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## A long-term study on the dynamics of guild structure among predatory vertebrates at a semi-arid Neotropical site

Fabian M. Jaksic, Peter Feinsinger and Jaime E. Jiménez

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For 48 mo we monitored diets and populations of 10 species of predatory vertebrates (two foxes, four falconiforms, and four owls) in semi-desert scrub at Aucó, Chile. Pellets (birds) and feces (foxes) collected monthly contained identifiable remains of small mammals, birds, reptiles, amphibians, large insects, other arthropods, and (in some fox feces) fruits. For non-mammalian prey, seasonal variation in availability appeared to be more pronounced than longer-term variation. In contrast, availability of the eight species of small mammals varied relatively little between predators' breeding and non-breeding seasons but declined by an order of magnitude through the first 3 yr of the study. Rather than responding to these shifts in food availability by diverging in diet during "lean" times and converging opportunistically during "fat" times, predators at Aucó responded in idiosyncratic ways. Predators of all species tended to maintain species-specific means in size of prey taken regardless of shifts in the relative availability of prey size classes. Two owl species maintained strict mammal diets throughout the decline in mammal abundance, whereas two other owls plus the two fox species maintained a tight feeding guild based on arthropods as well as mammals and other food groups. The four falconiforms failed to maintain consistent diets from season to season, and consequently ended up temporarily in unique positions in "diet hyperspace" or else joined temporarily one of the two consistent guilds. The degree to which falconiform diets were unique in a given season showed no clear relation to food abundance. Changes in use of habitat did, however, relate to changes in food abundance. None of the falconiforms resided continuously in the study area throughout the period, and their occurrence was particularly sporadic late in our study even for falconiform species that were not particularly mammalivorous. The lack of clearcut patterns among Aucó predators in response to resource-"lean" and resource-"fat" times may result from one or more of the following: (a) from predators' viewpoints, food classes at Aucó may be quite discrete, inhibiting gradual diet shifts by owls and foxes at least; (b) truly opportunistic immigrants that might have increased overall diet overlap during "fat" times, as sometimes occurs in other consumer assemblages, do not exist in the Aucó landscape; and (c) despite the pronounced decline in small mammal densities, the predator assemblage may have remained above the threshold of food limitation through part or all of the study.

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During the early phases of development of consumer-resource theory, community ecologists proposed that fluctuations in the availability of resources should influence the niche dynamics and coexistence patterns of consumer populations (MacArthur and Levins 1964, 1967, MacArthur 1968). With the advent of long-term field studies that encompassed a full annual cycle, researchers realized that consumers' responses to changing resources were highly complex, with different species responding in quite different ways. These responses to alternating times of abundant and scarce resources, or "fat" and "lean" periods, depend partly on the degree of contingency (*sensu* Colwell 1974) of peaks and valleys in resource availability, on the life span of the consumers, on consumer mobility (which can vary greatly among the members of a single guild or even among related species), and on more obvious factors such as the diet flexibility of consumers or whether characteristics of resources are distributed in discrete or continuous fashion from the viewpoint of consumers (e.g., Wiens 1977, 1990a, 1990b, Feinsinger 1980, Erlinge et al. 1982, 1984, Feinsinger et al. 1985, Korpimäki 1985, Wiens et al. 1986).

One frequently noted effect of fluctuations in resource levels is a divergence of the diets of consumer species when resources are scarce. Of 30 studies examined by Schoener (1982), 27 demonstrated lower diet overlaps during resource-lean than during resource-fat periods. Some cases involved a consistent set of guild members that coexist year-round, whereas others clearly showed fat-season invasions by various numbers of immigrant species, often with convergent diets, overlaying a core of resident species. Examples of changes in guild structure in response to lean versus fat periods – which are often taken to characterize non-breeding versus breeding seasons, respectively – include fishes (Zaret and Rand 1971, Schmid-Hempel and Holbrook 1986), lizards (Dunham 1980), Mediterranean-climate passerines (Herrera 1978), Galápagos finches (summarized by Grant 1986), shorebirds (Baker and Baker 1973), foliage-gleaning birds (Root 1967, Ulfstrand 1977, Wagner 1981), nectar-feeding birds (Feinsinger 1976, Feinsinger et al. 1985), shrubsteppe or desert birds (Rotenberry 1980, Maurer 1985), tropical forest birds (Karr and Freemark 1983), and rodents (M'Closkey 1976, Llewellyn and Jenkins 1987).

Recently, however, Jaksic et al. (1990) reported that in two of three year-round studies of assemblages of raptorial birds in seasonal environments, there was little evidence of marked changes in diet overlaps and guild structure between breeding and non-breeding seasons. The possibility existed that the particular years of these studies did not involve prey fluctuations sufficiently intense to generate recognizable responses among raptors. Here we report on an extension of one of these three studies over a 4-yr period that included an irruption and prolonged decline of a major resource class, small mammals. Our results suggest that some predat-

tors simply lessened their use of the habitat patches in question and that guild structure changed surprisingly little among those populations remaining.

## Materials and methods

### Study site

The study site was Las Chinchillas National Reserve, near Aucó (31°30'S; 71°06'W), 300 km north of Santiago, Chile. Located in the coastal ranges, the 4229-ha Reserve has a rugged topography with numerous ridges dissected by deep ravines and few level areas. Elevations range from 400 to 1700 m. The climate is semi-arid, with rainfall concentrated during austral winter (June – August). Annual precipitation averages ca 200 mm but varies greatly from year to year (Fuentes et al. 1988). The thorn-scrub vegetation consists primarily of dicot shrubs, terrestrial bromeliads, and cacti. Slopes that face north (equatorial) receive higher solar radiation than south-facing slopes, and have sandy open soils with scattered gravel patches and rock outcrops. On the xeric north-facing slopes, grasses are scarce (mainly *Nassella* spp. and *Stipa* spp.), but cacti (*Trichocereus* spp., *Tephrocactus ovatus*), bromeliads (*Puya berteroniana*), and sclerophyllous shrubs (*Bahia ambrosioides*, *Cordia decandra*, *Bridgesia incisaefolia*, *Flourensia thurifera*) are abundant. In contrast, the more mesic slopes that face south (polar) support many grasses but few cacti and no *Puya*; furthermore, a different assemblage of shrubs prevails (*Adesmia* spp., *Porlieria chilensis*, *Colliguaya odorifera*, *Proustia* spp.). Gajardo (1978) provides further descriptions of the vegetation at Aucó.

### Monitoring small mammal populations

The most prevalent and distinctive habitats available to predators hunting mammalian prey were north- and south-facing slopes of ravines. We monitored small-mammal populations by establishing trapping grids on opposite north- and south-facing slopes of each of two ravines, El Grillo and El Cobre, separated by 2 km. We employed mark and recapture procedures, using live traps to estimate the minimum number of mammals known to be alive in the grids. We installed four trapping grids: two on opposite-facing slopes of El Grillo, and two on slopes of El Cobre. All 7 × 7 trapping grids had trapping stations separated by 15 m, providing a sample area of 105 × 105 m (including a boundary strip of 7.5 m), or 1.1 ha. Each station contained one Sherman trap (south-facing slopes) or one Sherman and one Tomahawk-like trap (north-facing slopes). Kept permanently in the field, traps were closed when not in use and were activated during five nights of each month (trapping effort = 735 trap-nights/mo over 2.2 ha).

Monthly trapping sessions alternated between El Grillo and El Cobre. Jiménez et al. (1992) provide full details on trapping methods.

### Monitoring predator populations

We kept monthly records of visual tallies of predators at the site. Twelve species were most commonly sighted: the falconiforms *Buteo polyosoma* (red-backed hawk), *Falco sparverius* (American kestrel), *Geranoaetus melanolencus* (black-chested eagle), and *Parabuteo unicinctus* (Harris hawk); the strigiforms *Athene cunicularia* (burrowing owl), *Bubo virginianus* (horned owl), *Glauucidium nanum* (austral pygmy owl), and *Tyto alba* (barn owl); the canids *Pseudalopex culpaeus* (Culpeo fox) and *P. griseus* (Chilla fox); the colubrid snake *Philodryas chamissonis* (long-tailed snake); and the teiid lizard *Callopistes palluma* (Chilean racerunner). We considered a given species to be "resident" at the site if we detected sustained occupation of roosts, perches, nests, or dens (raptors and foxes) or observed individuals (snakes, lizards) and in addition found at least five pellets (raptors) or feces (foxes and racerunners) per season.

### Monitoring predator diets

We sampled each month's accumulation of regurgitated pellets at known roosts, perches, or nests (raptors), or of feces along consistent transects (foxes, racerunners), from March 1987 through February 1991. In the laboratory, pellets and feces were carefully teased apart under a dissecting microscope, and prey or food plants were identified to the maximum level of resolution (specific for vertebrates and plants, ordinal for invertebrates). In particular, remains of mammal prey were identified to species level by reference to keys (Reise 1973) and locally collected voucher specimens. The minimum number of individual mammal prey present in pellets or feces was estimated by the minimum number of double or single anatomical elements such as crania, mandibles, or tooth rows (Marti 1987). Analogous techniques were used to determine minimum numbers for other prey taxa and for fruits consumed by foxes. Pavez et al. (1992) have shown that estimates of minimum prey numbers obtained through such techniques are precise and unbiased relative to other techniques for quantifying predator diets.

Analyses and the results reported below are restricted to raptors and foxes. Although the snake *P. chamissonis* was a permanent resident at the site, we could not find its feces. The racerunner *C. palluma* also resided permanently, but after the first year of data collection (reported by Castro et al. 1991) we were unable to obtain enough feces for analysis. It should be noted that, being ectotherms, the prey consumption rates of these two species should be considerably lower than

those of the raptors and foxes. In addition, their activity periods are restricted to the warmer months of the year.

### Characterizing guild membership and structure

We calculated geometric mean weight of prey as:

$$GMWP = \text{antilog} (\sum p_i \log W_i), \quad (1)$$

where  $p_i$  is the relative incidence of prey category  $i$  in a given predator's diet and  $w_i$  is the mean weight of prey  $i$  (Jaksić and Braker 1983). This procedure partially compensates for the skewed distribution of prey sizes in most predators' diets.

We computed diet overlap between two predator species (cf. Pianka 1973) as:

$$Ov = \sum p_i q_i / (\sum p_i^2 \sum q_i^2)^{1/2}, \quad (2)$$

where  $p_i$  and  $q_i$  are the relative occurrences of prey category  $i$  in the diets of the two predators, respectively.  $Ov$  ranges from 0.0 to 1.0 (0–100% overlap). We applied both eqs (1) and (2) to diet data using the highest possible taxonomic resolution of prey (plant foods were not considered): species for vertebrates, orders for invertebrates (cf. Greene and Jaksić 1983).

Using entries in the diet similarity matrices constructed for calculating  $Ov$ , we applied the unweighted pair-group clustering method with arithmetic averaging (UPGMA, Sneath and Sokal 1973). Following Jaksić and Delibes (1987) and in order to compare results from throughout the study period, we set the threshold for assigning predators to trophic guilds at 50% diet similarity. Less arbitrary means of defining guilds (e.g., Jaksić and Medel 1990) would result in thresholds for guild designations that varied seasonally, rendering comparisons of guild structure between and among years much more difficult.

### Expressing seasonal trends

In order to increase sample sizes for computations, data were pooled into two biologically relevant seasons per year: non-breeding (from 1 March to 31 August) and breeding (from 1 September to 28 February). Thus, we examined four non-breeding and four breeding seasons over the 48 mo of the study. Below we discuss whether or not these corresponded to "lean" and "fat" seasons, respectively, from predators' viewpoints.

Because species present during a given non-breeding season typically remained for the subsequent breeding season, guild node values for consecutive non-breeding and breeding seasons are not independent. Thus, to compare guild structure in non-breeding and breeding seasons, we used Wilcoxon signed-rank paired-sample tests (Siegel and Castellan 1988) in which node values

Table 1. Numbers of pellets (raptors) and feces (foxes) collected at Aucó, by season. If number was < 5, species not considered "resident" (see text). NB = non-breeding season; B = breeding season. Mammal densities from Jiménez et al. (1992); nd = no data taken that season. Masses of predators from Jaksić et al. (1992).

Predator species	Mass (g)	NB87	B87	NB88	B88	NB89	B89	NB90	B90	Total
<i>Falco sparverius</i> (F.s.)	116	15	38	5	5	0	2	0	31	94
<i>Geranoaetus melanoleucus</i> (G.m.)	2378	15	8	9	0	0	0	0	2	32
<i>Parabuteo unicinctus</i> (P.u.)	876	4	0	28	27	11	0	0	0	66
<i>Buteo polyosoma</i> (B.p.)	975	0	40	19	69	0	0	0	0	128
<i>Glaucidium nanum</i> (G.n.)	81	100	76	129	118	81	68	73	23	668
<i>Athene cunicularia</i> (A.c.)	247	124	214	25	101	59	103	217	154	997
<i>Tyto alba</i> (T.a.)	307	51	104	181	71	21	0	56	0	484
<i>Bubo virginianus</i> (B.v.)	1227	187	194	260	433	62	64	71	10	1281
<i>Pseudalopex culpaeus/griseus</i> (P.c./P.g.)	7367/3807	84	176	804	378	484	315	286	249	2776
No. resident species		8	9	10	9	7	5	6	6	
Total small-mammal density (No./ha)		nd	222	209	98	30	25	17	21	
<i>Phyllotis darwini</i> (No./ha)	47	nd	165	140	65	18	17	11	20	
<i>Octodon degus</i> (No./ha)	123	nd	12	9	5	3	1	<1	0	

for a given non-breeding season were paired with their counterparts for the subsequent breeding season. Species present during only one or the other season were deleted from this analysis. All tests were two-tailed.

## Results

### Predator and prey populations

We captured eight species of small mammals (cf. Jiménez et al. 1992): seven rodents [*Akodon longipilis*, *Akodon olivaceus*, *Oryzomys longicaudatus*, and *Phyllotis darwini* (all Cricetidae), *Abrocoma bennetti* (Abrocomidae), *Chinchilla lanigera* (Chinchillidae), and *Octodon degus* (Octodontidae)] and a marsupial, *Marmosa elegans* (Didelphidae). During the winter of 1987 (June-August), an outbreak of small mammals occurred, apparently triggered by unusually high rainfall and subsequent vegetation production (details in Jiménez et al. 1992). Overall density soared to an estimated 222 small mammals/ha when we began monitoring during the breeding season of 1987, and declined thereafter to 17/ha during the non-breeding season of 1990, increasing only slightly in the following breeding season (Table

1). Thus, small-mammal densities at their lowest were estimated to be 7% of peak densities.

The number of endothermic predator species considered resident at the site peaked at ten (counting the two foxes separately) during breeding season of 1987 and dipped to five during breeding season of 1989. *Falco* resided at Aucó throughout breeding of 1988 and again during breeding of 1990 but not in-between. *Geranoaetus* resided at the site only during the first three seasons of the study, as did *Buteo*, which appeared at Aucó during breeding of 1987 and disappeared after breeding of 1988. *Parabuteo* first appeared as a resident later in the study, and resided through non-breeding of 1989. *Athene*, *Bubo* and *Glaucidium*, as well as both species of *Pseudalopex* (as verified by sightings), resided throughout the study. *Tyto* resided continuously at Aucó from non-breeding of 1987 through non-breeding of 1989, disappeared from the study site the following season, reappeared during non-breeding of 1990, and disappeared afterward. Even during these absences, though, we found evidence of active *Tyto* roosts in areas just outside the Reserve. Except for *Tyto*, we sighted all species of predators in the areas surrounding the study site even during seasons when they were not resident as defined above. Thus, seasons of non-occurrence pre-

Table 2. Geometric mean prey weights  $\pm$  SD (g) of Aucó predators over the seasons of the study. See Materials and methods for method of calculation. Predator abbreviations as in Table 1.

Seasons	Predators								
	G. m.	B. p.	P. u.	F. s.	T. a.	B. v.	G. n.	A. c.	P. c./P. g.
Non-breeding 1987	99.8 $\pm$ 2.2			1.6 $\pm$ 3.1	47.6 $\pm$ 1.8	67.4 $\pm$ 2.2	3.3 $\pm$ 5.9	1.2 $\pm$ 2.3	3.8 $\pm$ 7.7
Breeding 1987	44.5 $\pm$ 8.8	9.0 $\pm$ 7.5		1.6 $\pm$ 2.5	43.9 $\pm$ 1.5	43.3 $\pm$ 3.2	2.5 $\pm$ 4.6	1.4 $\pm$ 2.9	2.4 $\pm$ 6.0
Non-breeding 1988	81.6 $\pm$ 2.0	16.3 $\pm$ 5.6	62.7 $\pm$ 1.9	9.2 $\pm$ 7.5	28.1 $\pm$ 1.3	45.8 $\pm$ 2.1	6.1 $\pm$ 7.2	1.5 $\pm$ 3.0	2.2 $\pm$ 5.3
Breeding 1988		16.8 $\pm$ 7.2	101.3 $\pm$ 1.5	1.5 $\pm$ 2.8	41.5 $\pm$ 1.7	49.9 $\pm$ 2.0	2.3 $\pm$ 5.0	1.4 $\pm$ 2.8	1.7 $\pm$ 4.4
Non-breeding 1989			77.9 $\pm$ 2.7		45.3 $\pm$ 1.5	19.4 $\pm$ 8.9	4.7 $\pm$ 6.7	1.1 $\pm$ 1.8	2.0 $\pm$ 5.3
Breeding 1989						52.5 $\pm$ 2.0	2.1 $\pm$ 5.2	1.1 $\pm$ 1.5	1.7 $\pm$ 4.6
Non-breeding 1990					42.6 $\pm$ 1.4	46.9 $\pm$ 1.8	3.5 $\pm$ 6.3	1.1 $\pm$ 2.0	1.5 $\pm$ 3.6
Breeding 1990				1.5 $\pm$ 2.2		55.2 $\pm$ 1.7	2.6 $\pm$ 6.1	1.3 $\pm$ 2.4	1.3 $\pm$ 3.1

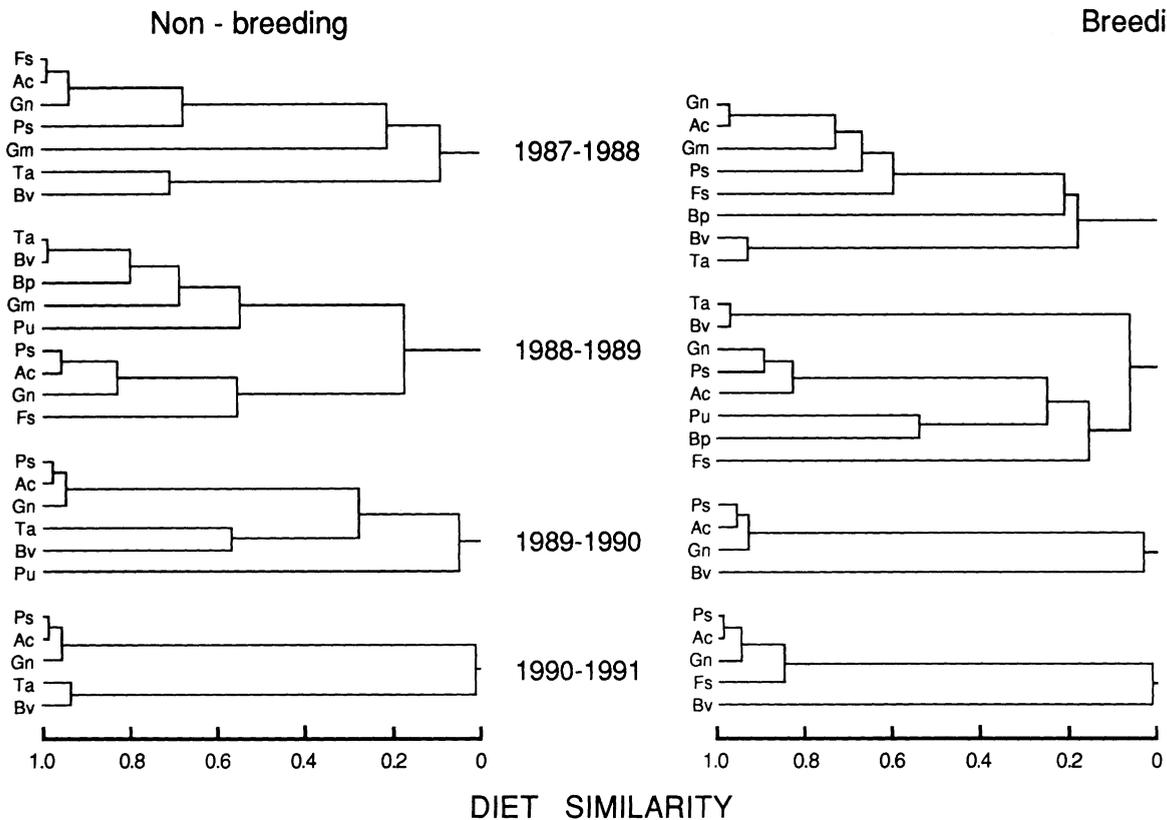


Fig. 1. Guild structure of predators in Aucó: results of UPGMA cluster analysis (see Materials and methods for details) of each season's diet data. Species clusters formed above the 50% level of diet similarity were designated as guilds. Abbreviations as in Table 1, except for Ps = *Pseudalopex* spp.

sumably represent seasons when predators chose not to utilize the habitat patches, perches, or nests we studied, not seasons of actual emigration from the region.

### Mean prey weights

Condensed diet matrices are presented in Jaksić et al. (1992) and thus are not reproduced here.

On average, during a given year, geometric mean prey weight in the diet declined from non-breeding to breeding season for *Glaucidium*, *Geranoaetus* (one complete year only) and the two *Pseudalopex* (Table 2). The opposite trend was apparent for *Bubo* and *Parabuteo* (one complete year only for the latter). The remaining four species showed no clear trends. *Geranoaetus* and *Parabuteo* took relatively large prey; *Athene*, *Falco*, *Glaucidium*, and the two *Pseudalopex* took relatively small prey, including many arthropods; and the remaining three species took intermediate prey sizes. Standard deviations of mean prey weight varied widely among and within species (Table 2).

### Guild membership

Two guilds with rather constant membership persisted throughout the study (Fig. 1). First, *Bubo* and (when present) *Tyto* maintained high diet overlap (Table 3) and formed a tight mammal-eating guild. Mammals, primarily *Phyllotis darwini*, made up 83–100% of the diet of either species in all seasons. When *Tyto* disappeared from the site during breeding of 1989 and of 1990, *Bubo* remained isolated dietarily (Fig. 1, Table 3) because no other species concentrated on *Phyllotis*. Species in the other consistent guild were omnivorous: *Athene*, *Glaucidium*, and the two *Pseudalopex* foxes remained consistently associated in cluster analyses due to their 36–98% arthropod diet component and their additional broad exploitation of all vertebrate classes available at the site.

Often these two guilds, hereafter labelled “mammalivorous” and “omnivorous,” included other consumer species as well. *Falco*, with an arthropod-rich (33–82%) diet and a secondary concentration on birds, joined the omnivorous guild during four of its five seasons of residence (Fig. 1). *Geranoaetus* varied widely in its guild

Table 3. Food-niche overlaps for predators at Aucó through successive non-breeding and breeding seasons. Figures are percent diet similarities. Those above the diagonal are for non-breeding seasons; below, for breeding seasons. Predator abbreviations as in Table 1.

Year	<i>G. m.</i>	<i>F. s.</i>	<i>T. a.</i>	<i>A. c.</i>	<i>B. v.</i>	<i>G. n.</i>	<i>P. c./P. g.</i>		
1987									
<i>Geranoaetus melanoleucus</i>		24.0	5.0	19.0	14.0	4.0	37.0		
<i>Falco sparverius</i>	53.0		0.2	99.0	0.3	94.0	94.0		
<i>Tyto alba</i>	43.0	6.0		0.3	71.0	2.0	56.0		
<i>Athene cunicularia</i>	71.0	69.0	6.0		0.4	94.0	0.2		
<i>Bubo virginianus</i>	41.0	1.0	93.0	3.0		2.0	14.0		
<i>Glaucidium nanum</i>	76.0	73.0	14.0	97.0	13.0		91.0		
<i>Pseudalopex culpaeus/griseus</i>	71.0	44.0	23.0	65.0	22.0	65.0			
<i>Buteo polyosoma</i>	49.0	12.0	8.0	22.0	34.0	6.0	18.0		
1988									
	<i>F. s.</i>	<i>T. a.</i>	<i>A. c.</i>	<i>B. v.</i>	<i>G. n.</i>	<i>P. c./P. g.</i>	<i>B. p.</i>	<i>P. u.</i>	
<i>Geranoaetus melanoleucus</i>	6.0	74.0	2.0	73.0	4.0	11.0	59.0	42.0	
<i>Falco sparverius</i>		2.0	53.0	3.0	59.0	54.0	24.0	10.0	
<i>Tyto alba</i>	1.0		2.0	99.0	22.0	12.0	80.0	55.0	
<i>Athene cunicularia</i>	15.0	4.0		3.0	80.0	96.0	44.0	1.0	
<i>Bubo virginianus</i>	0.1	98.0	4.0		24.0	13.0	80.0	56.0	
<i>Glaucidium nanum</i>	1.3	5.0	87.0	7.0		85.0	61.0	43.0	
<i>Pseudalopex culpaeus/griseus</i>	49.0	6.0	80.0	8.0	90.0		53.0	8.0	
<i>Buteo polyosoma</i>	16.0	13.0	39.0	15.0	52.0	47.0		65.0	
<i>Parabuteo unicinctus</i>	0.0	6.0	2.0	7.0	8.0	6.0	54.0		
1989									
	<i>A. c.</i>	<i>B. v.</i>	<i>G. n.</i>	<i>P. c./P. g.</i>	<i>P. u.</i>				
<i>Tyto alba</i>	0.1	57.0	4.0	3.0	0.6				
<i>Athene cunicularia</i>		53.0	96.0	98.0	0.1				
<i>Bubo virginianus</i>	5.0		52.0	56.0	3.0				
<i>Glaucidium nanum</i>	93.0	2.0		95.0	16.0				
<i>Pseudalopex culpaeus/griseus</i>	96.0	2.0	92.0		7.0				
1990									
	<i>F. s.</i>	<i>A. c.</i>	<i>B. v.</i>	<i>G. n.</i>	<i>P. c./P. g.</i>				
<i>Tyto alba</i>		2.0	95.0	0.0	2.0				
<i>Athene cunicularia</i>	83.0		0.4	96.0	99.0				
<i>Bubo virginianus</i>	0.0	0.3		1.0	2.0				
<i>Glaucidium nanum</i>	88.0	95.0	3.0		97.0				
<i>Pseudalopex culpaeus/griseus</i>	84.0	99.0	2.0	95.0					

affiliation. During the 1987 non-breeding season, *Geranoaetus* emerged alone in the cluster analysis (Fig. 1, Table 3) due to a unique diet combination of the mammal *Octodon degus* (40%) and reptiles (also 40%). During the 1987 breeding season *Geranoaetus* joined the omnivorous guild, consuming not only a variety of rodents (but no *Octodon*) and reptiles but also some birds and arthropods. During the 1988 non-breeding season *Geranoaetus* switched to the mammalivorous guild, concentrating heavily on rodents (60%) that included *Phyllotis* but not *Octodon*.

*Parabuteo* joined the mammalivorous guild during the 1988 non-breeding season, consuming not only many *Octodon* but also many *Phyllotis* and thus converging on the diets of *Bubo* and *Tyto* (Fig. 1, Table 3). Increasing concentration on *Octodon* during the 1988 breeding season separated *Parabuteo* from the owls. Further concentration on *Octodon* during the 1988 non-breeding season isolated *Parabuteo* even further in the cluster analysis (Fig. 1). *Buteo* occupied a position inter-

mediate between the mammalivorous and omnivorous guilds during the 1987 breeding season, due to an unusual combination of rodents, reptiles, and invertebrates in the diet. During the non-breeding season of 1988, however, *Buteo* consumed relatively more mammals (including *Phyllotis*) and fewer reptiles, consequently joining the mammalivorous guild in the cluster analysis. In the 1988 breeding season, *Buteo* again increased consumption of reptiles and invertebrates, joining *Parabuteo* due to their shared concentration on *Octodon* (Fig. 1, Table 3).

### Guild structure

Except for 1988, when guild nodes were higher (diets were more similar among species) in non-breeding than in breeding season (Wilcoxon paired-sample signed-ranks test,  $P < 0.03$ ), levels of guild nodes in the cluster

analysis did not shift significantly from non-breeding season to subsequent breeding season (Wilcoxon tests, all  $P_s > 0.10$ ). Pooling all pairs of guild nodes from non-breeding and breeding seasons of each of the four years, species clustered significantly more tightly into guilds during non-breeding seasons than during subsequent breeding seasons (Wilcoxon test  $P < 0.001$ ). That is, diets of consumer populations converged during non-breeding seasons and diverged during breeding seasons.

Given the irruption and decline in small mammal densities that occurred during the study, we examined whether levels of diet similarity changed among those species that resided for the duration of the study (*Athene*, *Bubo*, *Glaucidium*, and the two *Pseudalopex*). Similarities among diets of these species in the cluster analysis (Fig. 1; cf. Table 3) tended to be greater on average during 1987–1988 than during 1989–1990, but not significantly so (Wilcoxon test;  $P > 0.25$ ). Thus, in terms of guild structure there was no clear response on the part of these five resident predators to the dramatic irruption or decline in mammal abundances.

## Discussion

### Fat and lean periods?

At Aucó, the onset of the typical breeding season as defined here is marked by a flush of vegetative production brought about by winter rains. Although we made no direct measures of productivity or standing crop for any group except small mammals, insects and small birds clearly increased in density soon after each springtime's vegetative flush. During the latter portion of the 6-mo breeding season (i.e., after winter/spring rains had ceased) density of foliage, insects, and birds began to decline (pers. obs.), a decline accentuated by the onset of the rainless non-breeding season. Nevertheless, as estimated by the trapping data summarized in Table 1 (see also Jiménez et al. 1992), the abundance of small mammals showed no such density changes between breeding and non-breeding seasons. While it is possible that trapping methods underestimated the availability of juvenile prey during the breeding season (thereby underestimating "fatness" of the resource base from the predators' perspective), it is also possible that a given number of small mammals was actually more accessible to predators in non-breeding than in breeding seasons due to the lack of foliage cover during the former. Apparently, then, annual breeding and non-breeding seasons most likely corresponded to "fat" and "lean" periods for Aucó predators when non-mammalian food resources, but not mammalian prey, were considered.

Instead, "fat" and "lean" periods among small-mammal prey involved a scale of several years (Jaksić et al. 1992, Jiménez et al. 1992, cf. Wiens 1977). Densities of these prey at the "lean" conclusion of our study were <

10% of densities at its "fat" onset. In contrast, through the course of the study we noted no marked long-term decline in the abundance of the other food classes, such as fruits, reptiles, insects, or passerine birds. Thus, there is no consistent "lean-fat" scenario at Aucó; rather, the site experiences a pronounced multi-year shift (cycle?) in density of a major prey category, superimposed on an apparent annual cycle in abundance of other prey classes.

### Predator responses

Based on the complex shifts in food availability for predators at Aucó, we might have expected the following responses among predators (cf. Erlinge et al. 1982, 1984): (a) seasonal diet shifts among the more omnivorous species, with convergence on preferred food sources during breeding seasons and divergence during non-breeding seasons; (b) emigration of small-mammal specialists, or else exploitation of alternate foods and thus convergence with omnivores as mammalian prey densities crashed; (c) overall, the most flexible guild structure, with great divergence among diets of the species still remaining on the site, during the leanest periods. Such an outcome would parallel those found in previous studies or models (e.g., Zaret and Rand 1971, Feinsinger 1976, M'Closkey 1976, Wiens 1977, Herrera 1978, Rotenberry 1980, Feinsinger et al. 1985). The observed outcome among Aucó predators, however, was actually much more complex than that expected despite the relative simplicity of the system (see also Jaksić et al. 1992).

Although shifts in guild structure (Fig. 1) imply that several mammal-eating species fled the region in response to declining prey abundance, among strict mammal-eaters we failed to record only *Tyto* either in visual or prey-remains censuses during two seasons late in the study. Even so, *Tyto* continued to appear sporadically during winter (non-breeding) seasons (cf. Table 1) and may actually have been present at the study site at undiscovered nests or roosts during the corresponding breeding seasons. Another strict mammal-eater, *Bubo*, remained throughout the study. The three mainly mammalivorous hawks decreased their use of the study site as mammalian prey declined (Table 1, Fig. 1) but remained in the region. In addition, reliance on mammalian prey alone cannot be proposed as the direct cause of hawks' altered patch choice. Diets of all three species – *Buteo*, *Geranoaetus*, and *Parabuteo* – varied greatly among seasons, frequently bringing one or another into close dietary proximity with the omnivorous group (Fig. 1). Furthermore, *Geranoaetus* and *Parabuteo* actually increased their relative consumption of the increasingly scarce mammals before abandoning the study site, whereas *Buteo* decreased mammal-eating and became more omnivorous before its departure.

Other than *Bubo* and *Tyto*, the resident species (*Ath-*

ene, *Glaucidium*, and the two *Pseudalopex*) remained in a relatively tight omnivorous guild throughout the study, regardless of season or year (Fig. 1). Only the omnivorous *Falco sparverius* demonstrated any sort of classic response to “leanness,” by decreasing its use of the study site during non-breeding seasons and leaving the study site (but not the region) entirely during the two non-breeding seasons late in the study. In short, nearly every species displayed a unique response to the complex scenario of food availability at Aucó.

### Responses of guild structure

The individualistic responses of many predator species did not overwhelm a basic, consistent guild structure at Aucó (Fig. 1), which persisted in the face of substantial changes in the food resource base. Clusters of four omnivores (*Athene*, *Glaucidium*, the two *Pseudalopex*) and two mammalivores (*Bubo* and *Tyto*) always occurred (except for the two breeding seasons when *Tyto* was not resident by our criteria). Superimposed on this basic structure were the four falconiforms that skipped about in diet hyperspace (Fig. 1) and apparently in feeding site as well. This correspondence between diet flexibility and wide-ranging habitat use apparently characterizes some members of other feeding guilds as well (e.g., Herrera 1978, Erlinge et al. 1982, 1984). Although none of the species we studied is apparently a true migrant (cf. Jaksic et al. 1990), the picture of a basic, consistent guild structure among sedentary species underlying more loosely organized dietary relationships among less habitat-specific species resembles that drawn for some consumer guilds consisting of resident species and complete seasonal migrants (e.g., Feinsinger 1976, M'Closkey 1976, Herrera 1978, Wagner 1981, Erlinge et al. 1982, 1984, Korpimäki 1985).

### Why don't predators respond “classically” to lean-fat periods?

Neither guild structure in general nor the relationships between predator diets in specific shifted as expected either among seasons or among phases in the abundance of small-mammal prey. Among many possible reasons, we stress three non-exclusive possibilities: (a) food classes may be quite discrete; (b) true “fat-season” immigrants did not exist in this landscape; and (c) food itself was never extremely limited from the point of view of the predators.

Most studies that demonstrate shifts in diet overlap in response to “fat” and “lean” seasons involve feeding guilds whose resources comprise a relatively continuous distribution of characteristics, such as the nearly continuous distribution of prey sizes available to fishes (Zaret and Rand 1971), of seed sizes available to granivorous mammals (M'Closkey 1976), or of flower characteristics

available to some tropical nectar-feeding birds (Feinsinger 1976, Feinsinger et al. 1985). In Aucó, prey categories (e.g., passerine birds, one species of snake, two or three of lizards, one racerunner, one toad, a few species of large insects, eight distinct small-mammal species) were relatively discrete from one another, each requiring quite different foraging techniques on the part of predators (see Jaksic et al. 1992). Although diets of many predators contained a variety of these groups, the discrete nature of prey categories may have inhibited some predators from “gliding smoothly” among resource classes and making gradual shifts in diet in response to seasonal or supra-annual shifts in relative abundance of food. The mass of the mean food item in the diets of most predators varied surprisingly little in the face of major shifts in prey abundance (Table 2), indicating that most predators had fairly fixed preferences in terms of food particle size if not necessarily food species (see also Jaksic et al. 1992). Thus, predators at Aucó, although often flexible in diet, may not have been sufficiently flexible to feed entirely opportunistically on the distinct food items available to them.

The lack of clear shifts in guild structure at Aucó might also reflect the regional absence of truly migratory species able to respond to “fat” seasons (cf. Erlinge et al. 1982, 1984, Korpimäki 1985). Elsewhere (Jaksic et al. 1990) we point out that avian carnivore guilds on other continents are often joined by highly migratory, opportunistic species during prey outbreaks or other “fat” times. Apparently, no species that was present during the “fat” period we examined at Aucó was a true migrant; some individuals of each continued to persist in the larger-scale landscape. The absence of long-distance migrants from Aucó may be a consequence of Chile's unique geography: enclosed by the open ocean to the west and south, the high Andes to the east, and the Atacama desert to the north (Jaksic et al. 1990).

Finally, it is possible that predators did not perceive any part of the apparent fluctuations in food resources at Aucó as a “lean-fat” scenario. Even the seasons of lowest density among mammalian prey may not have been sufficiently severe to drive predator diets in divergent directions (cf. Wiens 1977, 1990b: 9). Alternatively, the sporadic occurrence of “lean” periods may limit predator populations regionally such that no tracking of “fat” periods is possible. Elsewhere (Jaksic et al. 1992) we demonstrate that local predators did not show either pronounced functional or numerical responses to the shifts in mammal density at Aucó, other than the falconiforms' abandonment of the study site as a hunting patch. In company with the absence of opportunistic complete migrants, and the discrete nature of food categories, irrelevance of the “fat-lean” scenario to Aucó predators may explain the complex patterns we found in their guild dynamics.

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