

Seasonal variations in microhabitat use and feeding habits of the pampas mouse *Akodon azarae* in agroecosystems of central Argentina

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Bilenca D. N. and Kravetz F. O. 1998. Seasonal variations in microhabitat use and feeding habits of the pampas mouse *Akodon azarae* in agroecosystems of central Argentina. Acta Theriologica 43: 195–203.

We studied microhabitat use and food habits of the pampas mouse *Akodon azarae* (Fischer, 1829), in agroecosystems of central Argentina. In summer (breeding season), *A. azarae* inhabited both cropfields and their weedy borders. Sexually active females were caught at microhabitats with 31% more green cover than inactive ones. The percentage of invertebrates in the stomach contents of females was 104% greater than in males. In winter (non-breeding season), individuals were restricted to the borders, selecting sites with high levels of forbs and green cover. There were no significant differences between the sexes, either in microhabitat use or in food habits. We propose that reproduction of females is influenced by green cover, and that a decrease of this resource may reduce breeding activity of females in the borders after most plants enter senescence. Females would feed on insects as a source of proteins, which are required for reproduction. In winter, when the population is sexually inactive, individuals of both sexes have similar requirements and occupy the most suitable sites available within a low-quality habitat. We conclude that seasonal variations in microhabitat use and food habits of *A. azarae* are mainly influenced by changes in resource availability and reproductive status of individuals.

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Key words: *Akodon azarae*, microhabitat use, food habits, seasonality, Argentina

Introduction

Seasonality is one of the major factors promoting variation in demography and resource use by rodent species (Kincaid and Cameron 1985, Ostfeld *et al.* 1985). Agroecosystems of the Pampean region in central Argentina show great seasonal variations in habitat structure. The schedule of agricultural practices in cropfields and the cover of grasses and forbs in the borders of cultivated areas are both primarily determined by seasonality (Busch and Kravetz 1992, Bonaventura and Cagroni 1995).

The pampas mouse *Akodon azarae* (Fischer, 1829) is one of the most abundant species inhabiting the agroecosystems of the Pampean region. This species inhabits

mainly cropfield edges, roadsides and fencerows (typically known as 'borders') and shows a strong seasonal variation in abundance, with a minimum in spring (October–November) and a maximum in late autumn and winter (late May–August), followed by a dramatic drop (Crespo 1966, Pearson 1967, Dalby 1975, Zuleta *et al.* 1988, Zuleta 1989, Mills *et al.* 1991, Busch and Kravetz 1992). Reproduction of *A. azarae* is also seasonal; the breeding season may last from 6 to 9 months (from September–October to April–June; Crespo 1966, Pearson 1967, Dalby 1975, Zuleta *et al.* 1988, Mills *et al.* 1992).

Little is known about how seasonality may influence the pattern of resource use of pampas mice. Previous studies observed intersexual variations in resource use during the breeding season (Bilenca *et al.* 1992, Bonaventura *et al.* 1992), which were attributed to differential investments and requirements of each sex in seeking reproductive success (Trivers 1972, Clutton-Brock *et al.* 1982). However, most previous studies of microhabitat use of *A. azarae* were restricted to the borders (Bonaventura and Kravetz 1989, Bonaventura *et al.* 1992, Bilenca *et al.* 1995), and information in cultivated areas is lacking. In this study we examined the interactions of a pampas mouse population with the varying conditions of the agroecosystems. Specific hypotheses addressed were: (1) variations in microhabitat use and food habits among seasons are directly related to habitat structure and resource availability, and (2) demographic subsets of the population (ie males and females, sexually active and inactive individuals) show differential patterns of resource use during the breeding season.

Study area and methods

Field work was carried out at Diego Gaynor (34°18'S, 59°14'W), NW Buenos Aires Province, Argentina. The study area belongs to the Pampa Ondulada, an agricultural region with moderate slopes (less than 2%) and a temperate climate. Mean annual temperature is 16°C, and annual rainfall averages 1000 mm. Phytogeographically, the Pampa Ondulada belongs to the Pampean Province, Chacoan Domain, Neotropical Region (Cabrera 1953). The original vegetation consisted of matted grasses 0.5–1.0 m high, and trees were absent. Nowadays, the area is intensely cultivated, and most native plants are restricted to cropfield edges, roadsides and fencerows. Major summer crops are corn, soybeans, sunflower and sorghum. After harvest, fields are planted with winter-wheat, or left as stubble until spring.

Trapping was conducted at 3 cropfields (1 of preharvest corn and 2 of sunflower) and 5 borders between late February and early March (summer, breeding season), and at 2 cropfields (postharvest corn and sorghum) and 3 borders in late August 1992 (winter, non-breeding season). Trap sites were selected spanning the typical range of microhabitat variation available for rodents in each season (Bilenca 1993). Sherman live-traps were placed at 5 m intervals along traplines in each type of habitat. There were 30–60 stations per trapline. Traps were baited with a mixture of peanut butter and bovine fat, and checked daily for 3–5 consecutive nights. Capture effort in summer was higher than in winter (3150 and 720 trap-nights, respectively), in order to have representative samples of rodents during low-density periods. Since capture effort differed among samplings, abundance of *A. azarae* was estimated by trapping success (number of captures / number of trap-nights; Mills *et al.* 1991). Each individual of *A. azarae* was sexed, and classified as reproductively active (males: scrotal

testes; females: opened vagina, pregnant or lactating) or inactive (males: abdominal testes; females: closed vagina, neither pregnant nor lactating).

We placed additional traplines with snap-traps in cropfield and borders, in order to perform stomach content analyses of *A. azarae*. Snap-traps were located at least 500 m far from live-traps, and were baited with the same mixture as that used for live-trapping. Stomachs of snap-trapped individuals were removed and fixed in 70% ethanol. Procedures for stomach content analyses followed those of Bilenca *et al.* (1992): contents were boiled for 5 minutes, cleared in 50% sodium hypochlorite for 3 minutes, then washed, filtered with Whatman Grade 1 qualitative filter paper (retention: 11 μ m) and spread on Petri dishes. Contents were examined at 12 \times and 50 \times magnification, and visual assessment was made of the relative (volumetric) quantities of seeds, invertebrates (mostly insects) and plant material; bait was removed and not counted in the measurements.

To describe the microhabitats available to pampas mice in cropfields and borders in each season, 12–30 1-m²-quadrats were randomly placed in each trapline. Five microhabitat variables were recorded for each quadrat as follows: % of grass cover (GRASS), % of forb cover (FORBS), % of green cover (GREEN), % of bare ground (BAREG), and total volume of the vegetation, in dm³ (VOLUM), multiplying the area of total cover by the mean height of the vegetation. Dominant species and their phenological phases were also recorded.

To examine the microhabitat selection of *A. azarae*, we compared the distribution of frequencies of each microhabitat variable recorded at the trap sites where individuals of this species were captured with the median available in each type of habitat obtained from all quadrats, using the Wilcoxon signed rank test (Daniel 1978). Thus, microhabitat use of *A. azarae* was considered selective if any of the variables recorded was exploited disproportional to its availability (Johnson 1980, Litvaitis *et al.* 1994). Since livetrapping produced more than one capture of the same individual, we only considered the first capture of each individual to examine microhabitat occurrence, thus avoiding dependence among data (Kincaid and Cameron 1985, Llewellyn and Jenkins 1987). Statistical comparisons in microhabitat use and food habits included ANOVA *F*-tests and Students *t*-tests for comparison of means of two samples with unknown variances not assumed equal (Bailey 1981: 49–51). Percentages of the vegetation variables (GRASS, FORBS, GREEN, and BAREG), and of the food items in the stomach contents were arcsin transformed prior to the analyses.

Results

Analysis of vegetation

Borders showed a sharp seasonal change in species composition of cover: in summer, grasses (*Stipa hyalina*, *Cynodon dactylon*, *Paspalum dilatatum*) and forbs (thistles, *Bidens subalternans*, *Eryngium* spp.) had nearly equal share in vegetation cover, whereas the latter prevailed in winter (Table 1). The volume of the vegetation in summer was highly significantly higher than in winter ($F = 309.58$, $p < 0.001$). On the other hand, borders had more green cover and less bare ground in winter than in summer ($t = 3.38$, $p < 0.05$ and $t = 2.55$, $p < 0.05$, respectively). Both seasonal changes were likely caused by the vegetative growth of winter forbs (*Senecio* spp., *Baccharis pingraea*), which show a dense cover at soil level.

In the cropfields, changes in vegetation and habitat structure were related to agricultural practices. In summer, crops were senescent (previous to the harvest) and weed grasses (*Digitaria sanguinalis*, *Echinochloa crus-galli*, *Sorghum halepense*) comprised the bulk of the green cover. After harvest, cropfields lost most

Table 1. Mean (\pm SD) values of microhabitat variables during summer (S) and winter (W), for borders and cropfields in agroecosystems of Diego Gaynor, Argentina. GRASS – % of grass cover, FORBS – % of forb cover, GREEN – % of green cover, VOLUM – total volume, in dm^3/m^2 , BAREG – % of bare ground. * $p < 0.05$, ** $p < 0.01$ (ANOVA F -test). ^^ $p < 0.01$ (Student's t -tests for two samples with unknown variances not assumed equal).

GRASS		FORBS		GREEN		VOLUM		BAREG	
S	W	S	W	S	W	S	W	S	W
Borders ($n = 60$ in summer, $n = 45$ in winter)									
45 \pm 25	** 21 \pm 24	48 \pm 22	** 67 \pm 30	56 \pm 14	^^ 68 \pm 30	656 \pm 142	** 194 \pm 123	26 \pm 19	^^ 18 \pm 18
	^^	**	**	*	**	^^	^^	^^	**
Crop areas ($n = 72$ in summer, $n = 24$ in winter)									
50 \pm 32	^^ 0 \pm 0	12 \pm 21	15 \pm 15	62 \pm 21	** 15 \pm 14	367 \pm 194	^^ 22 \pm 17	59 \pm 29	^^ 72 \pm 15

of their cover, the percentage of bare ground increased significantly, and the scarce seedlings of forbs provided most of the available green cover.

In general, the microhabitats of borders were more homogeneous and had more cover and less bare ground than those of the cropfields (Table 1). However, cropfields showed more green cover than borders in summer ($t = 2.20$, $p < 0.05$), due to the different phenological phases of dominant species in each habitat type: in the cropfields, most species were still flowering or dispersing, whereas in the borders they entered senescence.

Trap success and breeding activity of *Akodon azarae*

Trap success of *A. azarae* in the borders increased from 1.6% in summer to 11.1% in winter. In summer, pampas mice had the same trap success in borders and cropfields, whereas in winter the population was almost absent in the cropfields (0.2%). Eighty eight per cent of the males ($n = 26$) and 72% of the females ($n = 32$) were sexually active during the summer (pooling data from live and snap trapping; one female with uncertain reproductive status was excluded), while breeding activity dropped sharply to 0% in winter ($n = 20$ and $n = 15$, for males and females, respectively).

Microhabitat use of *Akodon azarae*

Altogether 57 trap sites of *A. azarae* were examined during the study period (Tables 2 and 3). In summer, microhabitat variables recorded in the borders at the capture sites of *A. azarae* showed no significant deviations from the microhabitat median, whereas in the cropfields pampas mice were highly selective, occupying grassy microhabitats, with scarce bare ground, and high levels of green cover and plant volume. Comparisons among sexes revealed no statistical differences in microhabitat use between males and females of *A. azarae*. However,

Table 2. Microhabitat medians, and median values of microhabitat variables at the capture sites of *A. azarae*, classified by season and type of habitat. "+" indicates a significant selection of *A. azarae* for a certain variable (larger than microhabitat median), "-" means avoidance (smaller than microhabitat median). * $p < 0.05$, ** $p < 0.01$ (Wilcoxon signed rank test). Mnemonics of the variables as in Table 1.

	<i>n</i>	GRASS	FORBS	GREEN	VOLUM	BAREG
Summer						
Habitat: Borders	60	43	45	60	640	20
<i>A. azarae</i> capture sites	25	40	50	60	650	10
Habitat: Cropfields	72	48	0	65	300	70
<i>A. azarae</i> capture sites	11	95	0	75	400	15
		+ **		+ *	+ *	- **
Winter						
Habitat: Borders	45	10	70	70	170	15
<i>A. azarae</i> capture sites	21	5	85	75	230	10
			+ **	+ **	+ **	

Table 3. Mean (\pm SD) values of microhabitat variables at the capture sites of *A. azarae*, classified by season, sex and reproductive status. * $p < 0.05$ (ANOVA *F*-tests). Mnemonics of the variables as in Table 1. ^a One female with uncertain reproductive status was excluded from the analysis.

	<i>n</i>	GRASS	FORBS	GREEN	VOLUM	BAREG
Summer						
Males	16	59 \pm 28	39 \pm 30	59 \pm 16	614 \pm 195	20 \pm 19
Females	20	59 \pm 36	36 \pm 34	63 \pm 16	587 \pm 144	17 \pm 17
Active females ^a	12	58 \pm 42	36 \pm 41	68 \pm 17	550 \pm 158	21 \pm 18
Inactive females	7	59 \pm 30	36 \pm 22	52 \pm 11	654 \pm 106	13 \pm 14
Winter						
Males	12	11 \pm 18	80 \pm 15	78 \pm 15	204 \pm 87	15 \pm 11
Females	9	10 \pm 13	80 \pm 16	78 \pm 13	286 \pm 199	15 \pm 13

sexually active females were caught at microhabitats with 31% more green cover than inactive ones (68 and 52%, for active and inactive females, respectively; $F = 4.49$, $p < 0.05$, Table 3). The low numbers of sexually inactive males did not allow us to perform statistical comparisons of microhabitat use between males.

During the non-breeding season (winter), most *A. azarae* individuals were restricted to the borders, selecting microhabitats with greater values of FORB, GREEN and VOLUM than the microhabitat median. There were no significant differences between sexes in microhabitat use.

Food habits of *Akodon azarae*

A. azarae showed significant seasonal shifts in the consumption of the different food items (Table 4). In summer, the mean volumetric percentage of invertebrates in the stomach contents was greater than in winter ($t = 3.20$, $p < 0.01$), whereas in the latter there was a greater percentage of plant material ($F = 16.28$, $p < 0.001$).

During the breeding season, the mean volumetric percentage of invertebrates in the stomach contents of females was 104% greater than in males ($F = 9.06$, $p < 0.05$). Considering only sexually active individuals in the analysis, consumption of invertebrates by females was 2.7 times greater than males (sexually active females: mean = 49, SD = 23, $n = 11$, sexually active males: 18 ± 18 , $n = 7$, $F = 10.05$, $p < 0.01$). There were no significant differences between the diets of males and females during the non-breeding season.

Table 4. Mean (\pm SD) volumetric percentages of seeds, invertebrates, and plant material in the stomach contents of *A. azarae* during summer (breeding season) and winter (non-breeding season). ** $p < 0.01$ (ANOVA F-test), ^^ $p < 0.01$ (Student's *t*-tests for two samples with unknown variances not assumed equal).

	<i>n</i>	Seeds	Invertebrates	Plant material
Summer	23	24 (26)	38 (23) ^^	36 (23) **
Winter	14	15 (23)	15 (10)	70 (24)
Summer				
Males	10	28 (25)	24 (18) **	46 (24)
Females	13	21 (28)	49 (21)	29 (21)
Winter				
Males	8	20 (29)	11 (5)	69 (30)
Females	6	8 (11)	19 (13)	71 (15)

Discussion

During the study, *A. azarae* showed great variations in population abundance and habitat distribution, reflecting both temporal and spatial changes in habitat quality and reproduction. The considerable drop in trap success in the cropfields during winter reveals that harvesting of cultivated areas makes the habitat unsuitable for *A. azarae* populations, whereas the high abundance in borders is a consequence of the recruitment that took place during the breeding season and postharvest recolonization from agricultural areas. These results are in agreement with previous studies showing that borders are the only type of habitat which can provide year-round favorable habitat for *A. azarae* (Zuleta *et al.* 1988, Mills *et al.* 1991, Busch and Kravetz 1992). However, cropfields may act as a temporarily

suitable habitat prior to the harvest, as revealed by the microhabitat selection of *A. azarae* for grassy sites in the crop areas (Table 2).

The higher level of green cover recorded at the capture sites of active females as compared with inactive ones during the breeding season (Table 3), is consistent with evidence from a livetrapping study conducted at the borders by Bonaventura *et al.* (1992). These authors found a negative correlation between the average distance travelled by females of *A. azarae* and the green foliage density recorded at the trap sites, and considered that green cover was an important resource for home-range election in *A. azarae* females. According to our results, the significantly higher proportion of pregnant female *A. azarae* in cultivated habitats as compared to the borders (Mills *et al.* 1992) could be related to the higher level of green cover in the former habitat (Table 1). Although we have no direct evidence to explain the effect of green cover in the breeding success of females of pampas mice, available evidence allow us to propose that reproduction of *A. azarae* females is influenced by green cover, and that a decrease of this resource may reduce the breeding activity of sexually active females in the borders after most plant species enter senescence.

In winter, many of the sites covered by forbs which are selected by *A. azarae* at the borders offer soft shoots (food), and provide high vegetation volume at ground level (Table 2). The selection of *A. azarae* for this type of microhabitats may have great adaptive significance, considering that, in winter, food availability is a limiting factor (Cittadino *et al.* 1994) and since frosts and low temperatures induce great rodent mortality (Crespo 1944, Dalby and Heath 1976).

The great seasonal variation in food habits of *A. azarae* (Table 4) reflects the high opportunism of the species in switching to those food items which are more abundant at a particular time, ie, more consumption of invertebrates in summer and more plant consumption in winter (Bilenca *et al.* 1992). Even though food habits of pampas mice are greatly influenced by food availability, the difference in the consumption of invertebrates between sexes observed in the breeding season reveals that *A. azarae* female are able to exploit food resources selectively. The higher consumption of invertebrates by females suggests that females of pampas mice feed on insects as a source of proteins, thus meeting both energetic and nutrient requirements for reproduction (Hoffmann 1958, Bomford and Redhead 1987).

In summary, we have observed that *A. azarae* shows a great seasonal variation in the pattern of resource use in agroecosystems of central Argentina. Available evidence suggests that differences in the pattern of resource use between the breeding and the non-breeding seasons can be explained by both changes in individual requirements and habitat structure. In *A. azarae*, as in many polygynous mammals (Suárez 1996), each gender has different constraints on reproductive success, leading to sex-specific reproductive tactics (Trivers 1972, Clutton-Brock *et al.* 1982, Ostfeld *et al.* 1985). For females, reproductive performance would rely on their ability to acquire specific resources (green cover, insects), while repro-

ductive performance of males would depend on their ability to be accepted by females for copulation, and probably not directly related to the abundance and distribution of resources (Zuleta 1989, Zuleta and Bilenca 1992, Bonaventura *et al.* 1992, this study). It can be suggested that during the non-breeding season, with harsher environmental conditions, all individuals have similar requirements. Thus, both sexes seek similar microhabitats which provide the highest levels of shelter and food. Clarification of these hypotheses must await experimental studies including manipulations of green cover in the field, along with feeding trials and assessment of the reproductive performance of *A. azarae* in the laboratory.

Acknowledgements: We are grateful to M. Busch, G. R. Cueto, G. A. Zuleta and 4 anonymous reviewers for reading and commenting on the manuscript. This study was funded by grants of the University of Buenos Aires and the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina).

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Received 3 March 1997, accepted 27 October 1997.