

Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site

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Summary. Occurrence and diet of ten carnivorous predators (four falconiforms, four owls, and two foxes), and population levels of their mammalian prey, were monitored over 45 months at a semi-arid site in north-central Chile. Early in this period, small mammals irrupted and then declined markedly to a density 7% of that at peak. All four falconiforms (*Buteo polyosoma*, *Falco sparverius*, *Geranoaetus melanoleucus*, *Parabuteo unicinctus*) and one owl (*Tyto alba*) responded numerically to the decline in mammalian prey by virtually abandoning the study site. The three other owls (*Athene cunicularia*, *Bubo virginianus*, *Glaucidium nanum*) and the two foxes (*Pseudalopex culpaeus* and *P. griseus*) remained. With few exceptions, throughout the study predators maintained species-specific preferences among small mammal species regardless of the absolute and proportional abundance of these prey. At no time did the two prey species most responsible for the irruption (the rodents *Phyllotis darwini* and *Akodon olivaceus*) occur in predators' diets out of proportion to their estimated relative abundance in the field. Predators were clearly unable to prevent the irruption from occurring. Given the absence of a clear functional response to the most irruptive species, predators seemed unlikely to have been responsible for the observed crash. At present, however, predators may be prolonging the crash and delaying the return of small-mammal populations to typical densities.

Key words: Functional response – Numerical response – Vertebrate predators – Mammalian decline – Chile

Predator-prey interactions among vertebrates involve both the effects of predators on their prey and the effects of changing prey densities on predators. The predation literature concentrates on the former (see reviews in Jaksic and Simonetti 1987; Marti 1987). Ecologists have

long been intrigued by the role of terrestrial vertebrate predators in affecting population levels of their prey (e.g., Elton and Nicholson 1942; Errington 1946; Lack 1954), particularly where prey appear to cycle in density (e.g., Keith 1963; Erlinge et al. 1984; Lindström et al. 1986). Many such studies have been conducted in boreal areas of the Holarctic region, where population cycles of microtines and other vertebrates have provided a testing ground for many hypotheses of population regulation (e.g., Chitty 1960; Andersson and Erlinge 1977; Hörnfeldt 1978; Angelstam et al. 1984; Korpimäki 1985). Relatively few studies exist on the interaction of predators and cycling populations in temperate or subtropical zones (Pearson 1966, 1971; Lidicker 1973).

The other side of the predator-prey interaction, how prey levels may affect the ecology of vertebrate predators, is poorly understood by comparison. Numerous theories, models, and hypotheses exist (e.g., Gilpin 1975; Murdoch and Oaten 1975; Krebs 1978; Rosenzweig 1978; Taylor 1984) but few empirical data (e.g., Holling 1959; Huffaker 1970; Sih et al. 1985; Corbett and Newsome 1987). Most studies that compare diet composition of vertebrate predators to availability of prey in the field are short term, conducted in boreal or temperate areas of the Holarctic region, and restricted to one or a few carnivorous predators that exploit cycling prey populations (see Sih et al. 1985 and Marti 1987 for recent reviews). Exceptions include a study on three temperate-zone hawk species over a 10-year period that included a complete jackrabbit population cycle and a ground squirrel population crash (Steenhof and Kochert 1988), and a 7-year study on predation by dingos following a mammal irruption in arid Australia (Corbett and Newsome 1987).

Predators' reaction to fluctuations in their prey levels involves two complementary phenomena (Taylor 1984): their numerical and functional responses. Numerical responses to a local increase in prey abundance involve immigration from peripheral areas and/or in situ reproduction (Solomon 1949). Conversely, numerical re-

sponses to a local decline in prey abundance involve emigration, decreased reproduction, higher mortality among predators, or some combination. Functional responses involve changes in the individual foraging behavior of a predator (Holling 1959). With increasing abundance of certain prey, an individual predator increases consumption of that prey, either linearly or curvilinearly in proportion to prey abundance, but in either case reaches an asymptote set by satiation levels (Taylor 1984).

We report here on a study covering 45 months in a semi-arid neotropical site. We consider the patterns of numerical and functional response by ten sympatric vertebrate predators concurrent with a marked, post-irruption decline in the density of their mammalian prey.

Methods

Study site

Las Chinchillas National Reserve, near Aucó, Chile (31° 30' S; 71° 06' W), 17 km north of Illapel and 300 km north of Santiago, encompasses 4229 ha of rugged terrain with elevations ranging from 400 to 1700 m and slopes between 18° and 40°. The semi-desert vegetation is related to the prevailing arid climate: rainfall averages 206 mm, 85% of it concentrated in May–September (the austral winter). Annual temperatures average 16° C, with hot summers and cool winters. The dominant vegetation, a low thorn scrub composed primarily of spiny dicot shrubs, bromeliads, and cacti, is described in more detail by Durán et al. (1987).

Monitoring small mammal populations

Amidst the vegetational and physiognomic diversity of the study site, the most prevalent and distinctive habitats available to predators hunting mammalian prey were north-facing and south-facing slopes of ravines. We monitored small-mammal populations on opposite north- and south-facing slopes of each of two ravines 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 ravine, and two on slopes of El Cobre ravine. 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, where colonies of *Chinchilla lanigera*, too large for Sherman traps, existed). Kept permanently in the field, traps were closed when not in use and were activated during 5 nights of each month (trapping effort = 735 trap-nights/month over 2.2 ha). Monthly trapping sessions alternated between El Grillo and El Cobre. More details of trapping procedures are given in Jiménez et al. (in press).

Assessing predators' diets

To estimate predator diets at Aucó, we sampled each month's accumulation of feces along consistent transects (foxes) or of regurgitated pellets at known roosts, perches, or nests (raptors) from March 1987 through November 1990 (45 months). 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. In particular, remains of mammalian prey

were identified to species level (see Greene and Jaksic 1983 for justification) by reference to keys (Reise 1973) and locally collected voucher specimens. The minimum number of individual 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. To provide adequate sample sizes for analysis, pellets and feces were pooled by season: summer (December through February); fall (March through May); winter (June through August); and spring (September through November). Thus, the 45 months of the study were pooled into 15 seasons.

Numerical response of predators

Each month's collection of pellets and feces represented the number accumulated only since the last visit. Deterioration during 1 month was apparently minimal. Because sampling took place along consistent routes, sampling intensity did not vary among months. Thus, numbers of feces and pellets can be used to determine the occurrence and estimate the relative abundance of the predators producing them. Absence of pellets or feces during a given collecting period may be interpreted as absence, or reduced activity, of a given predator at the study site. Substantial increases or decreases in numbers of pellets or feces should reflect changes in activity or density of the local predator population.

Functional response of predators

For those predators that appeared to reside continuously at the site or nearly so, we monitored the relative representation of major prey groups in diets over the 15 seasons of the study. From data pooled within a given season, we estimated diet diversity as $B = 1/\sum(p_i^2)$, where p_i is the relative occurrence of prey category i in a given predator's diet. This index yields values ranging between 1 and n (for n equally used categories; see Levins 1968) and reflects population-wide use of resources regardless of their relative availability (Feinsinger et al. 1981). We computed diet diversity across broad prey categories only – i.e., mammals, birds, reptiles, amphibians, insects, and arachnids – each of which undoubtedly requires different detection abilities, foraging techniques, and capture methods on the part of the predators.

Differential use of mammalian prey by predators

To examine possible functional responses in more detail, we analyzed diets of predators to species level of mammalian prey. Trap data provided a rough index of relative prey availability. By comparing relative frequencies of prey species in predators' diets with estimates of those mammals' relative abundance obtained from trapping data, we could roughly assess whether predators were cueing in on, or avoiding, some prey taxa, and whether predators' preferences changed over time. Goodness-of-fit tests (χ^2) were made between observed (in diet) and expected (in traps) frequencies of small mammals. Small mammal species were pooled whenever necessary to obtain expected frequencies ≥ 5 , as required by the χ^2 test (Sokal and Rohlf 1981). When a given mammal species appeared in a predator's diet more than expected from its field abundance as estimated by trapping, we say that this prey species was "overconsumed" or "preferred", as a shorthand for "overrepresented in predator diet". Similarly, we say that a prey is "underconsumed" or "avoided" when it is found to be underrepresented in a given predator's diet, as gauged by trapping. Consistency of over- or underconsumption over time was evaluated by the sign test (Sokal and Rohlf 1981).

Table 1a, b. Small mammals trapped at Aucó (recalculated from Jiménez et al., in press). Estimated density (number/ha) and percentage of total sample that season, for each species, extrapolated from estimates of minimum number known to be alive on trapping grids

Species	1987		1988				1989							
	Spring		Summer		Fall		Winter		Spring		Summer		Fall	
<i>Abrocoma bennetti</i>	2.2	(1.3%)	0.0	(0.0%)	1.4	(0.5%)	0.4	(0.3%)	0.0	(0.0%)	1.0	(1.8%)	0.4	(1.2%)
<i>Akodon longipilis</i>	1.4	(0.8%)	1.4	(0.5%)	0.0	(0.0%)	1.0	(0.7%)	1.8	(1.3%)	0.0	(0.0%)	0.4	(1.2%)
<i>Akodon olivaceus</i>	16.8	(9.6%)	43.2	(16.0%)	52.2	(18.6%)	23.2	(17.1%)	22.2	(15.4%)	6.8	(13.2%)	3.6	(9.9%)
<i>Chinchilla lanigera</i>	5.0	(2.8%)	6.8	(2.5%)	4.6	(1.6%)	6.0	(4.3%)	6.0	(4.1%)	3.2	(6.1%)	3.2	(8.7%)
<i>Marmosa elegans</i>	6.0	(3.4%)	6.0	(2.2%)	13.6	(4.9%)	4.0	(3.0%)	8.6	(6.0%)	1.4	(2.6%)	3.2	(8.7%)
<i>Octodon degus</i>	12.2	(7.0%)	10.8	(4.1%)	8.2	(2.9%)	10.4	(7.7%)	8.2	(5.6%)	1.4	(2.6%)	3.2	(8.6%)
<i>Oryzomys longicaudatus</i>	1.0	(0.5%)	1.8	(0.7%)	6.8	(2.4%)	5.0	(3.7%)	5.4	(3.8%)	0.0	(0.0%)	0.4	(1.2%)
<i>Phyllotis darwini</i>	130.8	(74.6%)	199.0	(74.0%)	194.6	(69.1%)	86.0	(63.2%)	92.4	(63.8%)	38.0	(73.7%)	22.4	(60.5%)
Total (No./ha)	175.4	(100%)	269.0	(100%)	281.4	(100%)	136.0	(100%)	144.6	(100%)	51.8	(100%)	36.8	(100%)

Species	1989		1990				Species mean overall							
	Winter		Spring		Summer		Fall		Winter		Spring		Species mean overall	
<i>Abrocoma bennetti</i>	0.4	(1.9%)	0.4	(2.3%)	0.0	(0.0%)	0.0	(0.0%)	1.4	(9.7%)	0.0	(0.0%)	0.6	(1.5%)
<i>Akodon longipilis</i>	0.4	(1.9%)	0.0	(0.0%)	0.0	(0.0%)	0.0	(0.0%)	0.0	(0.0%)	0.0	(0.0%)	0.5	(0.5%)
<i>Akodon olivaceus</i>	3.2	(13.5%)	3.2	(15.9%)	1.8	(6.3%)	1.0	(4.8%)	1.8	(12.9%)	0.8	(4.3%)	13.8	(12.1%)
<i>Chinchilla lanigera</i>	1.8	(7.7%)	1.8	(9.1%)	1.8	(6.3%)	2.2	(11.9%)	0.0	(0.0%)	0.0	(0.0%)	3.3	(5.0%)
<i>Marmosa elegans</i>	1.4	(5.8%)	1.0	(4.5%)	2.2	(7.8%)	1.8	(9.5%)	2.2	(16.1%)	1.8	(8.7%)	4.1	(6.4%)
<i>Octodon degus</i>	1.8	(7.7%)	1.8	(9.1%)	0.4	(1.5%)	0.4	(2.4%)	0.0	(0.0%)	0.0	(0.0%)	4.5	(4.6%)
<i>Oryzomys longicaudatus</i>	1.8	(7.7%)	0.0	(0.0%)	0.0	(0.0%)	0.4	(2.4%)	0.0	(0.0%)	0.0	(0.0%)	1.7	(1.7%)
<i>Phyllotis darwini</i>	12.8	(53.8%)	11.8	(59.1%)	22.8	(78.1%)	13.2	(69.0%)	8.6	(61.3%)	18.2	(87.0%)	65.4	(68.2%)
Total (No./ha)	23.6	(100%)	20.0	(100%)	29.0	(100%)	19.0	(100%)	14.0	(100%)	20.8	(100%)	93.9	(100%)

Results

Mammalian prey species and abundances

Eight common species of small mammals were captured at the site (Table 1). Seven were rodents: *Akodon longipilis*, *A. olivaceus*, *Oryzomys longicaudatus*, and *Phyllotis darwini* (all Cricetidae), *Abrocoma bennetti* (Abrocomidae), *Chinchilla lanigera* (Chinchillidae), and *Octodon*

degus (Octodontidae). The only marsupial was *Marmosa elegans* (Didelphidae).

A small-mammal outbreak occurred during winter of 1987 in the study site (Jiménez et al., in press). Overall density of small mammals, about 175 individuals/ha when we began monitoring them in spring 1987, increased steadily to a peak of 281/ha in fall 1988 and then declined markedly through 145/ha in spring 1988, to 20/ha in spring 1989 and 21/ha in spring 1990 (Table 1).

Table 2. Numbers of pellets (raptors) and feces (foxes) collected at Aucó. A zero indicates that a predator species was infrequent or absent that season, except for foxes in winter-spring 1987, when no sampling of their feces was undertaken for logistic reasons

Predators	1987			1988			1989			1990			Total	
	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer		
<i>Buteo polyosoma</i>	0	0	22	18	18	1	0	69	0	0	0	0	0	128
<i>Falco sparverius</i>	5	10	37	0	0	4	5	0	0	0	2	0	0	81
<i>Geranoetus melanoleucus</i>	15	0	2	6	9	0	0	0	0	0	0	0	0	32
<i>Parabuteo unicinctus</i>	4	0	0	0	28	0	0	27	11	0	0	0	0	70
<i>Athene cucularia</i>	102	22	114	100	25	0	70	31	59	0	90	13	61	935
<i>Bubo virginianus</i>	184	0	0	194	204	56	245	188	53	9	47	17	4	1276
<i>Glaucidium nanum</i>	91	9	0	76	69	60	18	100	36	45	28	40	33	658
<i>Tyto alba</i>	50	1	104	0	157	24	29	42	21	0	0	0	0	484
<i>Pseudalopex</i> spp.	84	0	0	176	531	273	148	230	293	191	129	186	95	2674
Total samples	535	42	279	571	1041	418	515	687	473	245	296	256	193	6338

Thus, small-mammal densities at the end of the study were about 7% of densities at peak.

Only 3 of the 8 species clearly irrupted (Table 1). *Phyllotis darwini* was by far the most abundant (peak density = 199/ha, crash density = 9/ha), followed by *Akodon olivaceus* (peak = 52/ha, crash = 1/ha) and *Marmosa elegans* (peak = 14/ha, crash = 1/ha). More or less in phase with one another, these species contributed relatively stable proportions to the overall small-mammal population, averaging 68%, 12% and 6% respectively. Four less abundant species disappeared entirely from trap samples toward the latter part of the study (Table 1): *Abrocoma bennetti* (peak density = 2/ha), *Akodon longipilis* (peak = 2/ha), *Octodon degus* (peak = 12/ha), and *Oryzomys longicaudatus* (peak = 7/ha), whereas *Chinchilla lanigera* decreased to very low densities (peak = 7/ha).

Predator species and diets

Apart from two small predatory reptiles, the snake *Philodryas chamissonis* and the racerunner *Callopistes palluma* (see Castro et al. 1991), ten species of endothermic carnivores occurred frequently at the study site (Table 2): the falconiforms *Geranoaetus melanoleucus* (black-chested eagle), *Buteo polyosoma* (red-backed hawk), *Parabuteo unicinctus* (Harris' hawk), and *Falco sparverius* (American kestrel); the strigiforms *Athene cucularia* (burrowing owl), *Bubo virginianus* (great horned owl), *Glaucidium nanum* (austral pygmy owl), and *Tyto alba* (common barn owl); and the canids *Pseudalopex culpaeus* (colpeo fox) and *P. griseus* (chilla fox).

We collected pellets of the eight local raptors, but only pellets of the four owls were found consistently throughout the study (Table 2). Aside from presenting data on the four falconiforms in Table 2 and elsewhere (Jaksić et al. 1990), we do not further discuss those species. At Aucó, owls exhibited much greater site fidelity than did the widely foraging falconiforms. The latter shifted perching sites often; they nested within the study site but apparently foraged well away from it.

At Aucó, burrowing owls consumed greater numbers of invertebrates than of vertebrates (Table 3). Great horned owls (Table 3) ate mammals almost exclusively. Austral pygmy owls took many avian prey in addition to mammals (Table 3; see also Jiménez and Jaksić 1989). Common barn owls resembled great horned owls in preying almost exclusively on mammals (Table 3).

We obtained large numbers of fox feces (Table 2). At the time of our study, techniques were not available to distinguish feces of the two species known to be present at Aucó. Thus, for analyses reported below we pooled all fox feces, following Durán et al. (1987). Pooling dietary data from *Pseudalopex culpaeus* and *P. griseus* does not necessarily weaken our analyses. In central Chile, at least, these congeners have been shown to have quite similar diets (Jaksić et al. 1980). Diet similarity at Aucó is now being evaluated using current techniques (J. Jiménez, pers. comm.).

Table 3. Diets of predators at Aucó, by percent of total prey found in pellets or feces that season. For computation of diet breadth prey were categorized to class level. n.p. = No pellets were found, and thus the species was presumed not active in the study site during that season. n.c. = Although the species was present, feces were not collected owing to logistic problems.

Predators	1987				1988				1989				1990			
	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer
<i>Athene cucularia</i>																
Mammals	1.2	1.4	10.0	4.5	3.6	n.p.	8.1	12.5	0.5	n.p.	0.3	0.0	0.5	1.2	1.8	
Other Vertebrates	3.7	8.9	10.2	5.5	7.7	n.p.	3.2	8.1	2.6	n.p.	1.2	2.4	1.6	4.5	6.1	
Invertebrates	95.1	89.7	79.8	90.0	88.7	n.p.	88.7	79.4	96.9	n.p.	98.5	97.6	97.9	94.3	92.1	
No. Prey	1012	213	488	1017	195	n.p.	407	136	634	n.p.	1728	208	959	943	774	
Diet Breadth	1.3	1.3	1.6	1.3	1.6	n.p.	2.4	2.0	1.4	n.p.	1.5	1.4	1.1	1.3	1.7	
<i>Bubo virginianus</i>																
Mammals	94.3	n.p.	n.p.	93.1	98.8	88.5	98.6	96.1	66.1	100.0	96.6	100.0	96.0	100.0	100.0	
Other Vertebrates	5.7	n.p.	n.p.	1.4	1.2	4.2	1.2	1.8	0.0	0.0	1.7	0.0	3.0	0.0	0.0	
Invertebrates	0.0	n.p.	n.p.	5.5	0.0	7.3	0.2	2.1	33.9	0.0	1.7	0.0	1.0	0.0	0.0	
No. Prey	635	n.p.	n.p.	422	487	96	422	338	112	11	58	20	100	4	35	
Diet Breadth	1.1	n.p.	n.p.	1.2	1.0	1.3	1.0	1.1	2.0	1.0	1.1	1.0	1.1	1.0	1.0	
<i>Glaucidium nanum</i>																
Mammals	10.5	4.3	n.p.	37.7	75.4	39.9	51.4	37.5	40.2	10.8	22.1	17.9	30.9	25.6	8.8	
Other Vertebrates	27.1	74.0	n.p.	5.4	6.1	5.9	5.4	7.8	18.2	30.6	26.4	9.5	17.9	13.9	29.4	
Invertebrates	62.4	21.7	n.p.	56.9	18.5	54.2	43.2	54.7	41.6	58.6	51.5	72.6	51.2	60.5	61.8	
No. Prey	313	23	n.p.	204	81	153	37	232	77	111	68	179	84	86	34	
Diet Breadth	2.4	2.1	n.p.	2.2	1.7	2.4	2.4	2.5	3.1	2.2	3.0	1.9	2.9	2.3	2.3	
<i>Tyto alba</i>																
Mammals	95.9	100.0	98.4	n.p.	99.3	98.0	97.7	96.8	96.9	n.p.	n.p.	n.p.	92.0	n.p.	n.p.	
Other Vertebrates	4.1	0.0	1.6	n.p.	0.7	2.0	2.3	1.6	3.1	n.p.	n.p.	n.p.	8.0	n.p.	n.p.	
Invertebrates	0.0	0.0	0.0	n.p.	0.0	0.0	0.0	1.6	0.0	n.p.	n.p.	n.p.	0.0	n.p.	n.p.	
No. Prey	97	1	193	n.p.	279	51	44	63	32	n.p.	n.p.	n.p.	88	n.p.	n.p.	
Diet Breadth	1.1	1.0	1.0	n.p.	1.0	1.0	1.1	1.1	1.1	n.p.	n.p.	n.p.	1.2	n.p.	n.p.	
<i>Pseudalopex</i> spp.																
Mammals	33.9	n.c.	n.c.	19.1	18.4	28.2	14.1	15.0	14.9	22.6	10.9	11.8	11.1	16.0	7.4	
Other Vertebrates	14.6	n.c.	n.c.	4.3	5.0	3.1	2.9	3.4	4.9	3.4	4.5	4.7	3.2	2.0	3.8	
Invertebrates	51.5	n.c.	n.c.	76.6	76.6	68.7	83.0	81.6	80.2	74.0	84.6	83.5	85.7	82.0	88.8	
No. Prey	295	n.c.	n.c.	1010	2545	706	1045	1228	1218	678	1138	1146	1145	530	1079	
Diet Breadth	2.6	n.c.	n.c.	1.7	1.7	1.8	1.4	1.5	1.6	1.7	1.4	1.5	1.4	1.5	1.4	
% Feces/Plants	29.8	n.c.	n.c.	49.4	62.7	50.9	31.1	62.2	78.5	69.6	34.9	58.1	57.6	54.7	27.2	

At Aucó, foxes appeared to act as generalist predators, consuming a variety of vertebrates, invertebrates, and fruits (Table 3), as previously noted by Durán et al. (1987).

Numerical response of predators

The highest density of raptor pellets and fox feces coincided with the peak density of small mammals in fall 1988 (Tables 1, 2), suggesting that overall predator abundance was highest at that time. Three of four owl species present during this irruption remained in the area throughout the study, despite the drastic decline in small-mammal prey. Pellets of burrowing, great horned, and austral pygmy owls were found during most months throughout the study period (Table 2). The same was true for fox feces (Table 2). Common barn owls, however, apparently left the study site after fall 1989, to return briefly during fall 1990 and then disappear again.

Density of falconiforms clearly declined in concert with mammal populations. Although we continued to sight occasional individuals throughout the study, we found no pellets of black-chested eagles after winter 1988, of red-backed hawks after fall 1989, or of Harris' hawks after winter 1989. Pellets of American kestrels have been found only sporadically since spring 1989 (Table 2).

Functional response of predators

Overall, predators failed to shift diets away from mammal prey as abundance of the latter declined dramatically (Table 1). Both great horned and common barn owls (Table 3) continued to concentrate on mammals throughout the study. Burrowing owls and foxes, on the other hand, did not appear to respond functionally to the 1987–1988 mammal irruption (Table 3): the former continued to concentrate on invertebrates, while foxes consumed highly variable amounts of fruit regardless of the availability of mammalian prey. Only austral pygmy owls displayed an apparent functional response to changes in the availability of mammalian prey (Table 3). Their relative consumption of mammals increased from winter 1987 to a peak in fall 1988, and then declined in favor of consumption of birds and invertebrates.

Had predators responded functionally to fluctuations in density of small mammals, diet diversities likewise would have increased as mammals declined in absolute abundance. Except perhaps for the austral pygmy owl, diet breadths failed to exhibit the expected trend and remained remarkably consistent (Table 3).

Differential use of mammalian prey by predators

No burrowing owl pellet ever contained remains of *Akodon longipilis*, *Chinchilla lanigera*, or *Octodon degus*, and only one pellet contained *Abrocoma bennetti* remains (Table 4). Of the other four prey species, *Marmosa*

Table 4. Percent numerical frequencies of small mammals in the diet of *Athene cucularia* at Aucó, by season. Not included are seasons when no mammal trapping was undertaken (fall–winter 1987), when no pellets were found (winter 1988–1989), or when no mammals were found in pellets (summer 1990). A + indicates that this species is found in the diet more than expected from its field abundance (Table 1); a – indicates the opposite; a = indicates that this species is taken as expected. P (bi) is the significance level of a binomial test applied to the signs; $P(\chi^2)$ corresponds to a χ^2 test applied to observed (this Table) and expected frequencies of small mammals (Table 1). n.a. = test not applicable

Mammalian prey	Sp. 87	Su. 88	Fa. 88	Sp. 88	Su. 88	Fa. 88	Sp. 88	Su. 88	Fa. 88	Sp. 89	Fa. 89	Wi. 90	Sp. 90	No. –	No. +	P (bi)
<i>Abrocoma bennetti</i>	0.0 –	0.0 =	0.0 –	0.0 =	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 =	16.7 +	0.0 =	5	1	= 0.50
<i>Akodon longipilis</i>	0.0 –	0.0 –	0.0 =	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 =	0.0 =	0.0 =	0.0 =	4	0	= 0.50
<i>A. olivaceus</i>	12.5 +	25.7 +	16.7 –	14.3 –	12.5 –	100.0 +	75.0 +	75.0 +	100.0 +	0.0 –	0.0 –	16.7 +	25.0 +	4	6	= 0.50
<i>C. lanigera</i>	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 =	0.0 =	8	0	< 0.05
<i>M. elegans</i>	18.8 +	22.9 +	33.3 +	21.4 +	25.0 +	0.0 –	25.0 +	25.0 +	0.0 –	0.0 –	0.0 –	33.3 +	25.0 +	2	8	> 0.10
<i>Octodon degus</i>	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 –	0.0 =	0.0 =	8	0	< 0.05
<i>Oryzomys longicaudatus</i>	12.5 +	22.9 +	0.0 –	28.6 +	12.5 +	0.0 –	28.6 +	12.5 +	0.0 –	0.0 =	0.0 =	0.0 =	12.5 +	3	5	= 0.50
<i>P. darwini</i>	56.2 –	28.5 –	50.0 –	35.7 –	50.0 –	0.0 –	35.7 –	50.0 –	0.0 –	0.0 –	100.0 +	33.3 –	37.5 –	9	1	< 0.10
Total	16	35	6	14	8	1	4	8	1	4	1	6	8			
$P(\chi^2)$	> 0.10	< 0.001	n.a.	> 0.05	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.			

Table 5. Observed frequencies of small mammals in the diet of *Bubo virginianus* at Aucó by season (see Table 4 for explanations). Not included are seasons when no mammal trapping was undertaken (fall-winter 1987), or when no pellets were found (spring 1987)

Mammalian prey	Su. 88	Fa. 88	Wi. 88	Sp. 88	Su. 89	Fa. 89	Wi. 89	Sp. 89	Su. 90	Fa. 90	Wi. 90	Sp. 90	No. -	No. +	P (bi)
<i>Abrocoma bennetti</i>	21.0+	5.0+	30.8+	6.3+	21.7+	46.8+	36.4+	8.1+	14.3+	5.9+	66.7+	9.7+	0	12	<0.001
<i>Akodon longipilis</i>	0.3-	2.1+	1.3+	0.3-	1.1+	0.0-	0.0-	2.7+	0.0=	1.2+	0.0=	0.0=	4	5	=0.50
<i>A. olivaceus</i>	14.2-	16.0-	6.4-	10.6-	13.2-	8.1-	9.1-	16.2+	14.3+	9.4+	0.0-	12.9+	8	4	=0.50
<i>C. lanigera</i>	0.6-	0.7-	5.1+	0.3-	1.1-	0.0-	0.0-	0.0-	0.0-	0.0-	0.0=	0.0=	9	1	<0.10
<i>M. elegans</i>	11.3+	6.8+	5.1+	3.8-	1.8-	3.2-	0.0-	5.4+	14.3+	7.1-	0.0-	6.5-	7	5	=0.50
<i>Octodon degus</i>	1.4-	0.5-	0.0-	0.8-	0.7-	0.0-	0.0-	0.0-	0.0-	0.0-	0.0=	6.5+	10	1	<0.05
<i>Oryzomys longicaudatus</i>	5.7+	4.6+	6.4+	7.1+	2.1+	3.2+	0.0-	2.7+	0.0=	3.5+	0.0=	0.0=	1	8	<0.10
<i>P. darwini</i>	45.6-	64.4-	44.9-	70.9+	58.4-	38.7-	54.5+	64.9+	57.1-	72.9+	33.3-	64.5-	8	4	=0.50
Total	353	438	78	395	281	62	11	37	7	85	3	31			
$P(\chi^2)$	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	>0.50	>0.50	n.a.	<0.001	n.a.	n.a.			

Table 6. Observed frequencies of small mammals in the diet of *Glaucidium nanum* at Aucó by season (see Table 4 for explanations). Not included are seasons when no mammal trapping was undertaken (fall-winter 1987), or when no pellets were found (spring 1987)

Mammalian prey	Su. 88	Fa. 88	Wi. 88	Sp. 88	Su. 89	Fa. 89	Wi. 89	Sp. 89	Su. 90	Fa. 90	Wi. 90	Sp. 90	No. -	No. +	P (bi)
<i>Abrocoma bennetti</i>	0.0=	0.0-	4.8+	0.0=	11.1+	0.0-	0.0-	11.1+	5.9+	0.0=	0.0-	33.3+	4	5	=0.50
<i>Akodon longipilis</i>	0.0-	0.0=	0.0-	0.0-	0.0=	0.0-	0.0-	0.0=	0.0=	0.0=	0.0=	0.0=	5	0	=0.10
<i>A. olivaceus</i>	52.5+	32.3+	26.2+	60.0+	22.2+	0.0-	25.0+	0.0-	29.4+	0.0-	0.0-	0.0-	5	7	=0.50
<i>C. lanigera</i>	0.0-	0.0-	0.0-	0.0-	5.6-	0.0-	0.0-	0.0-	0.0-	0.0-	0.0=	0.0=	10	0	<0.02
<i>M. elegans</i>	15.0+	16.1+	16.7+	6.7+	11.1+	7.1-	0.0-	0.0-	0.0-	0.0-	0.0-	0.0-	7	5	=0.50
<i>Octodon degus</i>	0.0-	25.8+	35.6+	13.3+	33.3+	78.6+	50.0+	77.8+	58.8+	100.0+	100.0+	66.7+	1	11	<0.02
<i>Oryzomys longicaudatus</i>	5.0+	9.7+	0.0-	6.7+	5.6+	0.0-	0.0-	0.0=	0.0=	0.0-	0.0=	0.0=	4	4	=0.50
<i>P. darwini</i>	27.5-	16.1-	16.7-	13.3-	11.1-	14.3-	25.0-	11.1-	5.9-	0.0-	0.0-	0.0-	12	0	<0.001
Total	40	31	42	15	18	14	4	9	17	4	7	3			
$P(\chi^2)$	<0.001	<0.001	<0.001	<0.001	<0.001	<0.005	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.			

Table 7. Observed frequencies of small mammals in the diet of *Tyto alba* at Aucó, by season (see Table 4 for explanations). Not included are seasons when no mammal trapping was undertaken (fall–winter

1987), or when no pellets were found (summer 1988, and after fall 1989 except for fall 1990)

Mammalian prey	Sp. 87	Fa. 88	Wi. 88	Sp. 88	Su. 89	Fa. 89	Fa. 90	No. –	No. +	<i>P</i> (bi)
<i>Abrocoma bennetti</i>	4.7+	0.8+	2.0+	4.7+	1.7–	0.0–	1.4+	2	5	=0.50
<i>Akodon longipilis</i>	0.6–	0.4+	0.0–	0.0–	0.0=	6.7+	0.0=	3	2	=0.50
<i>A. olivaceus</i>	12.2+	15.0–	20.4+	2.3–	13.3+	13.3+	27.5+	2	5	=0.50
<i>C. lanigera</i>	0.0–	0.0–	0.0–	0.0–	0.0–	3.3–	0.0–	7	0	<0.10
<i>M. elegans</i>	9.9+	9.6+	2.0–	9.3+	8.3+	6.7–	4.3–	3	4	=0.50
<i>Octodon degus</i>	1.7–	0.0–	0.0–	0.0–	0.0–	0.0–	0.0–	7	0	<0.10
<i>Oryzomys longicaudatus</i>	9.3+	5.8+	2.0–	4.7+	1.7+	0.0–	4.3+	2	5	=0.50
<i>P. darwini</i>	61.6–	68.4–	73.6+	79.0+	75.0+	70.0+	62.5–	3	4	=0.50
Total	172	260	49	43	60	30	69			
<i>P</i> (χ^2)	<0.001	<0.001	>0.05	<0.05	>0.90	>0.10	<0.001			

elegans was consistently consumed more frequently than expected from trapping data, both *Akodon olivaceus* and *Oryzomys longicaudatus* were taken roughly in proportion to their field abundances, and the abundant *Phyllotis darwini* was consistently underconsumed (Tables 1, 4). No prey shifts among small mammals were observed in burrowing owls.

Great horned owls consumed both *Abrocoma bennetti* and *Oryzomys longicaudatus* very frequently (Table 5) relative to their abundance in trap samples (Table 1), *C. lanigera* and *Octodon degus* less frequently than expected, and *Akodon longipilis*, *Akodon olivaceus* and *P. darwini* in about their proportional abundances in the field. A slight prey shift occurred over seasons: comparison of Tables 1 and 5 suggests that great horned owls preyed disproportionately more on *M. elegans* from summer through winter 1988, and thereafter preyed on this species at roughly the expected frequencies.

Austral pygmy owls did not prey at all on *Akodon longipilis* or *C. lanigera* (except for a single occurrence of the latter species). They consistently took more *Octodon degus* and fewer *P. darwini* than expected from trapping data (Tables 1, 6). *Abrocoma bennetti* and *Oryzomys longicaudatus* were taken at roughly their estimated abundances in the field (Table 6). Two clear prey shifts were noticeable over the seasons: Austral pygmy owls took more *Akodon olivaceus* and *M. elegans* than expected from summer 1988 to summer 1989, and thereafter took them at roughly the frequencies expected from trap samples (Table 1).

Except for a single occurrence among pellets, common barn owls did not prey on *C. lanigera*, and rarely did so on *Octodon degus*. They took more *Abrocoma bennetti*, *Akodon olivaceus*, and *Oryzomys longicaudatus* (Table 7) than expected from trapping data (Table 1). Consumption of *Akodon longipilis* and *P. darwini* roughly reflected their respective abundances in traps. Barn owls displayed a questionable prey shift from higher than expected consumption of *M. elegans* during spring 1987 and fall 1988, to taking it in roughly its proportion in trap samples (Tables 1, 7).

Foxes consistently ate *Abrocoma bennetti* and *Octodon degus* more frequently than expected from trapping

data, underconsumed *Akodon longipilis*, *C. lanigera*, *M. elegans* and *P. darwini*, and ate *Akodon olivaceus* and *Oryzomys longicaudatus* apparently in approximate proportion to their abundance in the field (Tables 1, 8). Foxes did not noticeably shift prey preferences among small mammals (Table 8) despite marked changes in mammal abundance (Table 1).

Discussion

Numerical and functional responses

Judging by abundance of pellets, all four falconiforms and the common barn owl displayed a dramatic numerical response to the decrease in their primary prey resources (small mammals). Occasional sightings of hawks, at least, proved that they did not abandon the area entirely, but obviously fidelity to the study site declined to zero. Because we had no baseline data prior to the mammal irruption, we cannot state whether these species had been in Aucó previously, or whether they had converged on the site in positive numerical response to the irruption. Four of the species that abandoned the site – black-chested eagle, Harris' hawk, red-backed hawk, and common barn owl – are wide-ranging foragers. In contrast, the three owl species that remained at the site are all known to be quite sedentary foragers. The decline in abundance of American kestrels, also known to be quite sedentary in their foraging habits, is difficult to explain, particularly as their main prey, arthropods and birds, did not appear to have declined as did small mammals.

Foxes also remained at Aucó despite the marked decline in mammalian prey. Martínez, Rau, and Jaksić (in manuscript), using scent lines, demonstrated that fox numbers remained stable between the fall 1988 mammal peak and the winter 1990 crash. Possibly, fluctuations in abundance of vertebrate prey are buffered by consumption of fruits; this demands more study.

Other than a possible functional response on the part of austral pygmy owls, the other resident predators failed to show clear functional responses to overall shifts in small-mammal densities. At least three possible explana-

Table 8. Observed and expected frequencies of small mammals in the diet of *Pseudalopex* spp. at Aucó by season (see Table 4 for explanations). Not included are seasons when no mammal trapping was undertaken (fall-winter 1987), or when no feces were collected owing to logistic problems (spring 1987)

Mammalian prey	Su. 88	Fa. 88	Wi. 88	Sp. 88	Su. 89	Fa. 89	Wi. 89	Sp. 89	Su. 90	Fa. 90	Wi. 90	Sp. 90	No. -	No. +	P (bi)
<i>Abrocoma bennetti</i>	13.6+	5.4+	10.6+	15.2+	21.6+	29.9+	25.9+	17.2+	21.2+	14.3+	5.6-	17.4+	1	11	<0.02
<i>Akodon longipilis</i>	0.0-	0.0=	0.0-	0.0-	0.0=	0.0-	0.0-	0.0=	0.0=	0.0=	0.0=	0.0=	5	0	=0.10
<i>A. olivaceus</i>	16.7+	16.0-	31.0+	12.4-	8.8-	4.6-	8.6-	14.1-	1.5-	4.1-	27.8+	8.7+	8	4	=0.50
<i>C. lanigera</i>	0.6-	1.2-	0.9-	2.9-	1.0-	2.3-	1.7-	4.7-	4.5-	0.0-	0.0=	0.0=	10	0	<0.02
<i>M. elegans</i>	3.1+	3.6-	0.0-	0.0-	0.0-	1.1-	0.0-	0.0-	1.5-	0.0-	0.0~	0.0-	11	1	<0.02
<i>Octodon degus</i>	17.3+	16.9+	15.9+	32.4+	33.3+	39.1+	43.1+	34.4+	51.5+	57.1+	44.4+	43.5+	0	12	<0.001
<i>Oryzomys longicaudatus</i>	6.2+	5.1+	2.7-	0.0-	0.0-	1.1-	3.4-	6.3+	0.0=	2.0-	0.0=	0.0=	6	3	=0.50
<i>P. darwini</i>	42.6-	51.7-	38.9-	37.1-	35.3-	21.8-	17.2-	23.4-	19.7-	22.4-	22.2-	30.4-	12	0	<0.001
Total	162	331	113	105	102	87	58	64	66	49	18	23			
$P(\chi^2)$	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.005	n.a.			

Table 9. Summary of apparent prey preferences for predators at Aucó, assuming that data in Table 1 provide at least a rough index to relative prey availability (see text for explanation). Symbols: + = taken more frequently than expected from trapping data; - = taken less frequently; 0 = taken about as expected; +/0 = apparent preference shift over time. Activity periods are: D = Diurnal; C = Crepuscular; N = Nocturnal; DCN = Continuously active

Mammal prey	Weight (g) $\bar{x} \pm 2SE$ (n)	Activity	<i>A. cunicularia</i> 247 ± 22(3)CN	<i>B. virginianus</i> 1227 ± 197(6)N	<i>G. nanum</i> 81 ± 13(3)DCN	<i>T. alba</i> 307 ± 22(8)N	<i>Pseudalopex</i> spp. 3623 ± 636(4)CN*
<i>Abrocoma bennetti</i>	182 ± 58 (10)	N	-	+	0	+	+
<i>Akodon longipilis</i>	61 ± 11 (5)	N	-	0	-	0	-
<i>A. olivaceus</i>	28 ± 1 (151)	DCN	0	0	+/0	+	0
<i>C. lanigera</i>	306 ± 55 (22)	N	-	-	-	-	-
<i>M. elegans</i>	26 ± 3 (41)	N	+	+/0	+/0	+/0	-
<i>Octodon degus</i>	123 ± 8 (45)	DC	-	-	+	-	+
<i>Oryzomys longicaudatus</i>	27 ± 3 (20)	N	0	+	0	+	0
<i>P. darwini</i>	47 ± 1 (622)	N	-	0	-	0	-

* Figures for juvenile *P. culpaeus*; *P. griseus* weighs 2000 g (n=1), and its activity period is DCN

tions exist: (1) Trapping data did not reflect prey densities accurately; i.e., no irruption and crash actually occurred but rather shifts in mammalian trappability. This is highly unlikely, as all other evidence also points to a dramatic irruption and crash of small mammals. (2) Other food resources declined at the same rate as did small mammals, such that proportional availability of foods did not change and no basis for a functional response was provided. We cannot assess this possibility quantitatively, but observations of invertebrate, bird, and fruit densities suggest that no overall decline in these food resources occurred in 1988–1990. (3) The decline in overall consumption of mammalian prey by all predators combined was essentially compensated for by the numerical response, as indicated by the shrinking number of pellets and feces found (Table 2). We believe that this is the most likely explanation for the lack of a clear functional response on the part of the predators that stayed at the site.

Mammalian prey vulnerability

Assuming that trapping data reflect true population densities of rodents in rough terms at least, we found that some small mammals appeared to be more vulnerable to predation than others. Jaksić and Simonetti (1987) and Simonetti (1989) have discussed at length the presumable escape responses displayed by central Chilean small mammals, thus here we will concentrate only on those responses that we have observed at our study site.

The two most frequent prey in the diets of local predators differed markedly. *Abrocoma bennetti*, the second largest mammal at the site, was “preferred” prey of the four largest predators in Aucó, was “opportunistic” prey (i.e., taken as available) for austral pygmy owls, and was “avoided” by burrowing owls (Table 9). This nocturnal rodent displays an unrefined escape response as judged by its behavior when released from traps. Upon release, *A. bennetti* first seems dazed and nearly immobile for a few seconds, then runs for cover with a slow trotting gait. Thus, those predators capable of hunting for larger prey may end up capturing *A. bennetti* with high efficiency relative to other prey species. The marsupial *Marmosa elegans* was the preferred prey of the four local owls, at least temporarily (Table 9). This nocturnal mammal is the smallest prey species at Aucó, and when released from traps it runs for cover directly but relatively slowly. When cornered, *M. elegans* stands its ground against predators, uttering distress calls. Only the two foxes appeared to avoid this prey species.

The rodents *Akodon olivaceus* and *Oryzomys longicaudatus* were either preferred or opportunistic prey of local predators (Table 9). They are very similar in body size but differ greatly in escape response. The continuously active *A. olivaceus* runs directly for the nearest cover when released from traps. The nocturnal *Oryzomys longicaudatus* escapes by springing about rapidly in such a zigzag fashion that it often misses the nearest cover.

Both *Akodon longipilis* and *Phyllotis darwini* were either avoided or opportunistic prey of local predators

(Table 9). They are medium-sized rodents of nocturnal habits, whose escape response involves a direct run for the nearest cover. However, *P. darwini* displays a unique phenomenon when grabbed by the tail: it sheds its integument across a neatly round section, close to the tail's base. How frequently predators misdirect their attacks to the tail of *P. darwini*, and thus the effectiveness of its tail shedding as an escape response, is difficult to evaluate.

The nocturnal *Chinchilla lanigera* appeared to be the most consistently avoided prey of local predators. The largest rodent species at Aucó (Table 9), *C. lanigera* appeared to us to be extremely secretive and shy, and extraordinarily sensitive (they possess greatly inflated auditory bullae) to the presence of potential predators. In our study site, chinchillas rarely ventured far from dense clones of the spiny terrestrial bromeliad *Puya*. Thus, it is quite possible that *C. lanigera* is a particularly difficult species to locate and capture by predators.

Among Aucó species, *Octodon degus* exhibited the unique combination of large size and diurnal/crepuscular activity (Table 9). The former feature may have rendered *O. degus* difficult to catch and subdue by the weakly equipped burrowing owls, whereas the latter makes it less accessible to the powerful but strictly nocturnal great horned and common barn owls. In contrast, *O. degus* appeared to be a preferred prey of the continuously active foxes and austral pygmy owls. The loosely colonial *O. degus* emits warning calls (Fulk 1976), thereby revealing its location to predators. Escape behavior is a straight and quick dash for the nearest cover.

No obvious single feature distinguishes “more vulnerable” from “less vulnerable” mammalian prey in Aucó. Neither abundance alone, as suggested by Jaksić (1986), nor size alone, as discussed by Bozinović and Medel (1988), but a combination of both, as proposed by Jaksić (1989), may best account for the patterns described. Other investigators have come to similar indecisive conclusions. Corbett and Newsome (1987, p 215) concluded that “prey availability (catchability, accessibility) appeared to be more important than prey abundance (numbers, biomass)” in determining the diet of dingos in arid Australia. Studying three hawk species in temperate North America, Steenhof and Kochert (1988, p 37) concluded that “prey choice was generally consistent with predictions of the original optimal diet model,” in that raptors generally took differently-sized prey in agreement with their respective profitabilities. How prey availability, catchability, accessibility, or profitability are to be objectively determined under field conditions is a major challenge faced by students of predator-prey interactions.

Predator selectivity and mammalian prey fluctuations

The six resident predators demonstrated clear differences in diet composition (Table 3). However, burrowing owls, great horned owls, common barn owls, and foxes maintained highly consistent preferences despite marked changes in mammalian prey abundance (Table 1). Obvious prey switching (Murdoch 1969) from mammals to

other prey classes did not take place even when small mammals decreased to 7% of peak abundance, either because other food resources experienced somewhat of a decrease as well, or because these predators were highly efficient at capturing their preferred prey. Only austral pygmy owls demonstrated an apparent shift away from mammals when they crashed (Table 3).

At the level of mammalian prey consumption, all local predators took some prey either less or more frequently than expected based on trapping data (Table 9). However, prey switching between mammalian prey was not common. Only austral pygmy owls demonstrated clear switching from a concentration on *Akodon olivaceus* and *Marmosa elegans* when they were abundant to other prey when these species declined drastically. In contrast, great horned owls and common barn owls showed either slight or questionable prey switches, and burrowing owls and foxes did not shift at all (Table 9).

Pearson (1964) hypothesized that carnivorous predators in California were able to continue consuming their preferred prey, *Microtus californicus*, even at very low densities because energy needs were supplemented with less preferred species whose populations did not cycle in phase with *Microtus*. Corbett and Newsome (1987) reported similar findings for Australian dingos (*Canis familiaris dingo*), which preyed disproportionately on rabbits (*Oryctolagus cuniculus*) throughout a prolonged drought period. In Idaho, Steenhof and Kochert (1988) found that both golden eagles (*Aquila chrysaetos*) and prairie falcons (*Falco mexicanus*) maintained strong preferences for specific mammalian prey (*Lepus californicus*, *Spermophilus townsendii*, respectively) despite marked changes in densities of those prey. It appears, then, that despite substantial reductions in their preferred prey, or substantial increases in non-preferred prey, some carnivorous predators can continue to prey on their staple species through both lean and fat times.

Predators at Aucó clearly did not prey on the most irruptive species at the site (*Phyllotis darwini* and *Akodon olivaceus*) at a rate that tracked prey abundance (Table 9). Possibly, then, small mammals remained at high densities for a longer time than would have occurred had predators been more effective and demonstrated a clear-cut functional response. Likewise, Pearson (1964, 1966, 1971, 1985) proposed that carnivorous predators are not effective at keeping small mammals such as cycling voles from increasing their population levels, but may function in keeping crash densities down for longer than would otherwise be the case. Corbett and Newsome (1987) concluded that Australian dingos were able to suppress the population growth of rabbits during drought periods, but were unable to regulate rabbits during flush periods. Sinclair et al. (1990) demonstrated that Australian raptors regulated populations of the house mouse (*Mus musculus*) at low and intermediate mouse densities but not during mouse outbreaks, when both numerical and functional responses of the predators reached plateaus. Thus, Pearson's hypothesis may apply widely: carnivorous predators do not seem to be effective agents in regulating populations of small-mammal prey unless the latter have already been depressed by lowered

food resources brought about either by their own feeding activities or by climatic harshness.

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