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What do carnivorous predators cue in on: size or abundance of mammalian prey? A crucial test in California, Chile, and Spain

¿Qué pista usan los predadores carnívoros: tamaño o abundancia de micromamíferos? Una prueba crucial en California, Chile y España

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ABSTRACT

Studies of carnivorous predators that consume mammalian prey have often demonstrated functional responses of the former to changes in the profile of abundance/size of the latter. Researchers disagree on whether the functional responses observed relate to opportunistic or selective behavior of the predators with respect to their prey. Re-analyzing data by Jaksic *et al.* (1981) on small mammal predation in central Chile, Bozinovic & Medel (1988) challenged conclusions therein that predators opportunistically take the most abundant prey, and showed instead that predators appear to selectively take the most profitable prey as scaled to their own energy requirements. I devised a test of these competing hypotheses by using partial correlation analysis, and applied it to comparable data sets from California, Chile, and Spain. Results were inconclusive in Chile, but predators in the other two localities appeared to cue in on prey size rather than on prey abundance. I re-define the terms "opportunistic" and "selective" predator, indicating the type of statistical results expected from realization of either of these two predatory modes. I also discuss the relationship between this dichotomy and those represented by the terms "generalist" versus "specialist", and "time-minimizer" versus "energy-maximizer".

Key words: Vertebrate predator, mammalian prey, prey selection, opportunist, selective, California, Chile, Spain.

RESUMEN

Los estudios de predadores carnívoros que consumen micromamíferos han frecuentemente demostrado respuestas funcionales de dichos predadores a los cambios en el perfil de abundancia/tamaño de tales presas. Los investigadores no concuerdan sobre si las respuestas funcionales observadas se deben a conductas oportunistas o selectivas de los predadores en relación a sus presas. Reanalizando datos publicados por Jaksic *et al.* (1981) acerca de la depredación sobre micromamíferos en Chile central, Bozinovic & Medel (1988) disputan las conclusiones alcanzadas allí, de que los predadores consumen en forma oportunista las presas más abundantes, y proponen en cambio que los predadores seleccionan las presas más redituables en términos de sus propios requerimientos de energía. Yo pongo a prueba estas hipótesis alternativas usando análisis de correlación parcial, aplicado a tres bases de datos comparables de California, Chile y España. Los resultados no son concluyentes en Chile, pero los predadores en las otras dos localidades parecen orientarse por el tamaño de la presa en vez que por su abundancia. Redefino los términos predador "oportunista" y "selectivo", indicando el tipo de resultados estadísticos esperables de la realización de estos dos modos de caza alternativos. También discuto la relación entre esta dicotomía y aquellas representadas por los términos "generalista" versus "especialista" y "minimizador de tiempo" versus "maximizador de energía".

Palabras claves: Predador vertebrado, mamífero presa, selección de presa, oportunista, selectivo, California, Chile, España.

INTRODUCTION

Mammalian species differ in their patterns of microhabitat use, activity periods, and morphological and behavioral traits, attributes that in different combinations may determine the mammals' potential susceptibility or vulnerability to predation. Similarly, carnivorous predators (i.e., including snakes, owls, hawks, and mammalian carnivores) also differ widely in locomotion and hunting modes, activity times, degree of specialization, perceptual features, and many other phenotypic

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characteristics. Surprisingly, the sheer complexity underlying the interactions between carnivorous predators and their mammalian prey has not discouraged determined efforts to understand these interactions.

Four approaches to such predator/prey systems may be recognized: 1) Studies that focus on a single, or a few, prey species, and evaluate the presumed effects of predation on their ecology, particulary on their abundance and fitness. Examples of this approach are the studies of Errington (1946 and references therein), Pearson (1964, 1966, 1971, 1985), MacLean *et al.* (1974), Boonstra (1977), Beacham (1979), Taitt & Krebs (1983), Janes & Barss (1985), and Desy & Batzli (1989). 2) Studies that focus on a single, or a few, predators, and evaluate their niche relationships, residence status, and/or reproductive success with respect to the size/abundance profile of prey and/or interactions with other sympatric predators. Examples are in Rusch *et al.* (1972), Nellis & Keith (1976), Brand *et al.* (1976), Beasom & Moore (1977), Phelan & Robertson (1978), Smith & Murphy (1979), Baker & Brooks (1981, 1982), Village (1982), Marks & Marti (1984), Nilsson (1981, 1984), Korpimaki (1985a, 1987), Steenhof & Kochert (1985, 1988), Sonerud (1986), and Korpimaki & Sulkava (1987). 3) Studies that integrate the population dynamics of both predators and their prey, often emphasizing the role of predation in determining cyclicity or lack thereof among the mammals studied. Representative studies are those of Craighead & Craighead (1956), Andersson & Erlinge (1977), Hornfeldt (1978), Erlinge *et al.* (1982, 1983, 1984), Angelstam *et al.* (1984), Korpimaki (1984, 1985b, 1986), Erlinge (1987), Hansson (1987), and Korpimaki & Norrdahl (1989). 4) Studies that relate predation levels (primarily by owls) to the structure of mammal assemblages, including their patterns of microhabitat use, foraging behavior, body size, and morphology (Kotler 1984, 1985, Kotler *et al.* 1988, Brown *et al.* 1988, Brown 1989, Derting & Cranford 1989, Kotler & Holt 1989).

Besides numerical responses of the predators to changes in prey abundance, functional responses (including prey switching) have also often been reported (e.g., Anderson & Erlinge 1977, Nilsson 1981, Erlinge *et al.* 1983, 1984, Korpimaki 1985a, 1985b, 1987, Steenhof & Kochert 1985, 1988, Korpimaki & Sulkava 1987, Korpimaki & Norrdahl 1989). Although not all studies have actually tested the statistical significance of the differences detected between abundance of mammalian prey in the field and that in the predators' diets, some of them have implied that predators take prey according to their relative abundances (Jaksic *et al.* 1981, Nilsson 1981, Village 1982, Jaksic 1986), whereas others have implied that predators take the most profitable, not necessarily the most abundant, mammalian prey (Korpimaki 1985a, Korpimaki & Sulkava 1987, Steenhof & Kochert 1988, Derting & Cranford 1989). The former authors consider predators to be "opportunistic" in their feeding, taking prey as they are encountered in the field, and the latter consider predators to be "selective", maximizing net energy intake (Griffiths 1975).

Because studies that arrive at different conclusions may be interpreted as simply reflecting the varied ecological settings and species involved, it is interesting that a recent re-analysis of a data set claimed to support the notion of opportunistic feeding by predators has produced the opposite conclusion. Jaksic *et al.* (1981, see also Jaksic 1986, Jaksic & Simonetti 1987) based on correlation analyses between rank abundances of mammalian prey in the field and in the respective diets of central Chilean predators, concluded that the latter took small mammals opportunistically. Based on the same data reported by Jaksic *et al.* (1981), Bozinovic & Medel (1988) computed the expected metabolic rate of central Chilean avian predators (KJ/day) and then their theoretical daily food requirements (g/day). Their hypothesis was that given that raptors' food requirements are rather constant, they should attempt to capture those small mammals that in a single bout provided for their daily energetic requirements. They demonstrated that results in Jaksic *et al.* (1981) could be interpreted in this light.

Bozinovic & Medel (1988) stated, in essence, that central Chilean avian predators cued in on prey size and not on prey abundance. That is, exactly the opposite of what Jaksic *et al.* (1981) had proposed before. Unfortunately, the central Chilean case was not very good for testing these two competing hypotheses: there was no trend for larger small mammals to be less abundant than smaller ones (see below), as expected by the allometry of abundance versus body sizes (Peters 1983). This was primarily because some large "small" mammals (e.g., the native rat *Octodon degus*, the introduced rabbit *Oryctolagus cuniculus*) were the most abundant species at the central Chilean site.

Here I present data on predator and prey sizes and abundances in a different locality, central California, where mammal sizes and abundances were negatively correlated (indicating that mammals of larger size tend to be comparatively less abundant than those of smaller size). This negative relationship between size and abundance may help unravel on which of these two attributes predators cue in, given that profitable prey are generally scarce and vice versa. Using statistical tools described below, I compare results from central California with those reported in Jaksic *et al.* (1981) for central Chile, and in Jaksic & Delibes (1987) for southern Spain. In this latter locality, the correlation between mammalian prey size and abundance was negative, similar to California.

MATERIAL AND METHODS

Study site and species

The study sites, their predator and prey composition, predator diets, and mammalian prey sizes and abundances for central Chile and southern Spain were described in Jaksic *et al.* (1981) and Jaksic & Delibes (1987), respectively. The San Joaquin Experimental Range (Madera County, central California) is a 1840-ha area in the rolling foothills of the Sierra Nevada, physiognomically characterized as a grassland interspersed with trees (oaks and pines), clumps of chaparral (an evergreen scrub formation), and piles of large granite boulders. Its climate is of the mediterranean type (Talbot *et al.* 1942).

The occurrence, residence status, and abundance of predatory vertebrates in San Joaquin were reported by Horn & Fitch (1942) and Fitch (1949). Food habits of 11 abundant resident species were studied by Fitch and collaborators between 1939 and 1941 (Fitch 1941, 1947, 1948, 1949, Fitch & Twining 1946, Fitch & Glading 1947, Fitch *et al.* 1946a, 1946b). A total of 9,053 prey items (including 8,175 vetebrate prey) was identified by them in the diets of the 11 predator species. Some ecological features of the predators studied are reported in Table 1.

Out of 15 small mammal species (13 rodents and 2 lagomorphs) present in San Joaquin, the most abundant were eight rodents and one lagomorph (Horn & Fitch 1942, Fitch 1947), whereas the remaining six mammal species (five rodents and one lagomorph) were scarcer and more localized. Species abundances were reported as average densities over the total area of San Joaquin, regardless of the areal extent of those habitat patches where different species were more common. Although crude, these average abundance estimates are in line with the relatively low level of resolution that can be attained when examining the diets of local predators: there is no way to know in which habitat patches the different prey were actually hunted down. Ecological features of the most abundant small mammals, reported by Horn & Fitch (1942) and (Fitch 1947), are summarized in Table 1. Common names of mammals follow Jones *et al.* (1986).

Trophic statistics

Food-niche overlaps (diet similarities) between the 11 predatory species were calculated with Pianka's (1973) index as $0 = (\Sigma\, pi\, qi)\, (\Sigma\, pi^2\ \ \Sigma\, qi^2)^{-1/2}$, where *pi* is the proportional representation of prey *i* in the

TABLE 1

Ecological features of the 11 predators and of the 7 most frequent small-mammal prey in central California. Both predators and prey are listed in order of decreasing abundance. "% Preyed" refers to a given small-mammal species' percent occurrence in predator diets, averaged over the 5 predatory species in the carnivorous guild (marked with an asterisk).

Características ecológicas de los 11 predadores y de los 7 micromamíferos más frecuentes en California central. Tanto los predadores como las presas se presentan en orden decreciente de abundancia. % Predado se refiere a la representación porcentual de un determinado micromamífero en la dieta de los predadores, promediada sobre las 5 especies predadoras del gremio carnívoro (marcadas con un asterisco).

Taxa	Locomotion	Activity	Weight (g)	Number/ha	% Preyed
Vertebrate predators:					
*Crotalus viridis**	serpentine	daylong**	300	4.3	
Pituophis melanoleucus	serpentine	daylong**	500	1.0	
Masticophis lateralis	serpentine	diurnal	150	<1.0	
Thamnophis elegans	serpentine	diurnal	75	0.5	
Lampropeltis getulus	serpentine	diurnal	280	0.1	
*Buteo jamaicensis**	aerial	diurnal	1,092	0.017	
*Bubo virginianus**	aerial	nocturnal	1,155	0.010	
*Urocyon cinereoargenteus**	quadrupedal	daylong	4,500	0.010	
*Canis latrans**	quadupedal	daylong	15,500	0.007	
Accipiter cooperii	aerial	diurnal	332	0.002	
Tyto alba	aerial	nocturnal	442	0.001	
Small mammal prey:					
Thomomys bottae	fossorial	daylong	100	10.0	11.6
Peromyscus spp.	quadrupedal	nocturnal	20	"several"	1.8
Dipodomys heermanni	ricochetal	nocturnal	60	2.0	12.6
Neotoma fuscipes	quadrupedal	nocturnal	200	1.2	10.0
Perognathus inornatus	quadrupedal	nocturnal	10	1.2	2.2
Spermophilus beecheyi	quadrupedal	diurnal	500	1.0	21.4
Sylvilagus audubonii	quadrupedal	daylong	800	0.4	12.6

* Member of the carnivorous guild.

** Diurnal in cold weather, crepuscular, and even nocturnal, in warm weather.

diet of one predator species, and qi is the representation of the same prey taxon in the diet of another predator species. This index yields values between 0 and 1 (or between 0 and 100%), signifying from null to complete similarity in prey use by two predator species. The diet similarity matrix was subjected to an UPGMA clustering technique (unweighted pair-group method using arithmetic averages, Sneath & Sokal 1973) because this clustering algorithm renders the best cophenetic coefficient, and consequently distorts to a lesser extent the information contents of the original data matrix (Jaksic & Delibes 1987). To determine which clusters of predator species (i.e., trophic guilds) are statistically significant we used the bootstrap procedure described by Jaksic & Medel (1987, in press). This procedure determines the overall probability level above which any given cluster is unlikely to occur under the assumption of stochastic processes. Using a one-tailed test with alpha = 0.05, the cutoff point for the phenogram as a whole is determined empirically. Only that significant grouping of strictly carnivorous predators, in consideration of the high representation of mammals in their diets (i.e., the carnivorous trophic guild), is subjected to intense scrutiny in this paper (see below).

Partial correlation analysis

The statistical procedures used to assess the relative contribution of prey size and abundance in accounting for predator diets involved the following steps: 1) Computation of Kendall's rank-order correlation coefficient (Siegel & Castellan 1988: 245-254), between occurrence of different mammalian prey in the diet of predators and their respective sizes and abundances in the field. The significance of these coefficients was consistently evaluated with one-tailed tests given that the expected departures had a known sign (e.g., according to Bozinovic & Medel's hypothesis, the correlation between prey in the diet and their respective body sizes must be positive and higher than that between prey in the diet and their respective abundances in the field; according to Jaksic's hypothesis, the opposite expectations hold). 2) Computation of Kendall's partial rank-order correlation coefficient (Siegel & Castellan 1988: 254-261), between diet composition and prey size, holding prey abundance statistically constant, and between diet composition and prey abundance, holding prey size statistically constant. This step resolves whether Bozinovic & Medel's or Jaksic's hypothesis is substantiated. Same as above, all tests were one-tailed. 3) Computation of the joint pattern of correlation for all carnivorous predators present at a site, using the combination of probabilities (Sokal & Rohlf 1981: 780), which was also tested unilaterally. This step allows generalization to the entire trophic guild of correlations detected at the species level.

RESULTS

California

A condensed diet matrix is presented in Table 2; the observed values of diet

TABLE 2

Consumption of prey species by 11 sympatric predatory species in central California. Names of predators are shortened to the initial of the genus and the first three letters of the species' epithet. Seventy-four prey taxa were consumed by the predators, but only those 7 most frequent mammalian prey are detailed by species name here. Numbers in the table are percentage occurrence of prey in the diet of predators (all columns add up to 100); subtotals are in brackets; tr = trace (< 0.5% of total prey).

Consumo de especies presa por 11 especies de predadores simpátridos en California central. Los nombres de los predadores estan acortados a la inicial del género y a las tres primeras letras del epíteto específico. Setenta y cuatro taxa de presas fueron consumidos por los predadores, pero sólo aquellos 7 micromamíferos más frecuentes en la dieta se detallan por su nombre específico. Los números en la tabla son los porcentages de incidencia numérica de las presas en la dieta de los predadores (todas las columnas suman 100%); los subtotales aparecen en corchetes; tr = traza (< 0.5% de las presas).

Prey/Predators	Carnivorous guild					Specialists & other guilds					
	Bjam	*Bvir*	*Cvir*	*Clat*	*Ucin*	*Acoo*	*Talb*	*Lget*	*Mlat*	*Pmel*	*Tele*
MAMMALS	[69]	[66]	[87]	[81]	[73]	[7]	[98]	[7]	[29]	[66]	[0]
Thomomys bottae	20	8	5	11	14	0	37	0	0	3	0
Dipodomys heermanni	1	16	11	17	18	0	7	0	0	1	0
Neotoma fuscipes	2	19	3	8	18	0	1	0	0	4	0
Perognathus inornatus	tr	1	7	3	0	0	43	0	0	1	0
Peromyscus spp.	tr	2	6	1	0	0	7	0	0	35	0
Spermophilus beecheyi	33	2	41	19	12	2	tr	0	0	7	0
Sylvilagus audubonii	9	15	10	18	11	5	1	0	0	4	0
Other mammals	4	3	4	4	0	0	2	7	29	11	0
BIRDS	[4]	[3]	[1]	[3]	[11]	[29]	[0]	[72]	[14]	[28]	[0]
REPTILES	[21]	[2]	[9]	[7]	[16]	[64]	[1]	[21]	[57]	[6]	[0]
Snakes	9	1	0	6	9	2	0	7	0	0	0
Lizards	12	1	9	1	7	62	1	14	57	6	0
AMPHIBIANS	[0]	[2]	[3]	[tr]	[0]	[0]	[1]	[0]	[0]	[0]	[100]
INVERTEBRATES	[6]	[27]	[0]	[9]	[0]	[0]	[0]	[0]	[0]	[0]	[0]
Insects	6	24	0	9	0	0	0	0	0	0	0
Arachnids	tr	3	0	tr	0	0	0	0	0	0	0
Diplopods	0	0	0	tr	0	0	0	0	0	0	0
TOTAL PREY	4,384	1,427	285	2,127	97	42	513	14	7	72	85

similarity are reported in Table 3, and their representation as a dendrogram is depicted in Fig. 1. Scrutiny of significant species clusters in San Joaquin demonstrated the existence of two trophic guilds (Fig. 1). One consisted of the Common Kingsnake (*Lampropeltis getulus*) and of the Gopher Snake (*Pituophis melanoleucus*), which clustered apparently because of their shared consumption of both birds and mammals. The other significant grouping of predators made up the carnivorous trophic guild, which was composed of a diverse array of predators (Fig. 1). They were the Great Horned Owl (*Bubo virginianus*), the coyote (*Canis latrans*), the gray fox (*Urocyon cinereoargenteus*), the Red-tailed Hawk *(Buteo jamaicensis)*, and the Western Rattlesnake(*Crotalus viridis*). They all were primarily mammal-eaters (small-mammals represented from 65% to 87% of their diet) and had many prey in common (Table 2). *Canis latrans, U. cinereoargenteus*, and *B. virginianus* consumed rather evenly the same variety of rodents and lagomorphs, whereas *B. jamaicensis* and *C. viridis* concentrated more heavily on a single rodent, the California ground squirrel (*Spermophilus beecheyi*). Interestingly, these five predator species encompassed diverse locomotion modes and activity periods (Table 1), but apparently had access to the same prey (Table 2), despite their broad differences in ecological features.

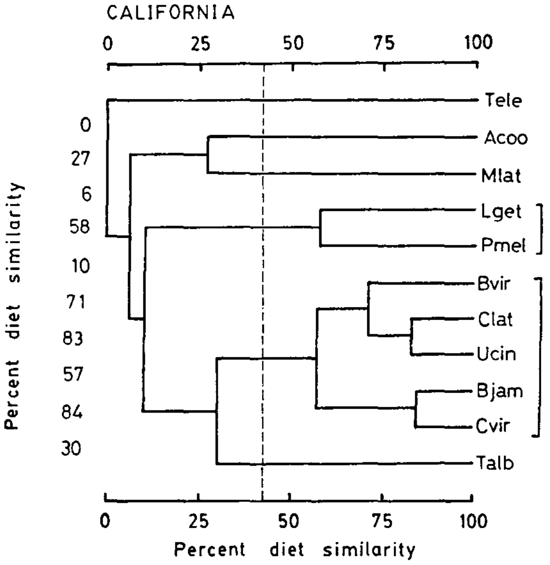

Fig. 1: Diet similarity dendrogram (UPGMA-generated) for 11 predatory species in central California. Species names abbreviated as in Table 2. Broken line at 42% diet similarity indicates that two trophic guilds (bracketed) are significant at P < 0.05.

Fenograma de similitud dietaria (generado por UPGMA) para 11 especies de predadores simpátridos en California central. Los nombres específicos están abreviados como en la Tabla 2. La línea segmentada al 42% de similitud dietaria indica que dos gremios tróficos (entre corchetes) son significativos con P < 0.05.

TABLE 3

Food-niche overlaps (diet similarities) between 11 sympatric predatory species in central California. Species names' abbreviations in the column header are the same as in Table 2. Numbers in the table are percent diet similarities.

Sobreposiciones de nicho alimentario (similitudes dietarias) entre 11 especies de predadores simpátridos en California central. Las abreviaturas de los nombres específicos en el encabezamiento de esta Tabla son las mismas que en la Tabla 2. Las cifras en la tabla son porcentajes de similitud dietaria.

Predators	*Acoo*	*Bjam*	*Bvir*	*Talb*	*Cvir*	*Lget*	*Mlat*	*Pmel*	*Tele*	*Clat*	*Ucin*
Accipiter cooperii	–	20.3	5.0	0.2	11.5	9.3	26.9	2.1	0.0	8.2	8.4
Buteo jamaicensis		–	35.6	32.9	83.7	3.4	9.1	18.4	0.0	77.3	60.1
Bubo virginianus			–	24.1	30.3	0.5	1.3	16.4	0.1	71.9	66.7
Tyto alba				–	24.1	0.1	2.3	16.3	0.0	33.5	32.5
Crotalus viridis					–	0.6	5.6	29.5	0.1	79.6	56.8
Lampropeltis getulus						–	10.1	58.4	0.0	1.8	0.6
Masticophis lateralis							–	10.7	0.0	2.1	0.0
Pituophis melanoleucus								–	0.0	20.8	15.9
Tamnophis elegans									–	0.0	0.0
Canis latrans										–	83.1
Urocyon cinereoargenteus											–

The natural history of the most frequently eaten small mammals can be scrutinized in detail with respect to their representation in the diets of the five predators that form the carnivorous guild (cf. Tables 1 & 2, Fig. 1). One of the least abundant species in the locality, the California ground squirrel (*S. beecheyi*), had the highest representation in predator diets. This species seemed to be selected by the predators, perhaps due to its large (profitable) size, use of very open habitat (grasslands), and diurnal habits (Table 1). Four other small mammals were consumed to a similar extent (they represented from 10.0 to 12.6% of the predator diets). Botta's pocket gopher (*Thomomys bottae*), was the most abundant small mammal in the locality, and despite being essentially fossorial it became easy prey when moving on the ground surface; it was active all day (Table 1). Heermann's kangaroo rat (*Dipodomys heermanni*) was the third most abundant small mammal. Although its density amounted to only one fifth that of the pocket gopher it was consumed to a slightly larger extent than the latter, and was nocturnal (Table 1). The dusky-footed woodrat (*Neotoma fuscipes*) ranked fourth in abundance, and it was only slightly less consumed than the former two species; it was nocturnal (Table 1). The desert cottontail (*Sylvilagus audubonii*) was the least abundant of the local small mammals, but was selected heavily, perhaps due to its day-long activity period and large size (Table 1). The least consumed small mammals, the San Joaquin pocket mouse (*Perognathus inornatus*) and the white-footed mice (*Peromyscus* spp.) shared nocturnal habits and small size (Table 1). Whether they were "skipped" by the predators due to their low profitability, or because they were more agile, secretive, or cryptic than the larger prey, is unknown.

Partial correlational analyses between representation of mammalian prey in the diet of California predators and the respective sizes and abundances of such prey in the field are listed in Table 4. Although often not significant, all but one correlation between diet composition and prey size are positive, when statistically removing the effect of prey abundance. The joint correlation pattern is highly significant, thus indicating that the carnivorous guild as a whole takes different mammalian prey in proportion to their sizes, independently of their abundances. In contrast, partial correlations between diet composition and prey abundance, holding prey size constant, are lower, sometimes negative, and do not reach statistical significance either singly or jointly. These findings indicate that California predators as a whole seem to cue in on prey size and not on prey abundance. The hypothesis proposed by Bozinovic & Medel (1988) for Chilean raptors may be consequently extended both to a different region and to a taxonomically broader predator assemblage (including not only avian predators but also snakes and mammalian carnivores).

It should be cautioned, however, that the lack of significant correlations between prey ranks in the diet of some predators versus prey sizes or abundances in the field may indicate some real biological phenomenon rather that simply lack of correlation. That is, there may be predators that do not use prey size or abundance as cues, but some other prey features such as odor or peculiar behavior. Or, that the investigator-determined prey abundances do not correspond to the perception of prey abundance that the predators have. Only the principle of parsimony warrants my treatment of insignificant correlations as no more than statistics that can be combined to search for global patterns of predator hunting behavior.

Chile and Spain

The same correlation analyses conducted in California can be applied to the Chilean carnivorous guild, using data in Jaksic *et al.* (1981) or in Jaksic (1986). Three species of hawks (*Buteo polyosoma, Geranoaetus melanoleucus*, and *Parabuteo unicinctus*) and one carnivore (*Pseudalopex culpaeus*) were shown to be mainly mammal-eaters (small mammals comprised from 89.7 to 96.4% of their diets). In this case, all coefficients are positive (Table 4) and most often significant, for partial correlations between diet composition and prey size, holding prey abundance constant. The joint correlation pattern is highly significant. For partial correlations between diet composition and prey abundance, holding constant prey size, all coefficients are positive, significant, and larger than in the previous case. The joint correlation pattern is highly significant as well. Because there is a better statistical fit between diet and abundance than between diet and size, it could be argued that these findings partially corroborate the hypothesis of Jaksic *et al.* (1981), but they also fail to refute the hypothesis of Bozinovic & Medel (1988). Further, the situation in Chile is confusing, provided the peculiar lack of negative correlation between mammalian prey size and abundance (Table 4), expected from the known allometry of body sizes. That is, large mammals such as the heavily preyed *Octodon degus* are more abundant than expected from their size, thus confounding the resolution of whether Chilean predators cue in on either size or abundance.

In Spain, Jaksic & Delibes (1987) showed that two hawks (*Aquila heliaca* and *Buteo buteo*) and one carnivore (*Lynx pardina*) were mainly mammal-eaters (small mammals represented from 58.2 to 81.0% of their diets). Applying the same analyses as above, partial correlations between diet composition and prey size, holding their abundance constant, demonstrate positive coefficients (often non-significant), which nonetheless are rendered significant as a joint correlation pattern (Table 4). Partial correlations between diet composition and prey abundance, with size held constant, are also positive (though non-significantly so), and often smaller than in the previous case. The joint correlation pattern does not reach significance, but is close enough to it.

TABLE 4

Kendall partial rank-order correlation coefficients (Tau) between representation of mammalian prey in the diet of predators and the respective prey sizes and abundances, holding constant either of these latter variables. Tau's between prey size and abundance in each region are not partial but simple. All tests are one-tailed.

Coeficientes ordinales de correlación parcial de Kendall (Tau) entre la representación de micromamíferos en la dieta de los predadores y los respectivos tamaños y abundancias de aquellos, manteniendo constante una u otra de estas últimas dos variables. Los Tau entre tamaño y abundancia de las presas en cada región no son parciales, sino simples. Todas las pruebas son unilaterales.

Sites/predators	diet/size (abundance = ct.)			diet/abundance (size = ct.)		
California (Tau size/abundance = −0.476; N = 7; P > 0.068):						
C. viridis	− 0.164;	N = 7;	P > 0.25	− 0.408;	N = 7;	P > 0.10
B. jamaicensis	+ 0.723;	N = 7;	P < 0.01	+ 0.244;	N = 7;	P > 0.20
U. cinereoargenteus	+ 0.380;	N = 7;	P > 0.10	+ 0.355;	N = 7;	P > 0.10
B. virginianus	+ 0.488;	N = 7;	P > 0.05	+ 0.257;	N = 7;	P > 0.20
C. latrans	+ 0.422;	N = 7;	P > 0.10	− 0.176;	N = 7;	P > 0.25
Combined P's (*)	X^2 = 21.640;	df = 10;	P < 0.025	X^2 = 3.665;	df = 10;	P > 0.90
Chile (Tau size/abundance = +0.133; N = 10; P > 0.300):						
B. polyosoma	+ 0.186;	N = 10;	P > 0.20	+ 0.752;	N = 10;	P < 0.001
G. melanoleucus	+ 0.872;	N = 10;	P < 0.001	+ 0.904;	N = 10;	P < 0.001
P. unicinctus	+ 0.509;	N = 10;	P < 0.025	+ 0.593;	N = 10;	P < 0.01
P. culpaeus	+ 0.867;	N = 10;	P < 0.001	+ 0.924;	N = 10;	P < 0.001
Combined P's (*)	X^2 = 38.228;	df = 8;	P < 0.001	X^2 = 50.657;	df = 8;	P < 0.001
Spain (Tau size/abundance = −0.467; N = 6; P = 0.136)						
A. heliaca	+ 0.853;	N = 6;	P < 0.01	+ 0.163	N = 6;	P > 0.25
B. buteo	+ 0.492;	N = 6;	P > 0.05	+ 0.427	N = 6;	P > 0.10
L. pardina	+ 0.107;	N = 6;	P > 0.25	+ 0.342	N = 6;	P > 0.10
Combined P's (*)	X^2 = 19.974;	df = 6;	P < 0.01	X^2 = 11.983;	df = 6;	P > 0.05

(*) See Sokal & Rohlf (1981: 780).

Although this case is not as conclusive as that in California, it is more in line with the suggestion that Spanish predators key on prey size rather than on prey abundance.

DISCUSSION

Prey abundance versus prey size

Jaksic *et al.* (1981) reported significant positive correlations between composition of prey in the diet of central Chilean predators, and the rank order of mammalian prey abundances in the field. Based on these findings, they proposed that local predators were opportunistic, preying on whatever prey was most abundant within those habitat patches where predators hunted, during their respective activity periods. Bozinovic & Medel (1988), analyzing the same data base of Jaksic *et al.* (1981), showed that avian predators took on average differently-sized prey in agreement with their daily energy requirements. This evidence was interpreted as indicating that central Chilean predators were selective, taking first those mammals with a size that provided for daily survival based on a single meal; and taking next those smaller-sized mammals that required more than a hunting bout.

A criticism that could be made of Bozinovic & Medel's (1988) analysis is that most of the predators examined by them ate the rat *Octodon degus*, which was not only the "best" meal size but also the most abundant rodent in the area. The concurrence of these two attributes on a single prey marred resolution of the competing hypotheses. Jaksic *et al.* (1981; see also Jaksic 1986) were aware of the anomalous situation in which a relatively large-sized mammal was more abundant than most or all of the smaller-sized mammals, but they did not test whether there were positive correlations between prey composition in the diet and the respective prey sizes available in the field. I have shown here that there is indeed a positive correlation between these variables, but that the peculiar situation posed in central Chile is not resolved by partial correlation analysis. A different approach is called for.

The comparative approach, exploring similar data sets from different continents, where large-sized mammals tend to be less abundant than smaller ones, provides a better basis for assessing the relative contribution of prey size and abundance as proximate factors on which predators cue in. Central California and southern Spain meet the requirements stated, and scrutiny of their respective predator/prey relationships give strong support to the hypothesis that carnivorous predators target on prey size rather than on abundance.

A different line of evidence indicates that Chilean predators may not be an exception to the rule. Two recent studies conducted in central Chile have reported that culpeo foxes (*Pseudalopex* [= *Dusicyon*] *culpaeus*) in two separate localities disproportionally take the two largest local rodents, thus pointing to some degree of selectivity by size (Meserve *et al.* 1987, Iriarte *et al.* 1989). The methodology used in these studies is more powerful than the correlational approach that has prevailed in dealing with predation phenomena in central Chile (Jaksic & Simonetti 1987): the composition of prey in the diet of the fox was compared with that expected were the fox to take prey in proportion to their respective abundances in the field (as evaluated by simultaneous trapping; Simonetti 1989 pointed that this requirement was not met in Meserve *et al.*'s study). Although time-consuming, it would be worth to analyze the diets of other central Chilean predators, concomitant with adequate trapping schemes, to determine whether they are size-selective as well. Carefully obtained data are needed from areas homogeneous enough as to insure that the prey abundances assessed in the field actually reflect their respective availabilities to predators that hunt in such areas.

Opportunism versus selectivity

To dispel potential confusion (cf. Simonetti 1988, 1989; Meserve 1988), I will address the point of how to determine whether predators are opportunistic or selective. Same as many other authors I have defined opportunist predators rather vaguely (e.g., Jaksic & Braker 1983, Jaksic 1988), and would like now to offer a clearer wording of the definition: "Opportunist" is a predator that takes all prey in the same relative abundances as present in those patches where the predator hunts (during the period when the predator is active, and within size limits imposed by the predator/prey size ratios and the perceptive and handling capabilities of the predator). Where, when and how a predator hunts should be determined by field observation; size limits should be determined from analysis of prey composition (and sizes) in the diet. An opportunistic predator so defined has a diet that correlates with the profile of prey abundances as weighted by their respective body sizes, present at a given place and time. Using partial rank-order correlation coefficients, the prey composition in the diet of such a predator shows a better fit with prey abundance than with prey size. Using goodness-of-fit tests (such as Chi-square or G), such a predator shows either no difference between observed and expected values of abundance of prey in the diet and in the field, or a disproportionately large consumption of the most abundant prey (when a search image has been formed).

In contrast, a "selective" predator takes some or all prey in different proportions than those present in patches where the predator hunts (during the period when the predator is active, and within size limits imposed by the predator/prey size ratios and the perceptive and handling capabilities of the predator). A selective predator so defined has a diet that does not correlate with the profile of prey abundances as weighted by their respective body sizes, present at a given place and time. Using partial rank-order correlation coefficients, the prey composition in the diet of such a predator shows a better fit with prey size than with prey abundance. Using goodness-of-fit tests, such a predator shows clear differences between observed and expected values of abundance of prey in the diet and in the field, and in particular, a disproportionately large consumption of the largest prey that it can handle. To avoid circular reasoning, the size of such largest prey should be determined either theoretically (by generalized allometric equations) or empirically. In this latter case, the largest prey species found in the diet should be partitioned by size classes, attempting to determine the maximum size represented in the diet by comparison with voucher specimens.

Although modern students of predators' trophic ecology (food-niche relationships) customarily assess prey densities in the field, and record their body sizes, they tend to relate only prey numbers in the field and in the predator diets by using either preference indexes (e.g., Nilsson 1981, Korpimaki 1985a, Kotler 1985, Steenhof & Kockert 1988) or Spearman's rank correlation coefficients (e.g., Steenhof & Kochert 1985, Korpimaki & Sulkava 1987). A problem with preference indexes is that analytic expressions of their variance are generally unavailable or are too complicated; consequently, statistical hypothesis testing is greatly hampered. A problem with Spearman's rank correlation coefficient is that it cannot be extended into a partial correlation coefficient (Siegel & Castellan 1988); consequently, the variables of interest cannot be dissociated and their relative importance cannot be assessed objectively. The statistical protocol here described has the advantage of resolving the question of whether a given predator cues in on prey abundance by partialling out the potential influence of prey size, and vice versa. Perhaps, wider use of the protocol discussed here will help resolve whether carnivorous predators are opportunistic or selective in other systems.

A criticism that could be made of the above definitions is that prey abundance is used in lieu of the more adequate prey "availability" (Simonetti 1989). The Ranking of prey availabilities to a given predator may not necessarily correspond to the ranking of those prey abundances in the field. However, I see no easy solution to this problem; to date, no one has come up with a realistic index for prey availability, except perhaps in laboratory conditions (Derting & Cranford 1989). For the time being, it seems that prey abundance in patches where (and at times when) predators hunt is the only reasonable substitute for prey availability.

Related dichotomic terms

Two other dichotomies are frequently found in the predation literature: generalist versus specialist, and time-minimizer versus energy-maximizer. I think that these two dichotomies refer to conceptual frameworks different from that implicit in the terms opportunist and selective. Opportunistic or selective refers to the foraging behavior of predators, which in turn becomes reflected in their respective trophic niches. It is almost a truism that an opportunistic predator has a generalized diet (or a broad trophic niche), whereas a selective predator has a specialized diet (or a narrow trophic niche). Of course, there are apparent exceptions: an opportunist predator faced with a profile of prey abundances that is strongly leptokurtic, will ostensibly demonstrate a narrow trophic niche. This point stresses the importance of classifying predators according to both their behavior and the local profile of prey sizes and abundances.

The ultimate cause of a predator behaving as opportunistic or as selective may be related to its hunting tactics. An opportunist predator may, more often than not, be a "time minimizer" (Schoener 1971, Hixon 1982), taking whatever prey comes within reach in the minimum amount of hunting time, ostensibly to use the remaining time in other activities. Why vertebrate predators may attempt to minimize time spent hunting is puzzling, however, given that they appear to have plenty of "leisure" time (Herbers 1981). Perhaps the time-minimizer tactic results from the avoidance of interspecific encounters, aimed at reducing both agonistic interactions and resource depression (Brown *et al.* 1988, Jaksic 1988). A selective predator, in contrast, may be an "energy maximizer" (Schoener 1971, Hixon 1982), using ample time to find, catch, and subdue the most profitable prey.

Consequently, all these dichotomic terms seemingly refer to different phenotypic components of the predators. Hunting tactics are dictated by decision rules involving either "time minimization" or "energy maximization"; these rules are reflected in the hunting behavior of predators, dichotomized as "opportunistic" or "selective"; and these behaviors, in turn, become transcribed in the trophic niche of the predators, be it broad/"generalized" or narrow/"specialized".

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