

Locomotion and Escape Modes in Rodents of the Monte Desert (Argentina)

Paula Taraborelli, Valeria Corbalán & Stella Giannoni

Grupo de Investigaciones de la Biodiversidad, Instituto Argentino de Investigaciones de las Zonas Áridas-CONICET, Mendoza, Argentina

Abstract

Modes of locomotion and escape tactics are attributes that affect the structure of animal communities, promoting exploitation of different microhabitats and the coexistence of different species. Bipedal locomotion is considered to be more effective than a quadrupedal gait in escaping attacks by predators because it allows for higher speed, a faster response to attack, sudden changes of direction and better detection of aerial raptors. The aim of this study was to determine the type of locomotion used at the moment of escape by three rodent species of the Monte desert – *Eligmodontia typus*, *Akodon molinae* and *Graomys griseoflavus*. The study was carried out in three plant communities of the Ñacuñán Reserve (Mendoza). All three species showed differences in both mode of escape and locomotory pattern. *Graomys griseoflavus* exhibited the highest proportion of escapes using quadrupedal saltation. The mode of locomotion employed by *E. typus* varied according to the type of plant communities it inhabited. Those occurring at open sites (Medanal community) exhibited a greater propensity to jump during escapes than those from more sheltered habitats (Algarrobal community). *Akodon molinae* relied primarily on a quadrupedal gait when fleeing from predators, which would explain its greater dependence on plant cover. Therefore, the morphological and behavioural characteristics of these species are related to their mode of locomotion and the strategies they employ to diminish the risk of predation.

Corresponding author: Paula Taraborelli, Grupo de Investigaciones de la Biodiversidad, Instituto Argentino de Investigaciones de las Zonas Áridas-CONICET, C.C. 507, 5500 Mendoza, Argentina. E-mail: ptarabor@lab.cricyt.edu.ar.

Introduction

Patterns of locomotion may help in explaining coexistence among desert rodent species because the way rodents move is related to their ability to exploit

microhabitats of varying degrees of predation risk (Brown & Lieberman 1973; Kotler 1984; Djawdan & Garland 1988; Price 1993; Vásquez 1996). Bipedality is strongly associated with life in arid regions (Mares 1983). In the United States, two genera of bipeds are rodents, while in other deserts, bipedal species may be marsupials, elephant shrews, or rodents (Mares 1993). Bipedality is regarded as an adaptation to the heterogeneous distribution of food in desert areas, where food is often found in open areas fraught with risk, but unavailable in protected sites or refugia (Costa 1995). In desert areas, the risk of predation is one of the most important factors influencing foraging behaviour (Hughes & Ward 1993; Hughes et al. 1994; Kotler et al. 1994; Vásquez 1994a; Kramer & Birney 2001), and the mode of locomotion employed by rodents plays a vital role in determining their ability to elude predators (Rosenzweig & Winakur 1969; Rosenzweig 1973; Thompson 1985; Djawdan & Garland 1988). When comparing species of similar size, bipedality permits more rapid acceleration, a faster response to predator attacks and sudden changes of direction. However, in terms of its energetic cost, bipedality does not differ from quadrupedality (Thompson 1985; Djawdan & Garland 1988).

Most studies addressing adaptations to harsh desert environments have focused on heteromyid rodents in North America (Reichman & Brown 1983; Randall 1993; Costa 1995). The type of locomotion employed appears to be related to escape/avoidance ability in different environments, with bipedal rodents (e.g. *Microdipodops pallidus*, *M. megacephalus*, *Dipodomys merriami*, *D. ordii* and *D. deserti*) being comparatively safer in open microhabitats, and quadrupedal rodents (e.g. *Perognathus* spp. and *Peromyscus* sp.) restricted to microhabitats affording at least some cover (Price 1978; Kotler 1984; Price 1986; Schroder 1987; Longland & Price 1991).

Among South American murids, *Eligmodontia* and *Oligoryzomys* are described as bipedal species (Mann 1978; Mares 1983). *Oligoryzomys longicaudatus*, in the Chilean matorral, uses bipedal locomotion when escaping, and quadrupedal locomotion when moving at a slow speed or over short distances (Vásquez 1994b). *Graomys griseoflavus* and *Akodon molinae* appear to use a quadrupedal gait although information about these rodents is only anecdotal. Straccia & De Santis (2000) compared the morphology of the limbs of *Dipodomys* (a strictly bipedal hopper) and *Eligmodontia typus* to establish a relationship between modes of locomotion used by small mammals and their adaptation to desert life. These authors provided evidence that *Eligmodontia* has good leaping abilities, although it is not as specialized a saltator as *Dipodomys*. *Eligmodontia*, with longer hind legs in proportion to its body size compared with other Monte rodents, should possess some degree of bipedality (M. Mares, pers. comm.). The aim of this study was to identify the type of locomotion employed in response to increased predation risk by three rodent species that coexist in the Monte desert – *E. typus*, *A. molinae* and *G. griseoflavus*. As *E. typus* occurs mostly in open habitats (Ojeda 1989) and is presumably bipedal (Straccia & De Santis 2000; M. Mares, pers. comm.), we expected it to escape using a bounding gait rather than a quadrupedal gait. *Graomys griseoflavus*, which inhabits a large diversity of

habitats, should exhibit different modes of locomotion when fleeing, depending on the complexity of the plant community in which it is found. However, we expected *A. molinae* to use a quadrupedal gait more frequently because its activity seems to be restricted to sheltered microhabitats (Corbalán in preparation).

Methods

The study was carried out in the reserve of Ñacuñán in the province of Mendoza, Argentina (34°0.2'S; 67°58'W). This reserve is located in the central area of the Monte desert (Cabrera & Willink 1980). The climate is semiarid, with large annual and daily thermal amplitudes (Ojeda et al. 1998). The reserve comprises a diverse mosaic of habitats and plant communities (Roig 1971). The study was conducted in the three most representative plant communities: 'Algarrobal' (Mesquite forest), 'Jarillal' (Creosote bush community) and 'Medanal' (sand dunes). The Algarrobal is the most complex community with three strata: an arboreal stratum, a shrub stratum and a grass stratum. In the Jarillal community, a shrub and a grass strata dominate, while the Medanal community is characterized by sandy soils with vegetation islands separated by open areas, with a rich herbaceous and shrub strata (Roig 1971).

We studied three species of murid rodents that inhabit the Monte desert (Argentina) (Table 1), but which occupy different microhabitats (Redford & Eisenberg 1992). *Akodon molinae*, locally known as Ratón Pajizo, utilizes habitats with high coverage of shrubs, herbs and litter (Corbalán & Ojeda 2001). *Eligmodontia typus*, locally known as Laucha Colilarga Baya, is abundant in the sand dunes where plant cover is scarce (Giannoni et al. 2001; Corbalán, in preparation). *Graomys griseoflavus*, locally known as Pericote Común, occupies highly diverse habitats, but it is more abundant in the Mesquite forest (Gonnet & Ojeda 1998; Corbalán & Ojeda 2000).

Potential predators of these species include some snakes (Fam. Colubridae and Viperidae), birds (Order Falconiformes, Fam. Accipitridae and Falconidae; Order Strigiformes, Fam. Tytonidae and Strigidae) and carnivorous mammals (Fam. Canidae, Mustelidae and Felidae).

The study was carried out in April–May 2001. In each community, two grids were established in a seven-by-seven configuration, with 15-m intervals between sampling stations. Sherman live traps were placed at each station, totalling 49 traps per grid. Traps were baited with oats during five consecutive nights. We determined species, sex and body weight for each rodent. After we recorded these data, the individuals were released to observe the type of locomotion used in an escape context (Vásquez 1994b). Only first captures of each individual were used in statistical analyses.

We recorded the following measures upon the release of an experimental subject: (1) number of leaps before reaching plant cover, and their length and height (cm); (2) any changes in direction (swift changes at an angle of 90° or in a zigzag pattern); and (3) the trajectory taken during escape (either towards shrubs or open sites). For analysing differences in escape mode between the sexes and

Table 1: Physical measurements (mean and SE) of *Graomys griseoflavus*, *Eligmodontia typus* and *Akodon molinae* and indices of bipedal morphology

Species	<i>G. griseoflavus</i>	<i>E. typus</i>	<i>A. molinae</i>
Body mass (BM) (g)	56.41 ± 0.9	18.1 ± 0.21	38.52 ± 0.69
Total length (TL) (mm)	256.5 ± 0.77	178.8 ± 0.27	182.7 ± 0.22
Tail length (t) (mm)	137 ± 0.07	87.5 ± 0.01	75 ± 0.49
Hind foot length (HF) (mm)	29.7 ± 0.09	22.3 ± 0.09	22.3 ± 0.03
Front foot length (FF) (mm)	9.3 ± 0.03	7 ± 0.01	10.7 ± 0.03
Index of bipedal morphology			
HF/FF	3.19	3.19	2.08
TL/t	1.87	2.04	2.44
HF/BM	0.05	0.12	0.06

among species, G-tests were used. When pair-wise comparisons between species were made, the Bonferroni correction was used to reduce the probability of type I errors (Byrkit 1987). The same procedure was used for assessing whether individuals occurring in different plant communities changed their escape mode significantly.

Locomotion Patterns

Eisenberg (1963) described three types of locomotion employed by heteromids: (1) in bipedal locomotion (e.g. *D. deserti*), the hind legs either move alternately (alternate walk) or strike the ground simultaneously (bipedal saltation); (2) in quadrupedal saltation (e.g. *D. ordii*), the forelimbs alternate with the hind legs in striking the ground simultaneously; and (3) in diagonal limb coordination (e.g. *Liomys pictus*), the contralateral limbs are in synchrony so that when the left hind and right front limbs are extended, the contralateral pair is flexed. Later studies viewed bipedal locomotion as a hopping movement, the body being propelled with the hind legs (Price 1978; Longland & Price 1991). In field observations, we categorized the locomotion pattern as 'run' or 'hop'. We viewed 'hop' as hopping mobilization, similar to the aforementioned description, but we were unable to determine, in the field, which limbs (hind or front) propelled the body of the rodent. Afterwards, in the laboratory, the limbs of individuals (three of each species) were painted with tempera to secure an imprint of the footprint pattern displayed by rodents while escaping. Fore legs and hind legs were painted with different colours to facilitate their identification. Each animal was then released into a box (300-cm long × 30-cm wide × 40-cm high), with a floor covering of black sandpaper to provide good traction, and permanent records of the limb movements were obtained.

Results

A total of 64 individuals of *G. griseoflavus* (37 from the Algarrobal, 20 from the Jarillal and seven from the Medanal), 62 *E. typus* (15 from the Algarrobal,

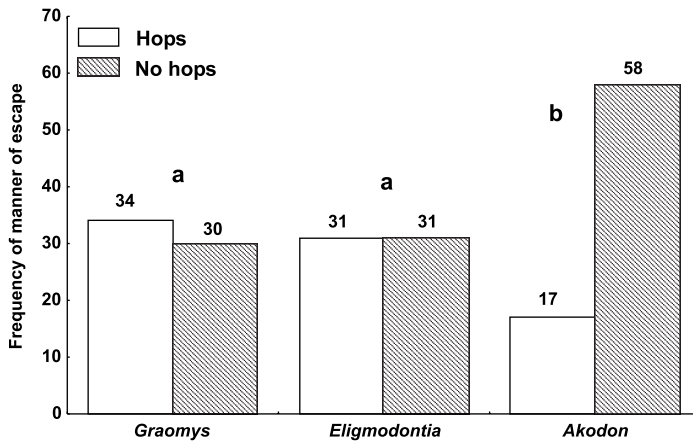


Fig. 1: Frequency of escapes with and without hops in rodent murid species. Different letters above bars represent significant differences between species

27 from the Jarillal, and 20 from the Medanal) and 75 *A. molinae* individuals (33 from the Algarrobal, 34 from the Jarillal and eight from the Medanal) were captured, and then released in the field.

There were no significant differences between the sexes in the mode of escape used in any of the species (*G. griseoflavus*: $G = 0.19$, $df = 1$, $p = 0.66$; *E. typus*: $G = 1.04$, $df = 1$, $p = 0.31$; and *A. molinae*: $G = 0.03$, $df = 1$, $p = 0.87$). There were, however, significant differences in the mode of escape among species ($G = 17.09$, $df = 2$, $p = 0.0002$). In particular, there were no differences between *G. griseoflavus* and *E. typus* ($G = 0.12$, $df = 1$, $p = 0.73$), but both species had a higher proportion of escapes involving hops than *A. molinae* ($G = 13.97$, $df = 1$, $p = 0.0002$; $G = 11.23$, $df = 1$, $p = 0.0008$, respectively; Fig. 1).

The number of hops exhibited by fleeing rodents differed across species ($G = 15.5$, $df = 2$, $p = 0.0004$). *G. griseoflavus* and *E. typus* showed a higher frequency of hops during escapes than *A. molinae* ($G = 15.4$, $df = 1$, $p < 0.0001$; $G = 7.08$, $df = 1$, $p = 0.008$, respectively).

Interspecific differences in jump length were also significant ($G = 16.80$, $df = 2$, $p = 0.0002$). *G. griseoflavus* had the highest frequency of escapes with at least one jump longer than 10 cm compared with *A. molinae* and *E. typus* ($G = 9.17$, $df = 1$, $p = 0.002$; $G = 13.80$, $df = 1$, $p = 0.0002$, respectively). However, there were no significant differences among species in jump height in escape situations ($G = 0.40$, $df = 2$, $p = 0.82$).

Individuals of *E. typus* from different plant communities differed significantly in their mode of escape ($G = 11.05$, $df = 2$, $p = 0.004$; Fig. 2). In the Medanal, individuals fled using a significantly higher frequency of hops than in the Algarrobal ($G = 10.98$, $df = 1$, $p = 0.0009$), moving especially to open sites (Table 2). The mode of escape used by individuals of *G. griseoflavus* and

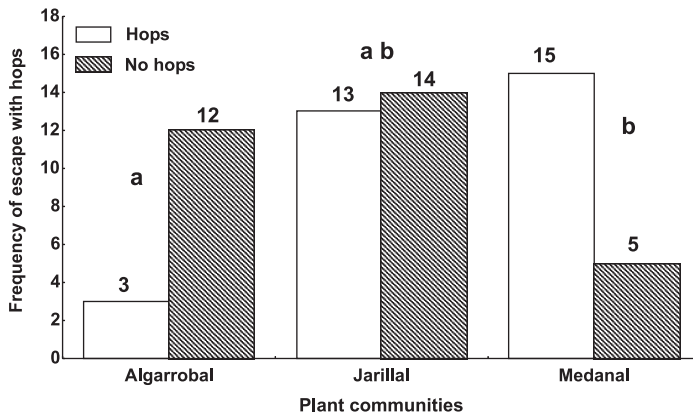


Fig. 2: Frequency of escapes by hops in *Eligmodontia typus*, in different plant communities. Different letters above bars represent significant differences between communities

A. molinae showed no significant differences among plant communities ($G = 1.10$, $df = 1$, $p = 0.57$; $G = 0.85$, $df = 1$, $p = 0.65$, respectively).

Eligmodontia typus used erratic escapes (zigzagging) on two occasions (Table 2). One was in the Medanal across an open site where the individual finally fled to a cave 6 m from the trap. The other was recorded in the Jarillal where the individual zigzagged across the grass and then ran toward shrubs that provided more protection. In 8% of the total escapes, *G. griseoflavus* changed direction by an angle of at least 90° . *Akodon molinae* never showed changes in direction upon release and often chose a trajectory towards sheltered sites under plant cover (Table 2).

Most of the individuals looked for shelter when released. They sought refuge under grasses, herbs (e.g. *Hyalis argentea*), subshrubs (e.g. *Acantholippia seriphioides*) and shrubs (e.g. *Lycium* spp., *Condalia microphyla*, *Capparis atamisquea* and *Larrea divaricata*).

Based on the footprint pattern recorded in the laboratory, we determined that *A. molinae* exhibits diagonal limb coordination (Fig. 3A), whereas *E. typus* (Fig. 3B) and *G. griseoflavus* (Fig. 3C) exhibit quadrupedal saltation.

Discussion

In desert areas, predation risk is one of the most important costs modulating the activities of rodents, patterns of habitat selection, species coexistence and community structure (Kotler 1984, 1985; Brown 1988; Longland & Price 1991; Hughes & Ward 1993; Brown et al. 1994; Kotler et al. 1994; Vásquez 1994a). Predation risk per unit time is higher in open places than near or under shrubs (Djawdan & Garland 1988; Hughes & Ward 1993). The three rodent species of the Monte desert varied in their mode of escape. *Akodon molinae* employed a quadrupedal gait also observed in other murid species such as *Reithrodontomys*

Table 2: Characteristics of escape modes used by *Graomys griseoflavus*, *Eligmodontia typus* and *Akodon molinae*

Species	<i>G. griseoflavus</i>	<i>E. typus</i>	<i>A. molinae</i>
Number of escapes			
Without jumps	30	31	58
With 1 jump	14	19	16
With > 1 jump	20	12	1
Number of jumps			
Length ≤10 cm	11	24	13
Length > 10 cm	23	7	4
Jump height (cm) ≥10	3	2	2
Direction			
Zigzag	0	2	0
90° changes	5	1	0
Number of escapes			
Across open sites	9	13	2

megalotis and *Gerbillus gerbillus*. Rodent species that use this locomotory pattern must restrict their activities to areas adjoining vegetation where predation risk is lower (Schröpter & Klenner-Fringer 1991). *Graomys griseoflavus* and *E. typus* used jumps in escape situations, and a quadrupedal run in short distances or under plant cover, similar to *O. longicaudatus* of the Chilean matorral (Vásquez 1994b).

Laboratory observations of *G. griseoflavus* and *E. typus* showed that all jumps were quadrupedal, so that these species would be categorized as 'quadrupedal saltators' (Eisenberg 1963). In quadrupedal saltation, the fore legs alternate with the hind legs in striking the ground, and the body of the rodent is propelled with the hind legs (Eisenberg 1963); therefore, the hind limbs are more developed than the fore legs (Price 1978). Morphological features such as tail length, hind foot length, the presence and length of the tuft at the end of the tail as well as the indices TL/t, HF/FF and HF/BM (see Table 1) are all related to the mode of locomotion employed (Rogovin et al. 1992; Kotler et al. 1994). The ability of these species to hop appears to be related to the greater development of their hind foot length relative to their body mass and front foot length. *Graomys griseoflavus* had the highest frequency of escape with at least one jump longer than 10 cm. This ability could be related to their greater body mass compared with the other species.

Both morphology and behaviour interact to influence the evolution of anti-predator strategies. For instance, a bicoloured tail has a distracting effect on predators, and the particular movement of the tail during a fast run promotes a frequent flipping of the tuft in the vertical plane, which may momentarily deflect a predator's attention (Rogovin et al. 1992). Another strategy, saltation, which allows for higher speed and changes of direction during an escape, may also be an effective tactic for avoiding or distracting predators (Djawdan & Garland 1988;

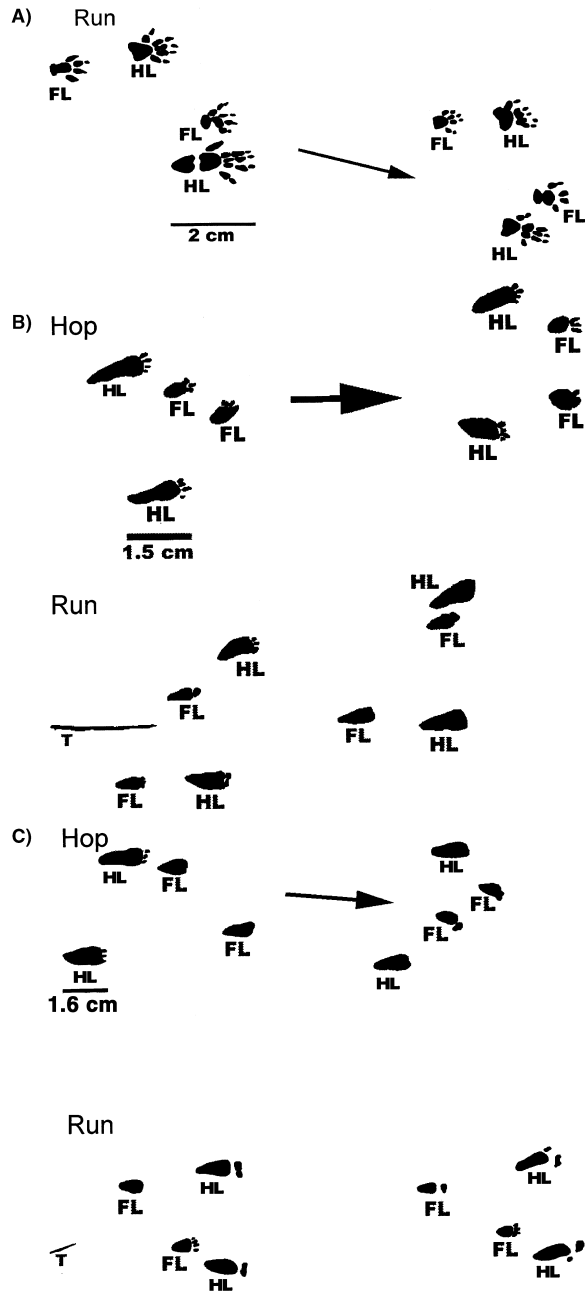


Fig. 3: Footprint pattern displayed by rodents during escapes. A: *Akodon molinae*, B: *Eligmodontia typus*, C: *Graomys griseoflavus*. References: T: tail, FL: forelimbs, and HL: hindlimbs

Vásquez 1996). *Graomys griseoflavus* has a strikingly bicoloured long tail and a tuft at the end. This species displayed abrupt and quick changes of direction when escaping. *Eligmodontia typus* used an erratic escape behaviour (zigzagging). These features would allow individuals of these species to efficiently avoid predator attacks, as has been found in the kangaroo rat, *D. merriami* (Harris 1984; Price et al. 1984; Djawdan & Garland 1988).

Individuals of *E. typus* that occur in the Medanal, a community characterized by vegetation islands separated by open areas, exhibited a higher number of jumps than individuals from the Algarrobal. Apparently, individuals inhabiting sites with high plant cover, such as the Algarrobal, are less reliant on jumping when running away because of a low risk of predation. However, *E. typus* has hairy cushions on the soles of its feet (Redford & Eisenberg 1992) to achieve greater speed and escape on sand substrata (Kotler et al. 1994). In these types of habitats, *E. typus* behaves differently, but we do not know if this is due to genetic or environmental differences because this species exhibits considerable geographical variation in karyotype (Redford & Eisenberg 1992).

Ojeda (1989) found that after a fire in the Jarillal community in the Reserve of Ñacuñán, *E. typus* became the dominant species when plant cover decreased dramatically, *G. griseoflavus* became the second most abundant species, and *A. molinae* became the least abundant. The results of our study provide additional evidence that there is a relationship between locomotion patterns and the exploitation of plant communities of varying complexity, which, in desert areas, is strongly related to predation risk.

Acknowledgements

This research was partly funded by CONICET Grant PIP no. 4684 and PICT no. 03281. The authors wish to thank Nelly Horak for assistance in the English version. We greatly appreciate the helpful comments made by Carlos Borghi, Paola Sassi, Scott Sakaluk, Burt Kotler and an anonymous reviewer. We also acknowledge Benjamín Bender's help in describing the footprint pattern displayed by rodents while escaping.

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Received: August 1, 2002

Initial acceptance: November 8, 2002

Final acceptance: February 8, 2003 (S.K. Sakaluk)