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. Jimenez


For 48 mo we monitored diets and populations of 10 species of predaceous vertebrates (two lizards, five falconiforms, and four owls) in semi-arid scrub at Asoro, Chile. Pollen (shrubs) and bees (sedges) collected monthly contained identifiable remains of small mammals, birds, reptiles, amphibians, large insects, other arthropods, and (in some 10 loci) 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 "fast" times and converging opportunistically during "fat" times, predators at Asoro 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 gleaning 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 hypercycles" or else occupied temporarily one of the two gleaning guilds. The degree to which falconiforms were unique in a given season showed no clear relation to food abundance. Changes in use of habitat did, however, resist to changes in food abundance. None of the microtines resided continuously in the study area throughout the period, and their presence was particularly sporadic late in our study even for falconiform species that were not particularly mammalivorous. The lack of simple patterns among Asoro predators in response to variation in "fast" and "fat" times may result from one or more of the following: (a) from predators' responses, food classes at Asoro may be quite diverse, inhibiting gradual diet shifts by owls and foxes to at least; (b) true opportunistic immigrants that might have increased overall diet overlap during "fat" times, as sometimes occurs in other consumer assemblages do not exist in the Asoro 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 "fast" and "slow" 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; Er- linge et al. 1982, 1984; Feinsinger et al. 1985; Korpimaki 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-rich periods. Some cases involved a consistent set of guild members that coexisted year-round, whereas others clearly showed fast-season invasions by various numbers of immigrant species, often with convergent diets, over layering 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 fish (Za- ret and Razi 1971; Schmid-Hempel and Holbrook 1986), lizards (Dunham 1980), Mediterranean-climate passerines (Hererra 1978), Galapagos finches (summa- rized by Grant 1986), shorebirds (Baker and Baker 1973), foliage-gleaning birds (Root 1967, Ulstrand 1977; Wagner 1985), nectar-feeding birds (Feinsinger 1976, Feinsinger et al. 1985), shrubsteppe or desert birds (Rosenberry 1980, Maurer 1985), tropical forest birds (Karr and Freeman 1983), and rodents (MClos- key 1976, Liljewall and Jenkin 1987). Recently, however, Jakub et al. (1990) reported that in two of three-year study of assemblages of raptors' 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 in tense to generate recognizable responses among raptors. Here we report on an extension of one of these three studies over a 43yr period that included an irrup- tion and prolonged decline of a major resource class, small mammals. Our results suggest that some pred- 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°17'S, 7°16'W). 300 km north of San- tiago, Chile. Located in the coastal ranges the 422ha Reserve has a rugged topography with numerous ridges dissected by deep ravines and few level areas. Eleva- tions 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 diot shrubs, terrestrial bromeliads, and cacti. Slopes that face north (equatorial) receive higher solar radi- ation than south-facing slopes, and have sunny open soils with scattered gravel patches and rock outcrops. On the xeric north-facing slopes, grasses are scarce (mainly Suaeda spp. and Sisyrh spp.), but cacti (Tricho- cereus spp., Trichocereus ovatus), bromeliads (Puya beterianua), and sclerophyllous shrubs (Babiana ambi- stoutetes, Cordia decandra, Bridelia insigniflora, Flos- rennaia shartifera) are abundant. In contrast, the more mesic slopes that face south (solar) support many grasses but few cacti and no Puya; furthermore, a differ- ent assemblage of shrubs prevails (Adecuenn spp., Po- lieaia chilensis, Collinsaea odorifera, Proctotrupes spp.). Gajardo (1978) provides further descriptions of the vegeta- tion 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 trap- ping grids: two on opposite-facing slopes of El Grillo, and two on slopes of El Cobre. All 7 x 7 trapping grids had trapping stations separated by 1 m, providing a sample area of 105 x 105 m (including a boundary strip of 7.5 m), or 1.1 ha. Each station contained one Sher- man trap (south-facing slopes) or one Sherman and one Tomahawk-like trap (north-facing slopes). Kept perma- nently in the field, traps were closed when not in use and were activated during five nights of each month (trapping effort = 735 trap-nights/ha over 2.2 hai
Monitoring predator populations

We kept monthly records of visual tallies of predators at the site. Twelve species were most commonly sighted: the falconiforms Buteo regalis (red-backed hawk), Falco sparverius (American kestrel), Geranoaetus melas (black-backed hawk), and Panaurus ussuriensis (Harris hawk); the striated plovers Arenaria cineraria (burrowing owl), Uto virginiensis (horned owl), Glau
colius magnirostris (pacific pygmy owl), and Tito alba (burn owl); the canids Canis latrans (red fox) and P. rufus (Chihuahua fox); the canidaphid Phalaenopsis chacota (long-tailed skunk); and the toxicid Cal
topia palliata (Chilean raccoon). We considered a given species to be "residents" at the site if we detected sustained occupation of nests, perches, nests, or dens (raptors and foxes) or observed individuals (snakes, lizards) in addition found at least five pellets (raptu
rs) or feces (foxes and raccoons) 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, raccoons), from March 1987 through February 1991. In the lab
atory, pellets and feces were carefully teased apart under a dissecting microscope, and prey or plant foods were identified by the maximum level of resolution (spe
ific for vertebrates and plants, ordinal for inverte
brates). In particular, remains of mammal prey were identified to species level by reference to keys (Reis 1973) and locally collected voucher specimens. The minimum number of individual mammal prey present in pellets or feces was estimated by the maximum number of double or single anatomical elements such as crania, nanatiles, or tooth rows (Mark 1987). Analytical tech
iques were used to determine minimum numbers for other prey taxa and for fruit 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. chacoensis was a permanent resident at the site, we could not find its feces. The rainforest C. palliata also resided per
manently, but after the first year of data collection (reported by Caso et al. 1991) we were unable to obtain enough feces for analysis. It should be noted that, using echotomography, the prey consumption rates of these two species should be considerably lower than those of the raptors and foxes. In addition, their activi
ty periods are restricted to the warmer months of the ye
ar.

Characterizing guild membership and structure

We calculated geometric mean weight of prey as:

\[ GMWP = \sum \frac{p_i}{5} \cdot S_i \cdot W_i \]

where \( p_i \) is the relative incidence of prey categories i in the given predator's diet, \( S_i \) is the mean weight of prey \( i \) (Jaksic and Braker 1983). This procedure partially com
pensates for the skewed distribution of prey sizes in most predator diets.

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

\[ O = \frac{2pq}{S_{12}} \]

where \( p \) and \( q \) are the relative occurrences of prey categories i in the diets of the two predators, respectively. \( O \) ranges from 0.0 to 1.0 (0.186 = overlap). We ap
plied 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 in
vertebrates (cf. Greene and Jaksic 1983).

Using entries in the diet similarity matrices con
structed for calculating \( O \), we applied the unweighted pair-group clustering method with arithmetic averaging (UPGMA, Smith and Saks 1971) following Jaksic and DeBiejs (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 sim
ilarity. Less arbitrary means of defining guilds (e.g., Jaksic and Model 1990) would result in results 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

OQTEC (1997)
Table 1. Numbers of peregrines (Falco peregrinus) and Merlin (Falco columbarius) at Aucu, 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). No = no data taken that season. Masses of predators from Liseo et al. (1992).

<table>
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<tr>
<th>Predator species</th>
<th>Mass (g)</th>
<th>NB75</th>
<th>NB75</th>
<th>NB85</th>
<th>NB85</th>
<th>NB85</th>
<th>NB85</th>
<th>NB85</th>
<th>NB85</th>
<th>Total</th>
</tr>
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<td>Falco peregrinus</td>
<td>116</td>
<td>15</td>
<td>8</td>
<td>5</td>
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<td>0</td>
<td>0</td>
<td>31</td>
<td>94</td>
<td>116</td>
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<tr>
<td>Gypaetus melvillii</td>
<td>2295</td>
<td>15</td>
<td>8</td>
<td>9</td>
<td>9</td>
<td>0</td>
<td>0</td>
<td>335</td>
<td>344</td>
<td>2295</td>
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<td>1</td>
<td>1</td>
<td>876</td>
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<td>19</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>375</td>
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<td>Glaucomys anomalus</td>
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<td>100</td>
<td>76</td>
<td>129</td>
<td>118</td>
<td>81</td>
<td>11</td>
<td>71</td>
<td>23</td>
<td>86</td>
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<td>Athene cunicularia (A.)</td>
<td>247</td>
<td>214</td>
<td>25</td>
<td>101</td>
<td>59</td>
<td>58</td>
<td>3</td>
<td>217</td>
<td>154</td>
<td>461</td>
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<td>Tody atricauda</td>
<td>307</td>
<td>31</td>
<td>104</td>
<td>81</td>
<td>71</td>
<td>21</td>
<td>0</td>
<td>56</td>
<td>104</td>
<td>361</td>
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<td>Bubo virginianus (B. v.)</td>
<td>1277</td>
<td>187</td>
<td>194</td>
<td>260</td>
<td>433</td>
<td>62</td>
<td>4</td>
<td>71</td>
<td>10</td>
<td>1348</td>
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<td>Porphyroptera rubra (P. r.)</td>
<td>7687</td>
<td>84</td>
<td>176</td>
<td>804</td>
<td>378</td>
<td>484</td>
<td>225</td>
<td>286</td>
<td>249</td>
<td>2776</td>
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<tr>
<td>No. resident species</td>
<td>3</td>
<td>8</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>5</td>
<td>5</td>
<td>6</td>
<td>6</td>
<td>23</td>
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<tr>
<td>Total small mammal density (No./ha)</td>
<td>222</td>
<td>228</td>
<td>209</td>
<td>98</td>
<td>30</td>
<td>15</td>
<td>21</td>
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<tr>
<td>Predators (No./ha)</td>
<td>47</td>
<td>nd</td>
<td>165</td>
<td>140</td>
<td>65</td>
<td>18</td>
<td>11</td>
<td>9</td>
<td>21</td>
<td>88</td>
</tr>
<tr>
<td>Owls (No./ha)</td>
<td>123</td>
<td>nd</td>
<td>12</td>
<td>9</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>&lt;1</td>
<td>0</td>
<td>123</td>
</tr>
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</table>

For a given non-breeding season were pired 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 longicaudus, Akodon olivaceus, Onychomys longicaudus, and Phytolepis darwinii) (all Cricetidae), Abrocoma fraxinis (Abrocomidae), Chinchilla laniger (Chinchillidae), and Otomys degus (Otomidae) and a mustelid, Marmota elegans (Didelphidae). During the winter of 1987 (July-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 values. 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 Aucu throughout breeding of 1980 and again during breeding of 1990 but not in-between. Geranoaetus not resident at the site only during the first three seasons of the study, as did Bubo, which appeared at Aucu 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 Glaucomys, as well as both species of Pseudopodopterus (as verified by sightings), resided throughout the study. Tody resident continuously at Aucu from non-breeding of 1987 through non-breeding of 1989, disappeared from the study site during the following season, reappeared during non-breeding of 1990, and disappeared afterward. Even during these absences, though, we found evidence of active Tody nests in areas just outside the Reserve. Except for Tody, we sighted all species of predators in the areas surrounding the study site even during seasons when they were not residents as defined above. Thus, seasons of non-occurrence pre-

Table 2 Geometric mean prey weights ± SD (g) of Aucu predators over the season of the study. See Materials and Methods for method of calculation. Predator abbreviations as in Table 1.

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</thead>
<tbody>
<tr>
<td>Non-breeding 1987</td>
<td>99.8±2.2</td>
<td>1.6±0.3</td>
<td>47.6±0.8</td>
<td>67.4±2.2</td>
<td>3.5±0.9</td>
<td>1.2±0.3</td>
<td>3.9±0.7</td>
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<tr>
<td>Breeding 1987</td>
<td>44.5±8.8</td>
<td>9.0±0.7</td>
<td>43.8±2.5</td>
<td>43.3±1.7</td>
<td>3.0±0.6</td>
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<td>1.8±0.7</td>
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<tr>
<td>Non-breeding 1988</td>
<td>81.6±2.0</td>
<td>62.7±1.9</td>
<td>62.3±2.0</td>
<td>45.6±1.5</td>
<td>1.6±0.3</td>
<td>1.1±0.2</td>
<td>2.6±0.5</td>
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<tr>
<td>Breeding 1988</td>
<td>18.5±2.7</td>
<td>1.0±0.1</td>
<td>18.9±2.0</td>
<td>41.5±0.7</td>
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<tr>
<td>Non-breeding 1990</td>
<td>77.9±2.7</td>
<td>16.8±0.9</td>
<td>16.8±0.9</td>
<td>16.7±0.9</td>
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<td>Breeding 1990</td>
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<tr>
<td>Non-breeding 1991</td>
<td>52.6±2.1</td>
<td>55.2±3.7</td>
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(8) (OKCOT/1/1990)
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 Jakić 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, Cereniornis (one complete year only for the latter). The remaining four species showed no clear trends. Cereniornis and Parahalcy took relatively large prey, Athene, Falco, Glaucidium, and the two Pseudalopex took relatively small prey, including many enoplaids; 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 consistent membership persisted throughout the study (Fig. 1). First, Falco and (when present) Tyto maintained high diet overlap (Table 3) and formed a tight mammal-eating guild. Mammals, primarily Phyllotis darmani, 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, Falco remained isolated diectically (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 non-mammal species as well. Falco, with an arthropod-rich (33-42%) diet and a secondary concentration on birds, joined the omnivorous guild during four of its five seasons of residence (Fig. 1). Cereniornis varied widely in its guild.

Fig. 1. Guild structure of predators in Acon. 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 in Table 1, except for Ps = Pseudalopex spp.
<table>
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<th>Year</th>
<th>G. m.</th>
<th>F. s.</th>
<th>T. s.</th>
<th>A. c.</th>
<th>B. v.</th>
<th>G. n.</th>
<th>P. c.-P. g.</th>
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<td></td>
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<td>70.0</td>
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Affiliation. During the 1987 non-breeding season, Gera-
nonias emerged alone in the cluster analysis (Fig. 1, Table 3) due to a unique diet combination of the mam-
mal Octodon degus (40%) and reptiles (also 40%). Dur-
ing the 1987 breeding season, Geranoonas consumed not only a variety of ro-
dents (but no Octodon) and reptiles but also some birds and antropods. During the 1988 non-breeding season, Geranoonas switched to the mammalivorous guild, con-
centrating heavily on rodents (60%) that included Phyl-
losis but not Octodon. The mammalivorous guild during the 1988 non-
breeding season, consuming not only many Octodon but also many Phyllosis and thus con-
venging on the diets of Bubo and Tyto (Fig. 1, Table 3). Increasing concentration on Octodon during the 1988 breeding season separated Parahano from the two. Further concentration on Octodon during the 1988 non-
breeding season isolated Parahano even further in the cluster analysis (Fig. 1). Parahano occupied a position inter-
mediate between the mammalivorous and omnivorous
guilds during the 1987 breeding season due to an un-
usual combination of rodents, reptiles, and inverte-
brates in the diet. During the non-breeding season of 1988, however, Bubo consumed relatively more mam-
mals (including Phyllosis) and fewer reptiles, conse-
quently joining the mammalivorous guild in the cluster analysis. In the 1988 breeding season, Bubo again in-
creased consumption of reptiles and invertebrates, join-
ing Parahano due to their shared concentration on
Octodon (Fig. 1, Table 3).

Guild structure
Except for 1988, when guild nodes were higher (with more similar species) in non-breeding than in breeding season (Wisconsin pairwise signed-ranks test, P < 0.05), levels of guild nodes in the cluster
analyzed did not shift significantly from non-breeding season to subsequent breeding season (Wilcoxon tests, all Ps > 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 (Arri- ene, Bufo, Glaucomium, and the two Pseudalpines). Similarities among diets of these species in the cluster analysis (Fig. 1; cf. Table 5) 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 measurements 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 associated with the onset of the rainless non-breeding season. Nevertheless, as estimated from 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 understimating "fattens" 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 (Jasik et al. 1992, Jiménez et al. 1992, cf. Wiens 1977). Densities of these prey at the "lean" conclusion of our study were < 30% 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. Erliing et al. 1982, 1983): (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 declined; (c) overall, the most flexible guild structure, with great divergence among diets of the species still remaining on the site, during the least periods. Such an outcome would parallel trends found in previous studies or models (e.g., Zaret and Rand 1971, Feininger 1976, M. C. 1976, Wiens 1977, Herrera 1979, Bartenberry 1980, Feininger 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 Jakie 1992).

Although shifts in guild structure (Fig. 1) imply that several mammal-eating species fixed the region in response to declining prey abundance, among strict mammal-eaters we failed to record only Tyro either in visual or prey-remains censuses during two seasons late in the study. Even so, Tyro continued to appear sporadically during winter (non-breeding) seasons (cf. Table 1) and may actually have been present at the study site at undetected nests or roosts during the corresponding breeding seasons. Another strict mammal-eater, Bufo, remained throughout the study. The three mainly mammalian hawks decreased their use of the site study at 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 — Bufo, Geranisus, and Phasianus — varied greatly among seasons, frequently bringing one or another into close dietary proximity with the omnivorous group (Fig. 1). Furthermore, Geranisus and Phasianus actually increased their relative consumption of the increasingly scarce mammalian prey, whereas Bufo decreased mammal-eating and became more omnivorous before its departure.

Other than Bufo and Tyro, the resident species (Arri-
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 omni-vores (Athene, Glaucomimus, the two Pseudotopas) and two mammalvores (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 families that specialized in diet hypervarice (Fig. 1) and apparently were feeding sites as well. This coexistence between diet flexibility and wide-ranging habitat use apparently characterized some members of other feeding guilds as well (e.g., Herrera 1978, Ernleig et al. 1982, 1984). Although none of the species we studied in apparently a true migrant (cf. Jakšić et al. 1996), the picture of a basic consistent guild structure among solitary 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., Feininger 1976, M'Closkey 1976, Herrera 1978, Wagner 1981, Ernleig et al. 1982, 1984, Kopninski 1985).

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

Neither guild structure is general nor the relationships between predator diets in specific shifts as expected either among species 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 (Feininger 1976, Feininger et al. 1985). In Aucó, prey categories (e.g., passerine birds, one species of three, two or three of lizards, one raccoon; one kind of one 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 Jakšić 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 class and making gradual shifts, in a response to seasonal or supra-annual shifts in relative abundance of food. The mass of the mean food item in the diets of most predator 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 Jakšić 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. Ernleig et al. 1982, 1984, Kopninski 1985). Elsewhere (Jakšić 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 high migratory density, and the open ocean to the west and south, the high Andes to the east and the Atacama desert to the north (Jakšić 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 different directions (cf. Wiens 1977, 1980, 1990). Alternatively, the sporadic occurrence of “lean” periods may limit predator populations regionally such that no tracking of “fat” periods is possible. Elsewhere (Jakšić et al. 1992) we demonstrated that local predators did not show either pronounced functional or numerical responses to the shifts in mammal density at Aucó, other than the facultative abandonment of the study site as a hunting patch. In company with the absence of opportunistic small-mammal species, the relative number of prey categories, the irrelevant of the “fat-lean” scenario to Aucó predators may explain the complex patterns we found in their guild dynamics.
References


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