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Nesting and digging behavior in two rodent species (*Akodon azarae* and *Calomys laucha*) under laboratory and field conditions

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Abstract

Nesting and digging habits as well as shelter locations were studied in *Akodon azarae* and *Calomys laucha* under laboratory conditions. Shelter locations were compared with burrow and nest locations in the field. Laboratory results showed that *A. azarae* built more burrows than surface nests while *C. laucha* built both surface nests and burrows and both species selected sods from external borders of cropfields (area out of the wire fences characterized by the most compacted soils and abundant plant cover) for building their shelters. Field observations showed that both *A. azarae* and *C. laucha* used burrows. In the field *A. azarae* shelters were located in the internal borders of cropfields (habitat with heavy plant cover placed under wire fences), while those of *C. laucha* were found in cropfields (the most perturbed habitat). We conclude that nesting and digging behavior in the laboratory reflects only soil selection while in the field it is also affected by interspecific competition, which causes spatial segregation of shelter locations between the two species.

Introduction

Akodon azarae and *Calomys laucha* are two of the most abundant murid rodent species that inhabit pampean agrarian ecosystems of central Argentina. Previous studies (Kravetz et al. 1981; Kravetz and Polop 1983; Busch et al. 1984; Mills et al. 1991; Busch and Kravetz 1992 a) suggest that these species show a differential habitat use. Rodents are distributed between two main macrohabitats: cropfields and their borders (marginal weedy areas below wire fences). While *Akodon azarae* uses more frequently cropfield borders, *Calomys laucha* occupies both habitats, but it is more abundant in the cropfields.

This spatial distribution is maintained, among other factors, by interference competition, *A. azarae* being competitively dominant over *C. laucha* (Busch and Kravetz 1992 a). In removal experiments, Busch and Kravetz (1992 b) demonstrated that the larger species, *A. azarae*, limited the abundance of *C. laucha* in the borders, and behavioral studies showed that competitive interference between both species may be expressed in spatial segregation produced from individual interactions (Busch and Kravetz 1992 b; Cueto et al. 1995).

In heterogeneous environments, habitat selection can exert marked effects on the outcome of interspecific interactions (Rosenzweig 1979; Pimm et al. 1985; Bowers and Dooley 1991; Danielson 1991), and differential habitat selection is considered one of the principal relationships that permit species to coexist (Rosenzweig 1981).

Evidences of direct methods as nesting and digging habits and the spatial location of the shelters (Kotler 1985) may contribute to elucidate the determinants of habitat choice and habitat occupancy patterns.

The aim of this work is to study the choice of habitat for nesting and digging habits in *Akodon azarae* and *Calomys laucha* under two situations: 1) Laboratory conditions (excluding intra- and interspecific competition) and 2) Natural conditions in the field.

Material and Methods

Laboratory experiments

Between August and December 1992, we studied habitat selection and the kind of shelters constructed by *A. azarae* and *C. laucha*. The experiment was conducted with 14 overwintering adult animals of *A. azarae* and 14 of *C. laucha* (7 females and 7 males in each case), which were caught in Diego Gaynor (34° 08′ S, 59° 14 W, Buenos Aires Province, Argentina) with Sherman live traps. Diego Gaynor is located in the Pampean region, the climate is temperate, and is characterized by agriculture and cattle farming. The landscape is composed of individual cropfields surrounded by wire fences with borders dominated by weedy species.

All mice were acclimated to laboratory conditions for two months before the experiment began. The animals were individually kept in laboratory cages (0.35 by 0.28 by 0.15 m) provided with sunflower seeds, water ad libitum and wood shavings as bedding materials. All individuals were maintained under a daily cycle of 14 h light: 10 h dark, an ambient temperature at 20 ± 4 °C and 60–80% of humidity.

The test apparatus used was a three glass boxes system (0.30 by 0.30 m side by 0.20 m high each box) connected with three equidistant wirework tubes (1.0 m long and 5 cm diameter each tube) (Fig. 1).

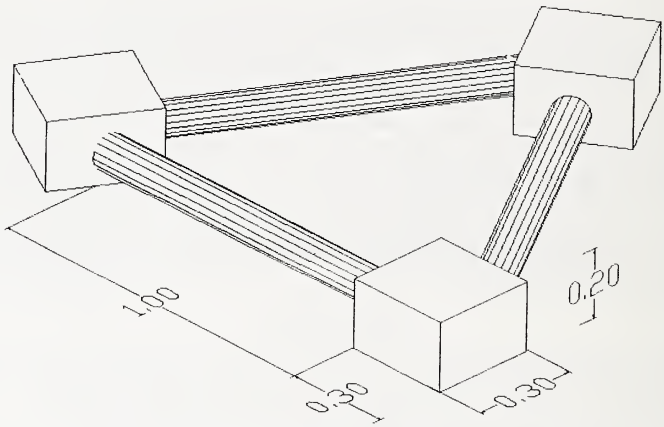

Fig. 1. A three glass box system connected with equidistant tubes used for laboratory experiences.

In each box one sod was used as substrate representing one of the three soil types being studied:

Soil type A: Cropfield characterized by a soil poorly compacted and strongly disturbed by agricultural activities.

Soil type B: Internal border (under wire fences limiting the cropfields) represented by strong and relatively stable plant cover and less compacted soil than the external one.

Soil type C: External border (out of the wire fences) characterized by abundant vegetation cover (with creeping species and rhizoma plants) and soil highly compacted by cattle.

Sods (0.30 by 0.30 m size by 0.15 m high each one) were taken out from D. Gaynor locality. Plant cover of types B and C sods were reaped at 0.10 m high previously to be placed into glass boxes. A water bottle and a supply of 50 g of oat seeds were offered into each box. Same conditions of day length, temperature and humidity were maintained previously and during the experiments.

Procedure

The animals were individually placed into the experimental system during 4 consecutive days. Each individual was randomly assigned to one box when it was introduced into the system. Observations started after 24 h of acclimatization to the experimental apparatus and they were initiated 2–3 h before the beginning of the dark period. There were two observations of 15 min per day. After each experiment the sods were removed and replaced by new ones; food and water were changed and the boxes were washed.

During each experiment we recorded:
Total permanence time: Total time (in min) spent by each animal in each habitat (Cropfield, internal border or external one).
Habitat types selectioned for building shelters.
Types of shelters built. They could be burrows (in deepness) or nests (at surface).

Field observations

The study was carried out during August 1993 on one 1.2 ha grid in a sunflower cropfield and its adjacent border in D. Gaynor locality. The experimental plot consisted of 120 Sherman live trap stations spaced at 10 m intervals.

From captured animals, all overwintering adult individuals (12 of *A. azarae* and 10 of *C. laucha*) were tracked using fluorescent pigments (Lemen and Freeman 1985), in order to determine their shelter locations. Selected animals were placed into a plastic bag containing a small amount of fluorescent pigment (Radiant Color, Richmond, CA), gently shaken and released at the site of capture. Animals covered with the pigment left a trail that could be followed at night with a longwave ultraviolet-light source locating shelters and identifying the type of shelter used and the habitat where it was placed.

Statistics

Kruskal-Wallis one-way analysis of variance was used to compare permanence times among habitat types. Dunn test for multiple non-parametric comparisons were performed if differences in permanence time were statistically significant (Siegel 1989). In order to compare the frequencies of types of shelters built and types of habitats selected we performed binomial tests (with grouped and ungrouped categories, Sokal and Rohlf 1980). In the first case the probabilities under the null hypothesis of random construction where $p = q = 0.5$, while in the second case the null hypothesis of random selection was $p = 0.33$ and $q = 0.67$. Fisher's exact probability test (Siegel 1989) was made for post-hoc analysis between laboratory and field results for both species. Values of $P < 0.05$ were considered to be significant in all analysis, except in Dunn multiple comparsions where the significant level was fixed at $P < 0.10$.

Results

Laboratory observations

Table 1. Total permanence time in each glass box. Time measures are in minutes (Median values are in parentheses).

	Species	
	A. azarae	*C. laucha*
Sod A	124 (0.5)	279.5 (2.5)
Sod B	473 (12.5)	217.5 (0)
Sod C	663* (56)	763* (69)
Total	1 260	1 260

Sods A, B and C: Sods from soil types A, B and C respectively. * Significantly different ($P < 0.05$ Kruskal-Wallis one-way analysis of variance).

In both species, individuals stayed significantly longer times in the soil type C (external border) than in the other 2 soil types (H: 6.00, $df = 2$, $P < 0.05$, Dunn $P < 0.10$ for *A. azarae* and H: 6.48, $df = 2$, $P < 0.05$, Dunn $P < 0.10$ for *C. laucha*) (Tab. 1).

Soil type C was also selected more frequently than the other types by *A. azarae* and *C. laucha* individuals for building their shelters (P(13): 0.008, $n = 22$, $P < 0.01$) and (P(10): 0.003, $n = 14$, $P < 0.01$), respectively (Tab. 2). Some *A. azarae* individuals built more than one shelter ($n = 22$) but all individuals of *C. laucha* built only one shelter ($n = 14$).

However, the kind of shelters built different according to the species. *A. azarae* built significantly more burrows in depth than surface nests (P(19): 0.0003, $n = 22$, $P < 0.01$), whereas *C. laucha* built surface nests as frequently as burrows (P(8): 0.183, $n = 14$, $P > 0.05$) (Tab. 3).

Table 2. Sod selection for building the shelters under laboratory conditions.

Species	Number of individuals	Number of observations	Number of shelters in each soil type		
			Sod A	Sod B	Sod C
A. azarae	14	22	2	7	13 **
C. laucha	14	14	0	4	10 **

Sods A, B and C: Sods from soil types A, B and C respectively.
** Significantly different ($P < 0.01$ Binomial test with grouped categories).

Table 3. Shelter types built under laboratory conditions

Species	Number of observations	Number of shelters	
		Burrows	Nests
A. azarae	22	19 **	3
C. laucha	14	6	8

** Significantly different ($P < 0.01$ Binomial test).

Surface nests were built with cut dry grasses delicately woven, as covered nests, and were placed in shallow depressions. They were cup-shaped nests with sides and a cover and they measured up to 5–6 cm in diameter for *C. laucha* and 8–10 cm for *A. azarae*.

Burrow systems of *A. azarae* had a branching structure. All burrows had a single nest chamber, packed with dry grasses and a variable number of tunnels to the surface. Rests of seeds and dry grasses in the central chamber and in the tunnels were observed in some cases.

Field results

According to fluorescent trails, burrows of *A. azarae* were located more frequently in the internal border ($P(8)$: 0.014, $n = 12$, $P < 0.05$) while *C. laucha* shelters were more frequently placed in the cropfield ($P(8)$: 0.002, $n = 10$, $P < 0.01$) (Tab. 4).

In agreement with laboratory observations *A. azarae* used burrows more frequently than surface nests in the field ($P(12)$: 0.0002, $n = 12$, $P < 0.01$). However, *C. laucha* used significantly more burrows than surface nests in the field ($P(9)$: 0.009, $n = 10$, $P < 0.01$) differing with laboratory observations (Tab. 5).

Table 4. Distribution of shelters in the 3 soil types under field conditions

Species	Number of individuals	Number of shelters in each soil type		
		Cropfield	Internal border	External border
A. azarae	12	4	8 *	0
C. laucha	10	8 **	2	0

* Significantly different ($P < 0.05$ Binomial test with grouped categories).
** Significantly different ($P < 0.01$ Binomial test with grouped categories).

Table 5. Shelter types located by marked animals under field conditions

Species	Number of individuals	Number of shelters	
		Burrows	Nests
A. azarae	12	12 **	0
C. laucha	10	9 **	1

** Significantly different ($P < 0.01$ Binomial test).

Shelter locations did not significantly differ under laboratory and field conditions for *A. azarae* (Fisher's exact test, $P = 0.154$), while *C. laucha* shelters were more frequently located in cropfields under field conditions, and in the external border in the laboratory (Fisher's exact test, $P = 0.0001$).

Discussion

According to our results, *A. azarae* individuals selected cropfield borders for building their burrows, both under laboratory and field conditions. However, in the first case the external border was more used, while under field conditions burrows were located in the internal border. The higher abundance of *A. azarae* in borders relative to cropfields is well documented (Mills et al. 1991; Busch and Kravetz 1992 a), but it is the first study in which it is confirmed that individuals of this species select borders for locating their burrows, thus these habitats are probaly the center of their daily activities and reproductive sites. The choice of a site for shelter location may be influenced by a number of factors, many of them being absent under laboratory conditions. Whether the selection is the same under such different circumstances, may depend on which keys animals use in order to identify a habitat. According to the theory of habitat selection, individuals may select those habitats where fitness is maximized (Morris 1987, 1988), assuming that animals are completely acknowledged with respect to the relative fitness rewards of different habitats. Habitat selection should be evolved through the identification of certain habitat cues, that bring out indirect information about these potential fitness rewards. In our case, which are the main features of each habitat that may be affecting its selection? From previous works (Bonaventura et al. 1989, 1992), it is clear that *A. azarae* abundance is correlated with high plant cover, which is found in both types of cropfield borders (external and internal one). However the borders are still selected in the laboratory, where plant cover was reaped at 10 cm high. The strongest difference between sods of different habitats are the characteristics of the soil. That from the external border is the most compacted soil, and apparently is the best fit to dig burrows, especially those of *A. azarae*, with a branching structure that needs the construction of tunnels. Cropfields soil is poorly structured due to plowing, and it was frequently disrupted when we tried to take out a sod, and the internal border soil is slightly less structured that the external one.

The selection of borders may then be related to both the presence of a good plant cover (under field conditions), that confers refuge from predators; and to soil characteristics, that favors burrow construction (under field and laboratory conditions). The difference between the relative use of external and internal borders under laboratory and field conditions must be related to the effect, in the first case, of only soil characteristics, while in the fields there are others factors, such as trampling by cattle, that may disturb more the external border than the internal one.

C. laucha located their nests and burrows in the borders under laboratory conditions, but it used the cropfield more in the field. This species shows more similar abundance in the two habitats than *A. azarae*, although it is generally more often captured in cropfields than in borders (MILLS et al. 1991; BUSCH and KRAVETZ 1992 a). Habitat segregation between these two species has been attributed to interspecific competition, which causes a shift in *C. laucha* towards cropfields (BUSCH and KRAVETZ 1992 b), and competitive dominance of *A. azarae* over *C. laucha* was also observed by CUETO et al. (1995) with respect to the access to food resources.

Our work provides another evidence that the apparent preference of *C. laucha* for cropfields, observed in natural conditions, may be caused by interspecific competition with *A. azarae*; since solitary individuals in laboratory, select sods of borders to build shelters and remain longer times in this type of habitat.

With respect to nesting and digging habits, *A. azarae* dug burrows and *C. laucha* built surface nests and burrows in the laboratory, while in the field both species used burrows. According to laboratory results, *A. azarae* probably uses burrows dug by its own, while *C. laucha* may occupy cracks and little modificated holds as burrows in the cropfields under field conditions, as observed by BUSCH et al. (1984) or dig own burrows as was demonstrated by YUNES et al. (1991). Living in an underground nest could be an adaptive response by *C. laucha* to avoid avian predators in cropfields where the plant cover is scarce, such as at harvest time or when the cropfields are recently tilled, and to survive at low temperatures, as was postulated by KRAVETZ et al. (1981) and YUNES et al. (1991).

The results of the present study suggest that *A. azarae* has the resident conditions in borders, which have the best habitability and limits the access of *C. laucha* to these habitats.

Therefore, *C. laucha* reduces direct competition with *A. azarae* in the field by moving to the cropfields that are less preferred habitats, because of being highly disturbed by agricultural activities and having low plant cover. The use of burrows may be favored in this kind of habitats instead of the more exposed surface nests. The ability of *C. laucha* to exploit unstable temporarily suitable habitats, such as the cropfields (MILLS et al. 1991) which are less often occupied by *A. azarae*, is in agreement with previous studies indicating that habitat shift is an adaptive behavior for subordinate species in two-species competitive system (ROSENZWEIG 1979).

In summary, we observed that *A. azarae* uses the most suitable habitat both under field and laboratory conditions, while *C. laucha* shifts its habitat use from the borders, when *A. azarae* is absent, and to the less suitable habitat when this species is present.

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Zusammenfassung

Nestbau- und Grabverhalten zweier Nagetierarten (Akodon azarae und Calomys laucha) unter Labor- und Feldbedingungen

Es wurden Verhaltensweisen beim Nestbau- und Grabverhalten sowie die Verteilung der Unterschlupfe von *Akodon azarae* und *Calomys laucha* unter Laborbedingungen untersucht. Die Lage der Unterschlupfe wurde dann mit der Lage der Erdhöhlen und Nester auf dem Feld verglichen. Die im Labor erzielten Resultate zeigten, daß *A. azarae* mehr Erdlöcher als Nester an der Oberfläche gebaut hatte, während *C. laucha* sowohl Nester an der Oberfläche, als auch Erdlöcher gebaut hatte. Beide Arten wählten Feldstücke vom äußeren Rand des Getreidefeldes (Standorte ohne Drahtzaun, mit am stärksten verdichteten Boden und einer artenreichen Pflanzendecke). Die Feldbeobachtungen ergaben, daß

A. azarae und *C. laucha* Erdhöhlen nutzten. Die Unterschlupfe von *A. azarae* befanden sich an den Innenrändern des Getreidefeldes (Standort unter einem Drahtzaun mit einer dichten Pflanzendecke), die von *C.laucha* jedoch befanden sich im Getreidefeld (Standort mit den meisten Störungen). Wir folgern hieraus, daß das Nestbau- und Grabverhalten im Labor nur von der Auswahl des Untergrundes abhängt. Auf dem Feld wird es hingegen auch durch interspezifische Konkurrenz beeinflußt, was eine räumliche Trennung der Aufzuchtgebiete beider Spezies zur Folge hat.

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