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SMALL-MAMMAL AVAILABILITY AND CONSUMPTION BY THE FOX, *DUSICYON CULPAEUS*, IN CENTRAL CHILEAN SCRUBLANDS

J. AGUSTIN IRIARTE, JAIME E. JIMENEZ, LUIS C. CONTRERAS, AND FABIAN M. JAKSIĆ

Departamento de Ecología, Universidad Católica de Chile, Casilla 114-D, Santiago, Chile (JAI, JEJ, and FMJ)
Departamento de Biología y Química, Universidad de Talca, Casilla 747, Talca, Chile (LCC)
Present address of JAI: Center for Latin American Studies, University of Florida, Gainesville, FL 32611

Three species of foxes occur in Chile, all in the genus *Dusicyon* (Honacki et al., 1982) or *Pseudalopex* (Berta, 1987). The small *D. fulvipes* is restricted to Chiloé Island and the Nahuelbuta ranges, whereas *D. griseus* and the larger *D. culpaeus* are found throughout the country. Previous reports on the ecology of *D. culpaeus* mainly have documented its food habits (Medel and Jaksić, 1988).

Indirect evidence led Jaksić et al. (1980) to conclude that *D. culpaeus* is crepuscular and chooses sparse scrub as its hunting grounds. Although these authors detected some differences between small-mammal availability in the field (based on trapping data), and their representation in the diet, they concluded that trap shyness and habitat selection by some small mammals accounted for the mismatch, and not prey selectivity by *D. culpaeus*. Jaksić et al. (1981a), by use of a different data set, showed that 83% of the prey in the diet of *D. culpaeus* was either diurnal or crepuscular, that there was a significant correlation (Spearman's $r = 0.833$; $P < 0.05$) between ranked abundances of prey in sparse scrub and in the diet, and that no such correlation was observed with the ranked abundances of small mammals in dense scrub. These observations led Jaksić et al. (1981a) to describe *D. culpaeus* as being a generalist predator that hunts diurnally or crepuscularly in sparse scrub.

However, data bases used to draw the foregoing conclusions are questionable. Assignment of small mammals as being diurnal, crepuscular, or nocturnal was based on Glanz's (1977) opinions, not on actual data on their times of activity. Habitat selection by small mammals was extrapolated from estimates of relative abundance in sparse and dense scrub by pooling trapping data reported by Jaksić et al. (1981b). Correspondence between the representation of small mammals in the field and in the feces was evaluated for statistical significance by pooling seasonal data to obtain a yearly estimate (Jaksić et al., 1980, 1981a). Most of these procedures were justifiable or mandated by internal constraints of the data bases (e.g., minimum sample sizes for cells in contingency tables mandated pooling of monthly or seasonal data).

Herein, we reexamine the feeding ecology of *D. culpaeus* in light of the more extensive data base reported by Iriarte et al. (1989). These authors conducted an 18-month live-trapping study of small mammals in a scrub habitat characterized by a shrub-cover gradient ranging from dense (80–100% shrub cover) to sparse (0–20% cover), with an overall cover of 55.6%. Sherman traps, capable of capturing all small mammals to the size of the rodent *Abrocoma bennetti* (231 g), and Tomahawk traps, capable of capturing European rabbits, *Oryctolagus cuniculus*, were used. Some traps were equipped with stopwatches so that captures could be timed precisely. Based on these data, Iriarte et al. (1989) provided monthly estimates of small-mammal numbers, mass, habitat selection (discriminating sparse, typical, and dense scrub), and activity times. Concomitant with the live trapping reported in our previous paper (Iriarte et al., 1989), we collected fox feces inside and within the periphery of the trapping grids, thus acquiring a sample to examine the relationship between small-mammal availability and consumption by foxes at the site in detail.

The study site was a relatively undisturbed scrub at 1,200 m elev. (15% E–W slope) within the Fundo San Carlos de Apoquindo (33°23′S, 70°31′W, 20 km E Santiago). The vegetation was an evergreen sclerophillous scrub locally known as "matorral." After removal of old fecal droppings, fresh fox feces were collected simultaneously with the monthly trapping sessions conducted May 1983–October 1984 inside the two adjacent grids (one was 0.35 ha, the other 0.49 ha) and within a strip of 200 m around them (thus totaling an area of 6.6 ha). In 18 months 202 feces were collected, and the prey contents examined by standard procedures (Jaksić et al., 1980). Small-mammal species found among the prey of *D. culpaeus* were examined with reference to their mass, habitat selection, activity time, and population abundance as documented by Iriarte et al. (1989). Owing to statistical constraints, monthly estimates of small-mammal abundance in the field and in the feces were pooled into the four seasons recognizable at the study site: winter, May–July; spring, August–October; summer, November–January; fall, February–April. Contingency tables and G statistics (Sokal and Rohlf, 1981) were used with those small mammals that provided sufficient sample sizes for analysis; expected cell values were at or above the minimum of five in all cases.

As first discussed by Pearson (1964), a major assumption in comparing prey availability with prey consumption by a widely ranging carnivore is that the area inside the trapping grids reflects without bias (or with the same bias) the composition of the small-mammal assemblage and relative population numbers of the larger area in which the carnivore hunts. Another major assumption with reference to Chilean scrublands (Jaksić et al., 1981b), is that the traps used sample the availability of small mammals without, or with the same, bias.

We reduced the first source of error by collecting fox feces only within the physiognomically similar surroundings of our two trapping grids, in hopes that *D. culpaeus* hunted in those surroundings or in similar areas outside. In addition, we sought a physiographically different site in the general area, to assess whether availability and consumption were biased toward some prey items. This second set of trapping data was obtained 21 July–2 August 1985 on the rugged terrain above the trapping grid at 1,200 m elev. (valley grid hereafter) established by Iriarte et al. (1989). This second grid (mountain grid hereafter) was located about 1,500 m southeast on the top of a rather low-elevation (1,825 m above sea level), gently sloping mountain (mean slope = 27%). The physiognomy and taxonomic composition of the vegetation was similar to that in the valley grid (Iriarte et al., 1989). Overall scrub cover on the mountain grid (58.5%) was similar to that

TABLE 1.—*Prey of* Dusicyon culpaeus *in* Fundo San Carlos de Apoquindo, *central Chile, by season in the valley, and in winter on the mountain. Integer numbers are the absolute numerical representation of each prey item; numbers in parenthesis are the percent numerical representation of major prey items.*

Prey items	Valley					Mountain
	May–July	August–October	November–January	February–April	Yearly	May–July
Rodents	(53.0)	(51.4)	(64.5)	(58.4)	(56.0)	(70.3)
Abrocoma bennetti	8	9	12	9	38	39
Akodon longipilis						1
Akodon olivaceus						1
Octodon degus	21	21	11	16	69	36
Oryzomys longicaudatus						3
Phyllotis darwini	1		1	3	5	3
Unidentified	5	7	5	7	24	7
Lagomorphs	(40.9)	(47.2)	(33.3)	(23.3)	(37.0)	(21.9)
Oryctolagus cuniculus	27	34	15	14	90	28
Marsupials						(0.8)
Marmosa elegans						1
Birds		(1.4)		(5.0)	(1.7)	(2.3)
Eggs				2	2	2
Unidentified		1		1	2	1
Reptiles	(6.1)		(2.2)	(13.3)	(5.3)	(4.7)
Liolaemus sp.						1
Philodryas chamissonis	4		1	8	13	5
Total prey	66	72	45	60	243	128
Total feces	54	60	41	47	202	72
Feces with plants (%)	11.1	15.0	22.0	19.1	16.3	11.1
Feces with insects (%)	3.7	15.0	9.8	4.3	8.4	4.2

in the valley grid (55.6%; Iriarte et al., 1989). During 14 days and 14 nights we trapped small mammals on four mountain slopes and at the summit. All five grids had a 7 by 7 configuration with one trap per station, alternating one Sherman with one Victor snap trap over both rows and columns, with stations separated by 7 m. The total area covered by the five grids, including 3.5 m-boundary strips, was 1.2 ha. Fox feces that appeared fresh were collected on the mountain slopes and on the top. We assumed that these feces accumulated over the last few months, probably representing the winter diet of the fox.

We reduced the second source of error (that traps sample availability without bias or with the same bias) by using traps of different size in the valley grid. As documented by Iriarte et al. (1989), there was no difference in population estimates obtained with each trap type (Sherman and Tomahawk) for the two largest rodents in the area (*Abrocoma bennetti* and *Octodon degus,* two of the three main prey of *D. culpaeus*); consequently, there was no bias owing to trap size or type for these species. There indeed was bias in population estimates for the third main prey of *D. culpaeus,* the European rabbit; only juveniles were captured in Tomahawk traps (Iriarte et al., 1989). However, *D. culpaeus* preyed essentially on juvenile rabbits, consequently the direction of the bias was the same between traps and foxes. On the mountain grid, where we used both Sherman live traps and Victor snap traps, we did not detect differences in the composition of small mammals captured by each (Jaksić et al., 1981b). Indeed, they were biased against rabbits, as none was captured despite being present.

Valley grid.—Rodent prey predominated in the fox feces during all seasons (51.4%–64.5% of the diet), peaking during summer and fall (Table 1). European rabbits followed (23.3%–47.2%), peaking during winter and spring. Ninety-five percent of the rabbit prey was juveniles, as determined by size of teeth. Birds and reptiles composed negligible amounts of the diet, except during fall, when snakes (*Philodryas chamissonis*) represented 13.3% of the diet. Plant consumption was relatively low throughout the year (11.1%–22.0% of feces contained plant material), peaking during summer and fall. Fruits were most common during spring and summer (mainly drupes of *Lithraea caustica* and *Quillaja saponaria*), and leaves and stems were

TABLE 2.—*Mass, habitat used (sparse scrub, dense scrub, or both), activity period, minimum number known alive (by season and year), and mean yearly density for small mammals captured on a 0.35-ha grid (Iriate et al., 1989) at 1,200 m elev. (valley) and on a 1.2-ha grid at 1,825 m elev. (mountain) near Santiago, Chile, 1984–1985.*

| Species | Mass (g) | Habitat | Activity | Valley | | | | | | Mountain | |
				Winter	Spring	Sum-mer	Au-tumn	All year	n/ha	Winter	n/ha
Abrocoma bennetti[a]	231	Sparse	Nocturnal	2	3	2	3	10	1.6	1	0.8
Akodon longipilis	63	Dense	Nocturnal	8	10	8	3	29	4.6	12	10.0
Akodon olivaceus	44	Dense	Nocturnal-crepuscular	6	3	13	4	26	4.2	5	4.2
Marmosa elegans	30	Dense	Nocturnal-crepuscular	6	5	11	12	34	5.5	19	15.8
Octodon degus	184	Both	Diurnal-crepuscular	16	11	16	17	60	9.6	29	24.2
Oryzomys longi-caudatus	36	Dense	Nocturnal-crepuscular	22	42	4	7	75	12.0	8	6.7
Phyllotis darwini	62	Dense	Nocturnal-crepuscular	38	40	29	22	129	20.7	34	28.3
Oryctolagus cuniculus[a]	447	Both	Diurnal-nocturnal	3	4	10	1	18	2.8	b	b
Totals				101	118	93	69	381	61.0	108	90.0

[a] Based on a grid of 0.49 ha (Iriarte et al., 1989:83, table 2).
[b] Present but not captured.

common during fall and winter. Insect consumption peaked during spring, when 15.0% of feces contained such items.

European rabbits were the most abundant prey species in the diet of foxes, followed by the rodents *Octodon degus*, *Abrocoma bennetti*, and *Phyllotis darwini*, in decreasing order. These species had a mean yearly abundance of 2.8, 9.6, 1.6, and 20.7/ha, respectively (Table 2), so that they were not captured by the fox in proportion to their abundance ($G = 407.20$; $d.f. = 3$; $P < 0.001$; field abundance data used to generate expected frequencies in the fox diet). Indeed, *A. bennetti*, *O. degus*, and *O. cuniculus* all were found in the feces more often than expected from their field abundances, whereas *P. darwini* was underrepresented in the fox diet. It is surprising that some abundant small mammals such as *Oryzomys longicaudatus* (12.0/ ha) were not found in the fox diet.

Three species rendered adequate numerical samples to explore whether they were taken homogeneously during the different seasons of the year, by considering as observed frequencies those obtained by analysis of fecal droppings (Table 1), and as expected frequencies those obtained by trapping (Table 2). *Abrocoma bennetti* was taken by the fox in about its seasonal availability in the field ($G = 3.27$; $d.f. = 3$; $P > 0.10$), whereas both *O. degus* ($G = 9.19$; $d.f. = 3$; $P < 0.05$) and *O. cuniculus* ($G = 60.53$; $d.f. = 3$; $P < 0.001$) were taken out of proportion to their seasonal availability. These two prey species showed similar trends; they were eaten more than expected during winter and spring, and less than expected during summer. During fall, *O. degus* was eaten less than expected, whereas *O. cuniculus* showed the opposite trend. These results suggest that *D. culpaeus* actively searches for *O. degus* and *O. cuniculus* during winter and spring, and apparently ignores them during summer. An alternative explanation is that the availability of these two prey species becomes so high during summer that the fox falls behind in cropping these prey populations swelled by recruits.

Mountain grid.—Small mammals trapped were of the same species found in the valley, except for rabbits. Although rabbits were present on the mountain, the traps used were too small to capture them. A comparison of these trapping data with those obtained during winter on the valley grid (Table 2; winter trapping data from the valley grid were used to generate expected values for the mountain grid) demonstrated that there was a significant nonhomogeneity between the two data sets ($G = 39.88$; $d.f. = 5$; $P < 0.001$; *Abrocoma bennetti* and *Akodon olivaceus* combined to produce an expected value >5.0). *Marmosa elegans* and *O. degus* were captured on the mountain more often than expected from the valley grid data, whereas *O. longicaudatus* and *P. darwini* were relatively underrepresented on the mountain. There was no significant difference between the representation of *A. bennetti*, *A. olivaceus*, and *Akodon longipilis* in the valley and on the mountain.

The diet of foxes on the mountain was composed of the same prey items as that of foxes in the valley (Table 1). In comparison to feces in the valley, however, those on the mountain had more rodents and fewer

rabbits, in agreement with our observation that rabbits were relatively scarce on the mountain. A comparison of the availability of rodents on the mountain with their representation in the diet of the fox rendered $G = 176.26$; $d.f. = 5$; $P < 0.001$ (trapping data used to generate expected values in the diet; *A. bennetti* combined with *A. olivaceus* to produce expected value >5.0). *Akodon longipilis, Marmosa elegans, O. longicaudatus,* and *P. darwini* were underrepresented in the fox diet, whereas *A. bennetti* and *O. degus* were found in the feces more often than expected from their availability at the mountain grid. These results are similar to those obtained in the valley grid; both *A. bennetti* and *O. degus* appear to be selected as prey items by the fox. Perhaps the same applies to *O. cuniculus,* but we were not able to estimate their abundance on the mountain grid.

Fox selectivity.—It may not be coincidental that the three major prey species of *D. culpaeus* were the same between valley and mountain, happened to be the largest sized small mammals on our study site, and the ones that used sparse scrub to a large extent (Table 2). The activity time of these species differed widely and did not explain further their high consumption by *D. culpaeus* (Table 2); apparently the fox is able to hunt at any time of the day, or able to catch inactive prey in burrows. Large size and occupation of sparse scrub seem to render these three small-mammal species more vulnerable to fox predation; the five species of smaller size that dwell in dense scrub appear relatively safe from the fox (Jaksić, 1986). Our results are in agreement with those of Meserve et al. (1986), indicating that *D. culpaeus* shows some degree of selectivity in diet. These authors demonstrated that in north-central Chile the fox consumed mainly *O. degus* (74% of total prey) and *A. bennetti* (24% of total prey), despite their rankings in abundance being third and sixth, respectively (*O. cuniculus* was not present in the area). The two most abundant small mammals (*P. darwini* and *A. olivaceus*) were not represented in the feces. Interestingly, in the study by Meserve et al. (1986), *O. degus* and *A. bennetti* were the largest-sized prey in the area.

Mere abundance seems not to be the small-mammal feature upon which foxes key. Two other features of potential small-mammal prey appear more important: large size and use of open scrub. As these two characteristics are associated among central Chilean small mammals, it is difficult to unravel their separate effect on attracting the attention of foxes. Studies of fox predation in areas where small-mammal size and habitat use are uncoupled should prove illuminating in this respect.

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