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Selection Of Cricetine Prey By The Culpeo Fox In Patagonia

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DIFFERENTIAL PREY VULNERABILITY: AN EXPLANATION FOR SELECTION OF CRICETINE PREY BY THE CULPEO FOX IN PATAGONIA

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ABSTRACT. The Patagonian culpeo fox (Dusicyon culpaeus) feeds mainly on the European hare, and secondarily on cricetine rodents, showing a marked preference for Akodon spp. In contrast, an approximately equally sized sympatric cricetine, Eligmodontia typus is rarely preyed upon in spite of being more abundant. Under the hypothesis that this preference is due to differential prey vulnerability we analyzed behavioral and morphological characteristics of the prey. The slightly lower weight of E.typus and its indiscriminate use of exposed habitats and microhabitats do not seem to explain the fox's selectivity. However we describe morphological adaptations related with an increased saltatorial ability, that could allow E.typus to display erratic and unpredictable flight responses. We conclude that this relative greater saltatorial ability of E.typus could imply a reduction of its relative vulnerability, thus being a plausible explanation for the fox's preference.

The culpeo fox (Dusicyon culpaeus) is the most important predator of the Patagonian steppe. It feeds mainly on European hares (Lepus capensis), sheep, and cricetine rodents (Crespo and De Carlo, 1963; Novaro, 1991). The silky mouse (Eligmodontia typus) is the most abundant potential prey that inhabit the steppe, however, it is hardly preyed upon by the fox. Species of the genus Akodon (Akodon longipilis, Akodon iniscatus, and Akodon xanthorhinus), are more common cricetine prey in spite of being less abundant.

A predator's prey selection is affected by antipredator behavioral adaptations as well as other attributes of prey which may not be directly related to their interaction (Sih, 1985). These adaptations in potential preys reduce their vulnerability, hence increasing their survival (Brown et al., 1979; Schall and Pianka, 1980; Pastorok, 1981; Ives and Dobson, 1987; Main, 1987; Sih et al., 1988; Kotler and Holt, 1989). Sih (1985) classified prey behavioral adaptations in two groups: predator avoidance behavior and prey escape behavior. The former would reduce the probability of them being found by the predator, and so occur before the prey has been detected. The latter, instead, occurs after detection and would reduce the probability of the prey dying during the encounter.

The most common examples of avoidance behavior found in desert rodents include the use of protected habitats, and the active use of refuges (Price, 1978; Hansson, 1987; Main, 1987; Wywialowsky, 1987; Brown et al., 1988; Sih et al., 1988; Gotceitas and Colgan, 1989). Escape behaviors are associated with the display of diverse flight mechanisms (Bartholomew and Caswell, 1951; Simonetti, 1989). Kotler (1984; 1985) showed that bipedism in desert rodents determines flight patterns that reduce their vulnerability to predators.

Some prey attributes which are not directly related to their chance of being preyed upon, such as body size, can in many cases affect their capture frequency (Iriarte et al., 1989; Endler, 1991). Capture frequency can also be affected by differences in activity time between prey and predator (Iriarte, 1986; Kufner, 1986).

The purpose of this paper is to compare differential vulnerability of E. typus and Akodon spp. through morphological and behavioral characteristics, in order to explain the fox's selectivity shown for the cricetine community.

METHODS

The study site was located in four cattle ranches of Junín de los Andes district

(Neuquén, Argentina). The area is a mixed steppe of grasses and shrubs no taller than 1 m. The most common species are Mulinum spinosum, Poa sp., Festuca sp., and Senecio sp. (Movia et al., 1982).

We can distinguish three different habitats in this area (Table 1):

1.-Pampa or plain: a flat , wide, and relatively high extension with poor vegetative cover and sandy substrata.

2.-Valley: a flat to undulated and relatively low extension surrounded by the slopes that give way to the pampas. It has good vegetative cover and human activities are concentrated there.

3.-Slope: They have rocky substrata with good vegetative cover and can be very steep.

Sampling was conducted during the winters of 1988, 1989, and 1990 in each of the above mentioned habitats. Grids of 10 by 10 Sherman live trap were installed leaving strictly 10 m between neighboring traps. The grids were revised twice every day (at sunrise and sundown). Captured animals were identified, weighed and marked (Beasley and Getz, 1986).

Population sizes were calculated using Chapman's index (Seber, 1982). In order to increase "a posteriori" the number of recaptures and so, reduce the coefficient of variation, we grouped capture days in pairs (Day et al., 1980). Densities were obtained from the ratio between the abundance and the area occupied by the grid plus a strip of width equal to half the average distance covered by the individual between captures (Brant, 1963; Seber, 1982).

Microhabitat use. We studied microhabitat use considering that the capture frequency is strongly related to it (Price, 1978; Kotler, 1984). Microhabitats were defined measuring the distance between the trap and the most proximate refuge (rock or shrub), grouping in 5 cm categories starting from the 20 cm value (maximum refuge). Each trap site was considered a random sample of the available microhabitats (Holbrook, 1979). Trapping success in each microhabitat was compared to expected random capture frequencies by means of the Kolmogorov-Smirnov test (Siegel and Castellan, 1988), considering that if rodents use microhabitats randomly, the captures in a given microhabitat will depend only on the number of traps placed in that microhabitat (Simonetti, 1989). A further analysis was done excluding recaptures of the same individual in the same trap, as these could bias the estimation of microhabitat use (Rosenzweig, 1973).

Although trapping methods could bias the estimates of the prey activity (Thompson, 1982), we considered this effect minimized by the systematic categorization of trap location as well as the low proportion of open areas found in these study sites.

Morphological adaptations. The escape efficiency of prey depends on its morphology and, in the case of a desert rodent, on the kind and development of its legs (Bartholomew and Caswell, 1951; Djwadan and Garland, 1988). We assumed that through measurements of the rodent's legs, we can determine their tendency to a certain kind of locomotive ability. Hence, we calculated the Index of Relative Bipedism (IBR) as the ratio between the length of the distal segment of the front limbs (carpus-metacarpus-phalanges) and the length of the equivalent segment of the hind legs (tarsus-metatarsus-phalanges). We measured 51 individuals of E.typus and 25 individuals of Akodon spp. and compared the IBRs of the studied species by means of the Mann-Whitney test (Siegel and Castellan, 1988).

RESULTS

We captured 150 individuals identified as E.typus, and 45 as Akodon spp., plus 12 Oligoryzomys caudatus, 1 Phyllotis darwini, and 2 Marmosa pusilla (Marsupialia). No captures we registered during the sunset revisions.

Body size implications. Akodon spp. shows an average weight of 23.8 g (SD 6.0) being significantly greater than E.typus's 18.9 g(SD 3.8) (P < 0.01). We excluded from this analysis individuals captured in areas where only one of the species was found.

In most of the sites, E.typus was the most abundant cricetine, in some cases four fold that of the grouped Akodon spp. (Fig. 1). Therefore, the available biomass of the former species calculated from its average weight was always greater than the latter one.

Habitat and microhabitat implications. E.typus was captured in the three habitats, whilst Akodon spp. was not found in Plain habitats.

Microhabitat use analysis shows that Akodon spp. was captured more frequently than expected in protected areas (uncovered patches smaller than 0.3 m ^{2}) but the differences were not statistically significant (P > 0.01)(Fig. 2). E.typus, instead, did not show preferences for any microhabitat, but there was a slight tendency to appear more often in open areas (Fig. 3). It must be taken into account that the results of this analysis considered for each habitat separately showed no differences in either species.

Morphological implications. The comparison of the IBR shows significant differences in favour of E.typus (P < 0.01), its hind legs being at least 25% longer than those of the Akodon spp. group.

DISCUSSION

Many predators prefer bigger prey and so the capture frequency can be higher for larger prey items than expected by their frequency (Krebs and Davies, 1981). Iriarte et al. (1989) found that Chilean populations of the culpeo fox selected preys according to size. But, to detect profitability differences associated to body size between potential prey, predators should be able to judge the size of each item and discriminate their nutritional value. This implies a specific search image which can only be a consequence of previous experience and so depend on the relative abundance of the prey items (Cheverton et al., 1985; Guilford and Slamdambuis, 1987). As E.typus is notably more abundant, selection against Akodon spp. would imply great perceptive specialization to detect a less than 5 g difference, which seems very unlikely considering that cricetine rodents are secondary prey items of a predator of rather poor environments.

Activity time segregation between predator and prey would reduce the latter's vulnerability to predation. Although Pearson (1983) states that Akodon spp. possess diurnal habits, we never captured any before dusk. E.typus is strictly nocturnal confirming previous descriptions (Pearson, 1983; Pearson et al., 1984; Mares, 1988). These findings suggest no activity time segregation with the culpeo fox (Crespo and De Carlo, 1963; Travaini, unpublished data.).

Prey availability as well as prey vulnerability could be affected by the structure of the habitat. Habitats with greater plant cover are less risky for prey, because the cover reduces the size of the exposed areas, hence, reducing the chance of being detected by the predator (Thompson, 1982; Wywialowsky, 1987). Vulnerability, also, can be affected by differential microhabitat use. In any given habitat prey can show either of two possible behavioral patterns: 1) to use protected and unprotected areas according to their availability, or 2) to reduce the activity to microhabitats that offer greater protection (under shrubs). The latter can imply differential predation.

In the three habitats here studied, E.typus was the most abundant cricetine, and the only species captured in those with the least cover, and therefore with greater risk of being preyed upon. Also, this species did not show activity restricted to less vulnerable microhabitats such as under protective shrubs. This ubiquitous behavior could be indicating that both habitat and microhabitat use are not responding to predatory pressure.

In contrast, Akodon spp. was only present in habitats with greater cover, and apparently uses protected microhabitats more frequently than E.typus, however our

results are not conclusive. However, this pattern can not be assigned exclusively to predatory pressure as in the best of cases it is the product of an integrate behavioral response to intraspecific and interspecific interactions , foraging activity and predator avoidance (Holbrook, 1979; Simonetti, 1989). Nevertheless, their space use pattern will ultimately reduce their vulnerability.

Previous studies of rodent space-use patterns in North American deserts report that bipedal species foraged in open microhabitats, showing little response to predatory pressure and greater efficiency in escaping predators than quadrupedal ones (Bartholomew and Caswell, 1951; Thompson et al., 1980; Harris, 1984; Kotler, 1984, 1985; Brown et al, 1988; Djwadan and Garland, 1988). Djwadan and Garland (1988) have demonstrated that bipedal locomotion permits greater instant velocity. This fact, together with the ability to change flight direction in an unpredictable manner and the possibility of more diverse escape responses undoubtedly contribute to escaping from predators, especially during the initial attack (Bartholomew and Caswell, 1951; Kotler, in litt.)

The differences here detected show that E.typus is more "bipedal" than the Akodon species. Field observations of E.typus's escape response are further evidence as every time an individual was released after its capture, it ran away by means of erratical hops. In contrast, the Akodon spp. always ran in a linear fashion to the nearest refuge (pers. obs.).

Although E.typus is not a bipedal rodent "sensu stricto", it shows certain features that allow "...a superficial comparison with the heteromyids rodents of North America, having long and thin hind legs..." (Mares, 1973). Pearson et al. (1984) indicate that E.typus has its hind legs 20% longer than the equally sized North American quadrupedal rodent , Peromyscus maniculatus .

Although the relatively greater development of E.typus hind legs is not comparable to the typical kangaroo rats of desert habitats, nevertheless, any relatively greater saltatorial ability in this kind of environments can imply a greater escape efficiency and consequently reduce its vulnerability.

CONCLUSION

The fact that E.typus, the most abundant rodent of the Patagonian steppe at Neuquén, is markedly less frequent in the culpeo fox's diet th in a sympatric group of other cricetines could be explained by its relatively reduced vulnerability. Our results support

the hypothesis that reduced vulnerability is acquired by a greater ability to display "bipedal" responses as the greater development of hind legs and the independence of habitat cover seem to show. Its morphology allows it to display erratic and unpredictable escape behaviors reducing its chance of being caught by the fox, and could in consequence enable this ubiquitous species to exploit unprotected microhabitats.

Although cuantitative data can only be obtained with experimental work, the mere comparison between prey species in totally natural conditions does allow us to analyze true prey availability and hence contribute to understand these complex predator's preferences.

ACKNOWLEDGMENTS

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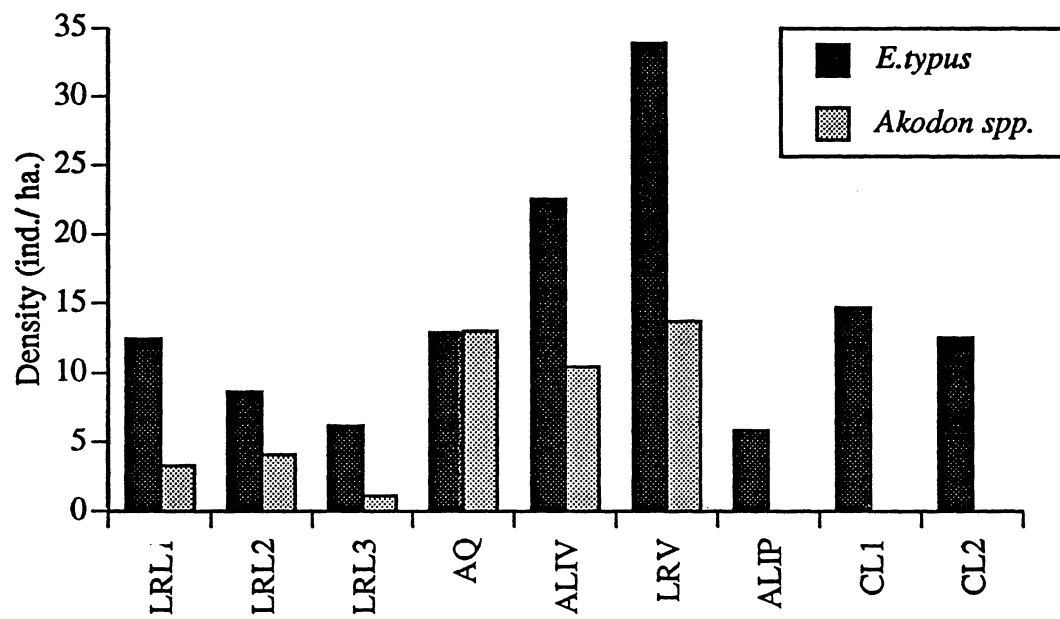SIMONETTI, J. 1989. Microhabitat use by small mammals in central Chile. Oikos, 56:309-318.

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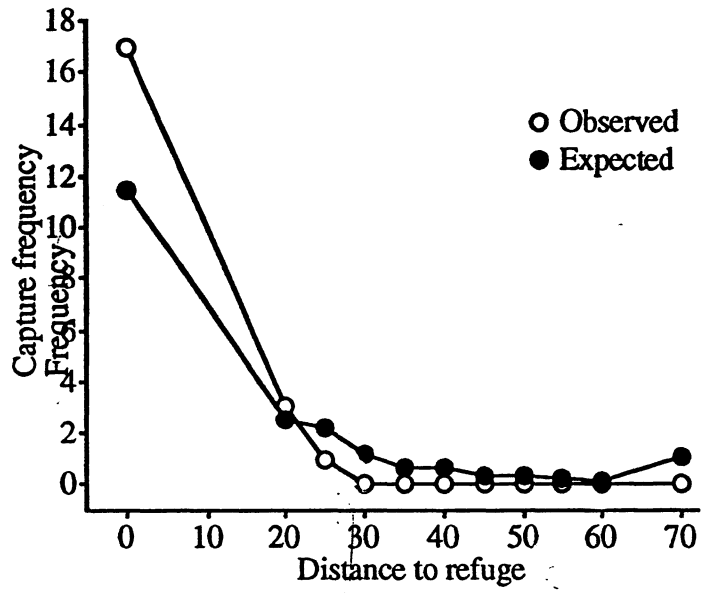
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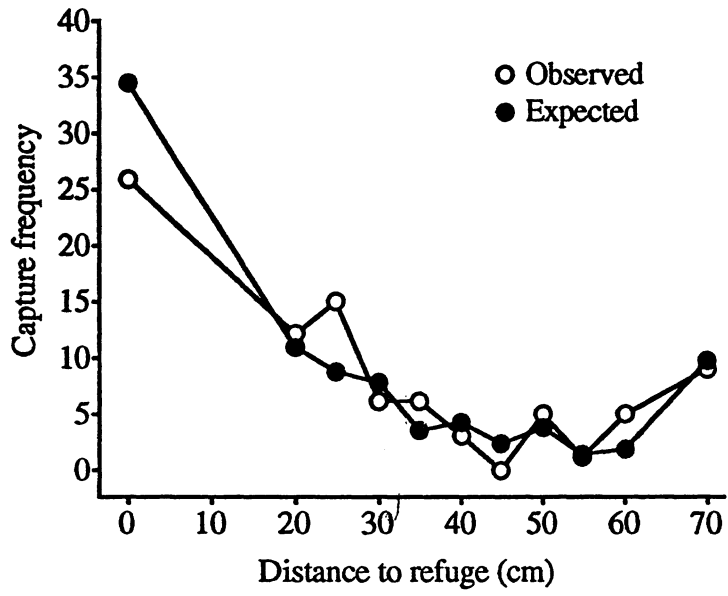
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Fig.1.- Densities of <u>Eligmodontia typus</u> and <u>Akodon</u> spp. in 9 different sampling sites (LRL1= La Rinconada ,slope 1988; LRL2=La Rinconada, slope 1989; LRL3=La Rinconada ,slope 1990; AQ=Aquinco; ALIV=Alicura valley; LRV=La Rinconada ,valley; ALIP=Alicura ,plain; CL1=Catan-Lil ,1989; CL2=Catan-Lil ,1990).

Fig. 2 · Observed and expected absolute capture frequency according to the distance of the trap to the nearest refuge of <u>Akodon</u> spp. grouping samples of three representative habitats of the Patagonian steppe.

Distance to refuge (cm)

Fig. 3 · Observed and expected absolute capture frequency according to the distance of the trap to the nearest refuge of <u>Eligmodontia typus.</u> grouping samples of three representative habitats of the Patagonian steppe.

Table 1.- Characteristics of 9 sampling sites of Neuquén Province (Argentina). Cover is expressed in percentage and the standard deviations are between brackets.

DATE	SITE	HABITAT	COVER
June 1988	Alicura	Valley	57.69 (14.6)
June 1988	La Rinconada	Slope	87.98 (4.6)
July 1988	La Rinconada	Valley	70.34 (15.7)
July 1988	Alicura	Plain	48.81 (19.8)
June 1989	La Rinconada	Slope	85.08 (7.7)
June 1989	Catan-Lil	Plain	24.46 (3.4)
June 1989	Aquinco	Valley	62.00 (22.5)
June 1990	La Rinconada	Slope	76.54 (9.3)
July 1990	Catan-Lil	Plain	18.32 (12.2)