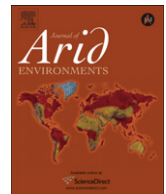




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Rodent selection by Geoffroy's cats in a semi-arid scrubland of central Argentina

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ABSTRACT

Small mammals usually constitute the main prey for *Leopardus geoffroyi* throughout its distribution. We studied the patterns of small rodent selection by this felid in a semi-arid scrubland of central Argentina, addressing whether prey choice may be related to the availability, morphology, and distribution of the different rodent species. Cat's diet was studied during 2005–2006 through the analysis of 182 scats, along with field estimates of rodent abundances from trapping. The cricetine rodents *Akodon molinae* and *Calomys musculus* were predated according to the availability expected by trapping, indicating that their use was opportunistic. *Akodon azarae* and *Graomys griseoflavus*, on one hand, and *Eligmodontia typus*, on the other hand, were consumed in lower and higher proportion than their availabilities, respectively. Our results suggest that some cricetine rodent characteristics such as abundance, escape ability, microhabitat use, and activity period, appear to be potential factors contributing to differential vulnerability to predation by Geoffroy's cat in central Argentina.

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1. Introduction

Predator-prey interactions are of particular interest in arid and semi-arid environments, where food resources are temporally fluctuant (Wiens, 1977). Prey may be captured in the same proportion as present in the environment by an opportunistic predator or in a different proportion by a selective one (Andersson and Erlinge, 1977; Futuyma and Moreno, 1988), and these patterns probably arises from the interaction between behavior and morphology of both predator and prey (Corley et al., 1995; Dickman et al., 1991; Kotler, 1984; Nishimura and Abe, 1988). Factors affecting prey choice by predators generally differ across landscapes, and this knowledge is essential to determine the ability of predators to deal with different prey compositions and habitat characteristics (Bekoff et al., 1984).

For several reasons, small mammals are a highly profitable prey for carnivores. First, small mammals are generally abundant in many ecosystems (Curtin et al., 2000; Pearson, 1964), which increase the encounter rate with predators. Second, they are usually easy to handle and digest by carnivores (Erlinge et al., 1974; Pearson, 1964). Third, small mammals typically contain a greater

percentage of digestible matter respect to similar-sized birds or reptiles (Hume, 2005; Johnson and Hansen, 1979). In consequence, small mammals-and particularly small rodents-comprise the bulk of the diet of several small-sized felids (<7 kg of body weight) (Lozano et al., 2006; Sliwa, 2006; Walker et al., 2007). Moreover, Mukherjee et al. (2004) estimated that up to 70% of the daily metabolizable energy in the jungle cat (*Felis chaus*) and the caracal (*Caracal caracal*), is obtained from small rodents.

Different small mammal species have evolved different strategies to avoid predation and reduce vulnerability, including morphological features (e.g., size of the auditory bullae, length of the forelimbs) or behavioral traits (e.g., bipedal locomotion, use of dense cover) (Dickman, 1992; Kotler, 1984; Rosenzweig, 1973; Taraborelli et al., 2003). Ultimately, these antipredatory traits and the structure of the small mammal assemblage result in interspecific differences in vulnerability to predation (see Corley et al., 1995).

Geoffroy's cat (*Leopardus geoffroyi*) is a small felid (ca. 4 kg) distributed from southern Bolivia and Brazil to southern Argentina and Chile (Nowell and Jackson, 1996). This species appears to be a highly adaptive predator, inhabiting a wide variety of habitat types including wetlands, dry forests, grasslands, and scrublands (Perovic and Pereira, 2006). Although the introduced European hare (*Lepus europaeus*) or waterbirds were found to be important prey items for Geoffroy's cat in some localities, small mammals usually constitute the main prey for this felid throughout its

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distribution range (Bisceglia et al., 2008; Canepuccia et al., 2007; Johnson and Franklin, 1991; Manfredi et al., 2004; Novaro et al., 2000; Sousa and Bager, 2008; Vuillermoz, 2001). However, the selection pattern of rodents in relation to their morphological and behavioral traits remains unstudied, impeding the recognition of how those factors may predispose different rodent species to greater predation rates by these cats.

A previous study about diet composition of Geoffroy's cat carried out in the Monte desert of central Argentina (Bisceglia et al., 2008) showed that small mammals constituted up to 94% of its diet. Here, we studied the seasonal patterns of small rodent selection by the same Geoffroy's cat population, addressing whether prey choice may be related to the availability, morphology, and habitat use of the different rodent species.

2. Study area

The study was conducted in Lihue Cale National Park (37° 57' S, 65° 33' W; 9900 ha). This protected area is located in the endemic Monte Eco-region of central Argentina (Burkart et al., 1999). The landscape is composed of a flat terrain, except for a large set of bare rock hills. The vegetation is characterized by a mosaic of creosote bush flats of the genus *Larrea*, open grasslands and isolated patches of xeric forests with *Prosopis caldenia* and *Prosopis flexuosa* as dominant tree species. The area is characterized by hot summers (January mean temperature = 24 °C), cool winters (July mean temperature = 8 °C) and low annual rainfall (414 mm), concentrated mostly in spring and summer (September–April).

3. Materials and methods

3.1. Availability of small rodents

We studied prey selection patterns by Geoffroy's cats considering the seven small sigmodontine rodents (*Akodon azarae*, *Akodon molinae*, *Calomys musculinus*, *Eligmodontia typus*, *Graomys griseoflavus*, *Oligoryzomys longicaudatus*, and *Reithrodon auritus*) highly preyed by this felid species at Lihue Cale throughout the year (collectively, these set of species composed >50% of the seasonal diet composition in terms of percent occurrence; Bisceglia et al., 2008). Although other small rodent species (such as the caviomorphs *Galea leucoblephara*, *Microcavia australis* and *Ctenomys azarae*) inhabit the study area, they were infrequently preyed upon by this felid (Bisceglia et al., 2008) and they were not included in the present study.

Abundance of small sigmodontine rodents was surveyed seasonally from winter 2005 (mid-August) to fall 2006 (mid-May), using the multiple capture-recapture method (Lancia et al., 1994) seasonally installed five grids of 7 × 8 live traps (7.6 × 8.9 × 22.8 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida), with 10 m between traps, in the three habitat types highly represented in the study area: a) two grids in mixed scrublands of *Condalia microphylla*, *P. flexuosa*, *Lycium chilense* and *Larrea divaricata*, b) two grids in rocky slopes, and c) one grid in tall grasslands dominated by the thistle *Centaurea solstitialis*. Since Pereira (2009) pointed out that Geoffroy's cats showed a similar intensity of use of the three habitat types, we consider the current sampling design adequately represents rodents' availability for this predator. Grids were operated for 5–6 consecutive nights (overall trapping effort = 6468 trap-nights), using rolled oats and peanut butter as bait. Captured individuals were identified to species level, sexed, weighed, marked by toe clipping, and released at the capture site. Toe clip material was preserved for further genetic analyses. Due to the low capture and recapture rate of some species throughout the year, we were unable to estimate the abundance of rodent species using capture-recapture models. Thus, the seasonal abundance of

each small rodent species was estimated using the minimum number of individuals known alive (MNKA). In each season, the proportion of each species in each habitat type was used as an index of its relative abundance.

3.2. Use and selection of small rodents by Geoffroy's cat

Diet composition of Geoffroy's cats was determined by analyzing fresh scats (see methods details and complete results in Bisceglia et al. (2008)). Scats were seasonally collected from winter 2005 to fall 2006, during a one-week period simultaneously with the small rodent surveys. Contribution of different small rodent species to the diet was reported as the number of times individuals of each species was found as percentage of all small rodents found (percent occurrence; PO). A goodness-of-fit chi-square test (Zar, 1996) was used to determine whether observed frequencies of each species in scats differed significantly from expected frequencies as estimated from trapping. Bonferroni confidence intervals were used to identify differences among species (Neu et al., 1974). When the expected proportion of consumption did not lie within the interval, we concluded that the expected and observed consumptions were significantly different at a level of significance of 0.05. Because the trapping protocol used during this study appeared to be not suitable to accurately assess the abundance of *R. auritus* (probably due to inadequate bait; see also Trejo and Guthmann (2003)), we did not consider this species for the selection analysis.

4. Results

4.1. Availability of small rodents

Globally, small rodents were more abundant during summer and fall than during spring or winter (Fig. 1). In each season, no significant differences were found in their abundance among habitats, except during summer ($\chi^2 = 11.51$, $df = 3$, $P = 0.003$) when the mixed scrubland showed the highest abundance and the rocky slopes the lowest one (Fig. 1). The grasslands showed a significant higher abundance of small rodents in summer and fall with respect to winter ($\chi^2 \geq 5.78$, $P \leq 0.016$), whereas the rocky slopes exhibit a significant higher abundance of small rodents in summer with respect to winter and spring ($\chi^2 \geq 7.76$, $P = 0.005$). The abundance of small rodents differed throughout the year in the mixed scrubland ($\chi^2 \geq 9.39$, $P \leq 0.002$), except between summer and fall ($\chi^2 = 0.19$, $P = 0.656$) when maximum abundances were reached (Fig. 1). *A. molinae* constituted >20% of the seasonal small rodent captures, with capture peaks in summer and fall (Fig. 2). *A. azarae* showed a similar pattern of captures of *A. molinae* throughout the year, but seasonal capture numbers were lower. *C. musculinus* was the most captured species in summer and fall. The remaining species were poorly represented in captures, except *G. griseoflavus* which showed a capture peak during fall (Fig. 2). *R. auritus* was not captured at all in spite of its presence in the study area was noticed from feces and burrows (Teta et al., 2009). Both *Akodon* species were more captured in the mixed scrubland than in the other habitats; in contrast, *C. musculinus* was more captured in the grasslands and the rocky slopes (Table 1). *G. griseoflavus* and *A. molinae* were the heaviest of the studied species, whereas *C. musculinus* showed the lowest body mass (Table 1).

4.2. Use and selection of small rodents by Geoffroy's cat

A. molinae was the most consumed small rodent throughout the year, followed by *C. musculinus* and *E. typus* (Table 2). Other species reached relative high values in the cat's diet in a single season, such

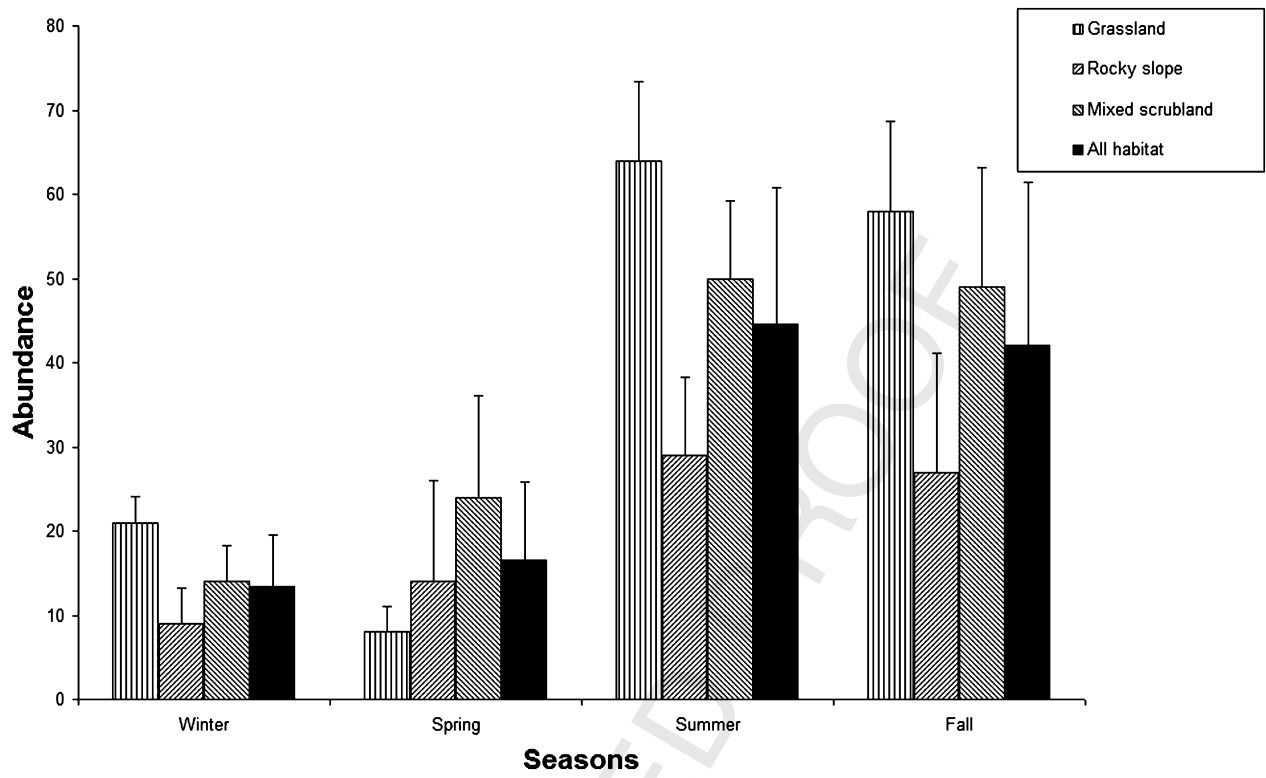


Fig. 1. Abundance of the small rodent assemblage (mean ± SE) in each habitat type and in all habitat types combined in Lihue Calel National Park, Argentina, during 2005–2006.

as *G. griseoflavus* in fall and *R. auritus* in summer (Table 2). The overall proportion of each species in the diet was significantly different ($P < 0.001$) to that expected as estimated from trapping in winter ($G = 32.36$; d.f. = 6), spring ($G = 61.73$; d.f. = 7), summer ($G = 64.41$; d.f. = 7), and fall ($G = 60.82$; d.f. = 4). *A. molinae* and *C.*

musculus were consumed in proportion to their availability throughout the year, whereas *G. griseoflavus* was negatively selected in summer and *E. typus* was positively selected in spring (Table 3). Finally, *A. azarae* (intervals not showed) was consistently “avoided” in all season.

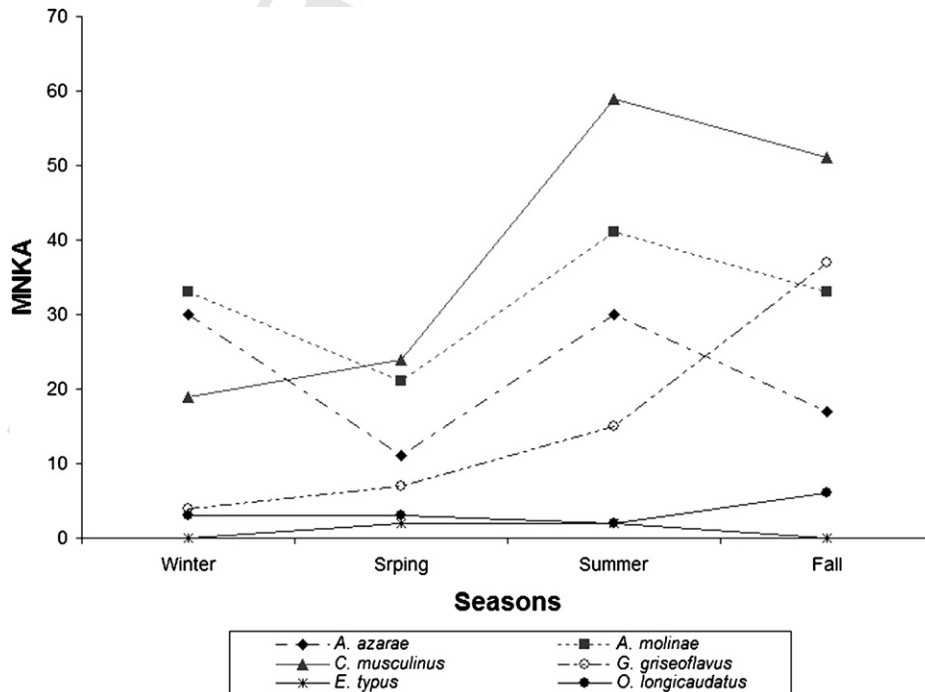


Fig. 2. Minimum number of individuals known alive (MNKA) of each small rodent species during each season in Lihue Calel National Park, Argentina, from winter 2005 to fall 2006.

Table 1
Morphological and behavioral traits and number of individuals of small rodent species captured in different habitat types, estimated as the MNKA, in Lihue Calel National Park, Argentina. Values in rocky slopes and scrubland were averaged between both grids operated in these habitat types. Escape and Activity were compiled from several sources: Contreras 1979, Pearson 1995, Taraborelli et al., 2003 and Teta et al., 2009.

Species	Body mass (mean ± SD)	Escape	Activity	Grassland	Rocky slopes	Mixed scrubland
<i>Akodon azarae</i>	20.2 ± 5.4	Quadrupedal	Diurnal/Nocturnal	13	0.5	37
<i>Akodon molinae</i>	37.6 ± 10.5	Quadrupedal	Nocturnal	25	7.5	44
<i>Calomys musculus</i>	14.7 ± 4.2	Quadrupedal	Nocturnal	50	30	21.5
<i>Graomys griseoflavus</i>	51.9 ± 15.7	Quadrupedal saltation	Nocturnal	4	13.5	16
<i>Eligmodontia typus</i>	19.2 ± 5.3	Quadrupedal saltation	Nocturnal	1	1	0.5
<i>Oligoryzomys longicaudatus</i>	25 ± 4.4	Bipedal	Nocturnal	0	0	7

5. Discussion

Our results showed that *A. molinae* and *C. musculus* were the most abundant small rodent species in the field as well as the most consumed rodent species by Geoffroy's cats. In fact, both species were consumed according to their availability, indicating that their use was opportunistic. Thus, Geoffroy's cat would be considered as plastic predator, which feeds on the most abundant prey in order to maximize consumption (Griffiths, 1975). Both *A. molinae* and *C. musculus* are short-legged rodents that have primarily a quadrupedal gait to escape from predators. This mode of locomotion is less effective than the bipedal one employed by other desert adapted species, which make them more vulnerable to predators and thus more dependent of plant cover (Taraborelli et al., 2003). Accordingly, both species reached high abundances in the more sheltered environments, such as the mixed scrubland and the grassland habitats. Several predation studies focused on raptor species have demonstrated that prey with low and predictable movements are often captured more frequently than those with rapid and erratic movements (e.g., Clarke, 1983; Glickman and Morrison, 1969; Kaufman, 1974; Spiegel et al., 1974;). This is probably due to predators preferring prey with the greater certainty of capture (Stephens and Krebs, 1986). As a result, both the high abundance and the poor escape response of these species probably enhance their profitability as prey for Geoffroy's cats.

However, a different pattern was observed with *A. azarae*. Although this small rodent was abundant in Lihue Calel and it have also a quadrupedal gait to escape from predators, its presence in Geoffroy's cat feces was low. This species also reached its maximum abundance in the mixed scrubland, that was the more sheltered habitat of the three studied. Prey selection on *A. azarae* and its congeneric *A. molinae* probably did not result from differences in habitat use, morphology, or prey size, because both species are associated with relatively complex and closed habitat with high shrub cover, are morphologically similar and have body weights within the size range taken by cats (Teta et al., 2009). In this context, the "avoidance" of *A. azarae* is probably related with the mostly diurnal habits of this species in the study area (Teta et al., 2009). Thus, even when Geoffroy's cats use habitats with dense

Table 2
Seasonal diet composition of *Leopardus geoffroyi* expressed in percent occurrence in Lihue Calel National Park, Argentina (see Bisceglia et al., 2008 for complete results).

Prey item	Season			
	Winter	Spring	Summer	Fall
<i>Akodon molinae</i>	55.1	27.3	34.7	24.4
<i>Akodon azarae</i>	7.1	7.6	2.7	5.4
<i>Calomys musculus</i>	20.4	31.8	36.0	27.0
<i>Graomys griseoflavus</i>	4.1	9.1	6.7	13.5
<i>Eligmodontia typus</i>	13.3	18.2	9.3	27.0
<i>Reithrodon auritus</i>	0.0	3.0	10.6	0.0
<i>Oligoryzomys longicaudatus</i>	0.0	3.0	0.0	2.7

cover in Lihue Calel, such as scrublands and dense grassland (Pereira et al., 2006; Pereira, 2009), its activity time does not coincide with the main activity time of this mouse. In consequence, *A. molinae* may be actually more vulnerable to predation than *A. azarae*, because its activity period and habitat use pattern coincide with those of Geoffroy's cat.

Ease of capture and body size are two important factors affecting differential capture rates among prey types (Derting and Cranford, 1989). For example, both *G. griseoflavus* and *E. typus* have the ability to use quadrupedal saltation to avoid predators, including abrupt and quick changes of direction when escaping or erradic zigzagging movements (Taraborelli et al., 2003). Quadrupedal saltation may be more effective than quadrupedal gait in escaping attacks by predators because it allows for higher speed, a faster response to attack, and sudden changes of direction (Taraborelli et al., 2003). Taking into account its large size, long legs and climbing abilities, *G. griseoflavus* was able to escape predators using jumps longer than 10 cm and/or climbing up on shrubs and trees (Taraborelli et al., 2003). On the other hand, despite its low weight and jumping locomotion, *E. typus* is easy to catch because it inhabits sites with low vegetation cover or bare ground and it runs in the open for long periods (Trejo and Guthmann, 2003; Trejo et al., 2005). Use of open habitats is associated with higher risk of predation (Kotler, 1984), and this feature can increase its vulnerability to Geoffroy's cat predation.

Our results suggest that some features such as abundance, escape ability, microhabitat use, and activity period appear to be potential factors that contribute to differential vulnerability to predation by Geoffroy's cat in scrublands of Argentina. In a similar study carried out in a wetland landscape, Canepuccia et al. (2007) found that abundance, distance of prey before attack, and prey size were significant predictors of prey (mainly waterbird)

Table 3
Prey selection by Geoffroy's cat in Lihue Calel National Park, Argentina, based on the Bonferroni confidence intervals. Positive (prey species consumed more than expected) or negative (consumed less than expected) selection are considered at the 0.05 level of significance.

	Season	Expected proportion	Bonferroni intervals	Selection
<i>Akodon molinae</i>	Winter	0.37	0.31 ≤ p ≤ 0.69	=
	Spring	0.30	0.12 ≤ p ≤ 0.42	=
	Summer	0.24	0.19 ≤ p ≤ 0.49	=
	Fall	0.23	0.05 ≤ p ≤ 0.42	=
<i>Calomys musculus</i>	Winter	0.25	0.09 ≤ p ≤ 0.31	=
	Spring	0.32	0.16 ≤ p ≤ 0.47	=
	Summer	0.35	0.21 ≤ p ≤ 0.51	=
	Fall	0.35	0.07 ≤ p ≤ 0.45	=
<i>Graomys griseoflavus</i>	Winter	0.03	0.00 ≤ p ≤ 0.09	=
	Spring	0.10	0.00 ≤ p ≤ 0.19	=
	Summer	0.35	0.00 ≤ p ≤ 0.14	Negative
	Fall	0.25	0.00 ≤ p ≤ 0.28	=
<i>Eligmodontia typus</i>	Spring	0.03	0.05 ≤ p ≤ 0.31	Positive
	Summer	0.01	0.00 ≤ p ≤ 0.18	=

consumption by this predator. Geoffroy's cat appears to consume different prey species in an opportunistic manner, maximizing the use of the most abundant "profitable" species. In arid and semi-arid regions where water is a limiting resource, drought periods can have a strong effect on the abundance of main prey of Geoffroy's cats (Pereira et al., 2006). Thus, both the foraging flexibility and the opportunistic dietary strategy may help this felid to survive in these fluctuant environments.

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