, caution must be used in examining these data for the importance of reptiles to predators. A prey taxon might be extremely important even if its overall representation in a predator’s diet is low, because of a seasonal or ontogenetic “bottleneck.” For example, at the California site reptiles make up only 9.2% of the prey of *C. viridis*, but a single lizard species (*Sceloporus occidentalis*) is the most important prey for juvenile rattlesnakes (Fitch 1949; HW Greene, unpublished).

Our results imply potentially great differences in the nature of predation on reptiles in three mediterranean-type ecosystems. It is clear that reptiles are important prey in Spain and California. Although relative abundance evidently affects predation levels, there are also indications of differential vulnerability. The situation in Chile is strikingly different, where lizards are abundant yet underrepresented in the diets of predators. We hope that these findings will stimulate similar research in other habitat types, and thereby contribute to a better understanding of predator/prey interactions and the factors influencing them.

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