The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent

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We studied effects of habitat structure on routine travel velocities, intermittent locomotion, and vigilance by the degu (*Octodon degus*), a diurnal rodent of central Chile. We predicted that travel speed, pauses during locomotion, and vigilance would be greater in open (riskier) than in shrub (safer) habitats. Video recordings of marked individuals in the wild were used to measure speed and other variables of spontaneous locomotion not triggered by predatory attack or any other noticeable stimulus during nonforaging periods. Time spent vigilant while foraging was also measured. Because degus use bare-ground runways for distant movements (e.g., between burrow openings and/or food patches), data on locomotion decisions were not confounded by effects of obstructive vegetation cover and/or resource abundance. When moving across the habitat between different feeding places, degus showed an intermittent pattern of locomotion, interrupting running events with short pauses. As predicted, travel speed and the duration of pauses between locomotion bursts were significantly greater in open habitats. Further, the duration of locomotion bursts between feeding sites or between feeding sites and burrows was significantly longer in open habitats. Our assumption that pauses and velocities are independent decisions was supported by the lack of correlation between pauses and speeds during locomotion events. During foraging, degus devoted more time to vigilance in open than in shrub habitats. The static position adopted by degus during pauses, the speeds attained during movements, and the concordance between pausing behavior and vigilance across habitats suggest that pausing has an antipredatory role and is not limited to orientation and/or physiological recovery. Our results support the view that degus perceive higher predation risk in open areas and that flexible movement behavior reflects an adaptive antipredator response. *Key words:* antipredator behavior, degus, *Octodon degus,* pausing behavior, predation risk, travel speed, vigilance. *[Behav Ecol 13:182–187 (2002)]*

Decisions about locomotion are integral to many fitness-related activities, such as foraging and predator avoidance (Djawdan and Garland, 1988; Garland et al., 1988; Houston, 1992; Swingland and Greenwood, 1983). For example, running speed has been widely described as a key attribute of escape behavior (Blumstein, 1992; Ydenberg and Dill, 1986). Smith (1995) showed that golden-mantled ground squirrels (*Spermophilus lateralis*) run faster than coexisting least chipmunks (*Tamias minimus*), which seems to allow the former species to use more exposed areas with lower predation hazard. Movement rates, distances, and changes in velocity may also influence feeding success (Gendron and Staddon, 1983; O'Brien et al., 1990). For instance, prey capture is greatly influenced by pausing behavior (i.e., pauses between movement bursts) and movement distance in flycatchers and owls (Davies, 1977; Sonerud, 1992).

The structural complexity of the habitat may affect movement behavior through (1) physically impeding locomotion (e.g., Brownsmith, 1977; Crist and Wiens, 1994; Schooley et al., 1996), (2) making movement more conspicuous and thus riskier (e.g., Brillhart and Kaufman, 1991), (3) providing a higher density of resources, hence favoring slower speeds so that resource opportunities are not missed (see Brownsmith,

1977), (4) increasing protection against predators through hiding cover (e.g., Thompson, 1982), and/or (5) increasing visual obstruction, thus reducing the ability to detect predators (Metcalfe, 1984; Schooley et al., 1996). The relationship between predation risk and habitat structure has stood out in the literature (e.g., see Lima, 1998; Lima and Dill, 1990; Ylönen and Magnhagen, 1992, for reviews). A common finding for nocturnal desert rodents is that vegetated shrub microhabitats provide safer conditions against raptors (e.g., Brown, 1988; Brown et al., 1988; Kotler, 1984; Kotler et al., 1991; Longland and Price, 1991). Despite the vast literature showing diverse effects of habitat structure over prey behavior such as foraging, refuge and space use, grouping, and vigilance (e.g., Brown, 1988; Elgar, 1989; Kotler and Blaustein, 1995; Korpimäki et al., 1996; Longland and Price, 1991), few investigations have addressed the influence of habitat structure on locomotion and running velocities. An exception is the study of Schooley et al. (1996), in which Townsend's ground squirrels (*Spermophilus townsendii*) exhibited slower escape speeds in shrub habitats than in open areas. According to these authors and contrary to the common finding that vegetation provides safer conditions, shrub vegetation obstructs movement and visual detection of predators, and hence squirrels seem to experience higher predation risk in shrub habitats. A drawback of the majority of studies that have measured running speed (e.g., Blumstein, 1992; Djawdan and Garland, 1988; Garland et al., 1988) is the measurement of velocities under laboratory or seminatural conditions, including artificial tracks, release of captive animals, and artificial stimuli to elicit running (e.g., humans, raptor models, trained animals). Moreover, there is a lack of studies measuring spontaneous or routine travel speeds under natural conditions.

Many animals do not move continuously through their habitat but show an overall pattern of intermittent locomotion, with pauses breaking up movement bursts (see Pennisi, 2000, for a recent discussion). Pauses may allow animals to increase detection both of predators and prey (Gendron and Staddon, 1983; McAdam and Kramer, 1998; O'Brien et al., 1990). If pausing occurs between bursts of rapid locomotion among feeding sites, it may improve predator detection (e.g., McAdam and Kramer, 1998); if it occurs between events of slow locomotion within feeding sites (i.e., while foraging), it may improve prey detection and capture (e.g., Anderson et al., 1997; Gendron and Staddon, 1983; O'Brien, 1990), as well as predator detection and avoidance (Lima and Dill, 1990). Pauses might also make prey more cryptic and reduce capture ability if predators are more likely to detect or attack moving prey (Curio, 1976; Martell and Dill, 1995). Pauses also may provide orientation cues for navigation throughout the habitat (Dyer, 1998). From a physiological point of view, pausing may serve as a resting period (Weinstein and Full, 1992). However, even if pausing functions to gain navigation cues and/or physiological recovery, it may also contribute to information processing and enhanced predator detection (Dukas, 1998). Also, during foraging activities not involving locomotion, animals normally interrupt feeding with vigilance events. Higher levels of vigilance are associated with higher perceived predation risk (Elgar, 1989). Although a faster speed may increase safety, it might also imply a higher cost, for instance, associated with greater energy expenditure (Taylor et al., 1982). Further, longer pauses favoring predator detection might also increase other costs such as increased total travel time (i.e., time exposed to predators), thus decreasing time that could be spent at feeding sites or refuges.

The purpose of this study was to assess the influence of habitat structure on routine travel speed, pausing behavior, and vigilance in the caviomorph rodent *Octodon degus* (Rodentia: Octodontidae; common name: degu). *Octodon degus* is a semifossorial, herbivorous rodent that inhabits xeric habitats of central Chile. Most daytime activities take place above ground (Fulk, 1976; Vásquez, 1997). Degus use shrub and open habitats when above ground, and previous studies suggest that shrub habitats provide lower predation risk than open areas (Lagos et al., 1995, Vásquez RA, unpublished data). Degus are social rodents that live in underground galleries, connected above ground by a system of runways (Fulk, 1976; Vásquez, 1997; Yáñez and Jaksic, 1978). These runways are highly conspicuous because frequent use by degus leads to bare ground along the runways (Fulk, 1976; Vásquez, 1997; Yáñez & Jaksic, 1978). Normally, these runways connect burrow entrances of different galleries in a straight line. Degus usually use the runways to move between distant locations within their home range, and they leave the runways only to forage (or sometimes to engage in social activities), particularly away from burrow openings (Vásquez, 1997; Vásquez RA and Bozinovic F, personal observations). Close to burrow entrances, degu activity often produces an area of completely bare ground where animals normally do not forage but engage in behaviors such as agonistic interactions, play behavior, reciprocal grooming, dust bathing, prolonged vigilance, resting, and burrow maintenance (Fulk, 1976; Vásquez, 1997; Yáñez & Jaksic, 1978; Ebensperger LA, unpublished data). The degu is an interesting animal model for testing hypotheses related to locomotion because its almost exclusive use of runways for distant movements and its exploitation of localized food patches allow the investigator to exclude the influence of physical obstruction and differential resource density on movement behavior.

If predation risk increases significantly in open areas, we predicted that degus should run faster when using open habitats, particularly if vegetation and food sources do not interfere with movement behavior, in spite of greater energetic costs of faster speed. We also predicted that degus should break locomotion bursts with longer pauses in open (riskier) habitats, particularly if pausing decreases overall predation risk, albeit accepting the cost of more time away from a feeding site or refuge. Our approach assumes that travel speed and the duration of (preceding and subsequent) pauses are independent decisions. This assumption was explicitly analyzed. To further support the view that habitat structure affects perceived predation risk, we measured individual vigilance of foraging degus in open and shrub habitats. During foraging activities, we expected degus to be more vigilant in open habitats. To our knowledge, this is the first study reporting habitat effects on routine travel speed under natural conditions.

METHODS

We studied a natural population of degus inhabiting a site in the oriental slopes of the coastal range (70°53′ W, 33°28′ S, 450 m above sea level) at the field station of the University of Chile, 30 km west of Santiago, central Chile. The area has Mediterranean climate characterized by warm, dry summers and wet winters and is located within the biogeographical zone known as matorral (Rundel, 1981). The studied population inhabited an area where two conspicuous habitats were distinguished: an open habitat comprising almost exclusively bare ground and dried small herbs with 2% of plant cover, and a shrub habitat comprising small shrubs (*Senecio* sp.) and herbs (*Erodium* sp., *Hordeum* sp.). In the shrub habitat, plant cover was 31%, and most vegetation had a height range of 10–50 cm. Degu predators such as culpeo foxes (*Pseudalopex culpaeus*) and black-chested buzzard eagles (*Geranoaetus melanoleucus*) were observed regularly in the area (see Vásquez, 1997).

Degus were recorded in a site of approximately 2 ha containing similar areas of both habitats. Because speed can be influenced by the arrangement of runways and burrow openings, we took special care to choose open and shrub habitats where runways and burrows had similar characteristics and densities, runways with few or no turns, similar lengths of straight lines, and even distributions of burrow openings. This was one of the reasons that we chose a shrub habitat with low and sparse vegetation (see Lagos et al., 1995, for degu populations dwelling in more densely vegetated habitats); the other reason was visibility of the degus being observed. We selected areas with similar sizes of each habitat to reduce any possible effect of total distance, total length of runways, and/or overall abundance of food patches. Observations were eased by the fact that most diurnal activities of degus, particularly foraging, take place above ground. From midsummer through early winter, most herbs are dried, and foraging is carried out almost exclusively in specific, well-delimited feeding sites with high densities of dried herbs and/or remaining green vegetation (Vásquez RA, unpublished data). During summer, degus show a bimodal period of above-ground activity with an interruption at midday when temperatures are highest (Kenagy et al., in press).

During a given period of activity, degus normally run between different feeding sites in bouts (bursts) of locomotion that include short pauses (i.e., intermittent locomotion). These running events are not triggered by predatory attacks or by any other noticeable stimuli. Overall, running episodes account for distances of up to 50 m in short periods of time (commonly ≤ 20 s), and often degus go across both habitats. To avoid the effect of neighboring habitat edges (see McAdam and Kramer, 1998), we recorded degus at 10 m or more from the closest habitat border.

Two weeks before recording locomotion behavior, we live-trapped 14 adult degus (mean ± SE weight: 172.3 ± 5.2 g; sex ratio male:female = 6:8) and marked them individually with distinct patterns using black hair-dye. Degus were immediately released after marking. Marking appeared not have any perceptible effect on the behavior of subjects. We video recorded marked subjects in the runways. We used two video cameras (Sony CCD-TR413). Video recordings were made from four different sites, all naturally hidden places located underneath shrubs in the margins of the study area, where degu activity was low or nil. Distance between recorded subjects and observer ranged from 15 to 40 m, and we stopped recording when we noticed that subjects were affected by observers or conspecifics, when animals got off the runways, or when a predator was present in the area. In this way, we only recorded routine travel on runways rather than responses to threatening stimuli. Recordings were made between 0700 h and 1100 h on target animals observed during a continuous time period of 5–40 min. Data collection began 30 min after arrival at the hide. After each recording day and in the study site, one of us watched the video recordings from the corresponding observation points, carefully distinguishing natural marks such as rocks and plants. In this way we identified accurately the runways used by subjects and later measured the distances traveled in each movement event to the nearest centimeter. The duration of running and pausing events was measured from the video recordings using stopwatches. The locomotion part of the study was carried out during the Southern Hemisphere summer between December 1998 and February 1999.

During different periods of observations, when animals were foraging and no locomotion occurred, we measured the time that individual degus devoted to vigilance. Degus were considered to be alert when motionless with the head raised or when standing erect on their hind feet (Vásquez, 1997). Observations began upon sighting an adult-sized degu. Then one of us voice tape-recorded the subject's activity. We stopped recording when the focal degu moved to a different habitat, when group size changed, or when the focal animal went out of sight. Animals were considered to be in the same group when interindividual distances were ≤ 2 m. Total observation time for each focal degu varied between 1.4 and 35.7 min (mean ± SE, 15.1 ± 1.1 min). We repeated these observations during periodic 1–2 day sessions once during midsummer (1999), midfall, and early winter. Both marked and unmarked degus were used as focal subjects. We observed unmarked degus at different locations within our study site to minimize pseudoreplication. Group size affects vigilance of degus (Vásquez, 1997), so we controlled this effect statistically (see below).

We averaged data for each individual for analyses. Data were transformed when appropriate to meet the assumptions of each analysis (Sokal and Rohlf, 1995). We carried out paired t tests to compare locomotion variables between habitats. To examine the influence of habitat type on time allocated to vigilance, we used ANOVA with group size and season as covariates.

RESULTS

Travel speeds and pauses

Degus traveled between feeding places in an intermittent pattern of locomotion and generally crossed shrub and open habitats during long trips. Of 14 marked individuals, we obtained records of 8 subjects (5 males, 3 females); 7 subjects were recorded in both habitats. We did not detect any perceptible difference in locomotion behavior between the sexes,
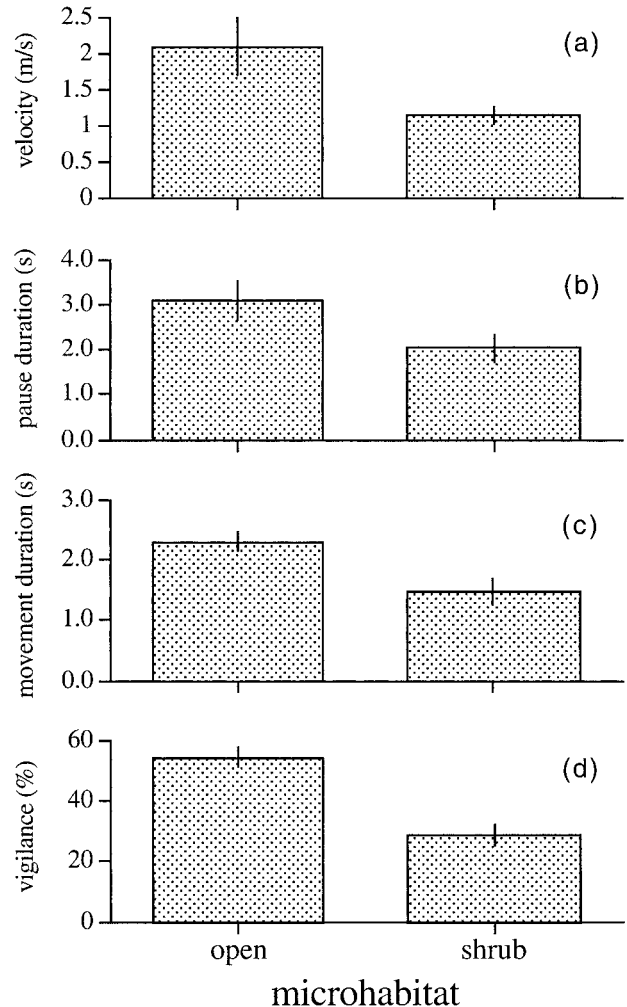

Figure 1
Results (means ± SE) on locomotion variables and vigilance of *O. degus* in open and shrub habitats. (a) Travel velocity during locomotion bursts; (b) pause duration between locomotion bursts; (c) duration of locomotion bursts ($n = 7$ for both habitats in panels a–c); (d) percentage of time devoted to vigilance by *O. degus* in open ($n = 48$) and shrub ($n = 16$) habitats.

and hence we pooled male and female subjects for analyses. Spontaneous travel speed was 1.82 times faster in the open than in the shrub habitat (paired t test: $t_6 = -4.52$, $p = .004$; Figure 1a). The ranges of observed speeds were 0.91–3.40 m/s in the open habitat and 0.83–1.59 m/s in the shrub habitat. The fastest speed recorded for an unmarked individual was 3.8 m/s in the open habitat. When running, degus adopted at least two different gaits: trotting for slow speeds, and bounding for faster speeds.

During trips between feeding sites or between feeding sites and burrows, degus normally interrupted their movement with short pauses. Pausing accounted for 44% of the total time spent traveling (i.e., pause plus movement). During these brief intervals, degus had their feet on the ground, often in a crouching posture, with the head raised in an alert position. This posture most likely allowed visual scanning of the surroundings and hence visual detection of dangerous events.

The mean duration of pauses was 1.51 times longer in the open than in the shrub habitat ($t_6 = 2.48$, $p = .048$; Figure 1b). Pauses showed a minimum and a maximum duration of 1.07 s and 4.10 s in the open habitat, and 0.50 s and 3.01 s in the shrub habitat, respectively.

The duration of locomotion bursts within a trip between feeding sites or between a feeding site and a burrow was also influenced by habitat. Locomotion bursts were 1.56 times longer in the open than in the shrub habitat ($t_6 = 3.52$, $p = .013$; Figure 1c). Locomotion bouts had a minimum and a maximum duration of 1.67 s and 2.71 s in the open habitat and 0.66 s and 2.48 s in the shrub habitat, respectively. Because degus moved faster and for longer time during locomotion bursts in the open habitat, the distance they traveled during each locomotion burst was 2.8 times greater in the open habitat ($t_6 = -7.84$, $p = .0002$). Mean burst distances ($\pm$ SE) were 4.8 ± 1.1 m and 1.7 ± 0.3 m in the open and shrub habitats, respectively. We found no correlation between speed during a movement burst and the duration of the preceding (Spearman correlation, $r_s = .22$, $p > .3$, $n = 8$) and subsequent ($r_s = -.40$, $p > .1$, $n = 8$) pause. Therefore, the analysis of pauses and movement bursts as independent decisions seems justified.

Vigilance during foraging

Because vigilance increased during winter as compared with summer and autumn ($t_{60} = 3.05$, $p = .003$) and it decreased with group size ($t_{60} = 2.7$, $p = .009$), we entered these factors as covariates. After doing so, we found that degus in open habitats were more vigilant than degus in shrub habitats (ANOVA, $F_{1,60} = 23.4$, $p < .00001$; Figure 1d). The majority of degu above-ground activities are allocated to foraging not involving long travel distances (Kenagy et al., in press).

DISCUSSION

As we expected, degus adjusted their locomotion behavior according to the type of habitat used. Degus ran faster and paused longer in the open habitat. Running faster in open habitats decreases the time animals spend moving in areas of high visibility, which may reduce predation risk, particularly if predators are more likely to detect and/or attack moving prey (Curio, 1976; Martell and Dill, 1995). We noted that it was far more difficult to detect a motionless degu than a moving one, and often we could only detect animals when they were moving. Open habitats between shrubs have been reported to present higher predation risk to rodents (Bowers et al., 1993; Brown, 1988; Kotler, 1984; but see Schooley et al., 1996). In experimental, large-scale exclusions, Lagos et al. (1995) found that degus use shrub and open microhabitats in similar proportions when predators were excluded, but they select shrub microhabitats when predators were present. Further, above-ground runways between shrubs were more linear in grids with predator access, suggesting that linear runways, by being shorter than more curvy runways, reduce exposure to predators (Lagos et al., 1995).

Longer pausing may increase the efficacy of antipredatory vigilance. Although longer pauses might increase total travel time, thus increasing exposure in riskier habitats, animals seem to overcome this cost with enhanced predator detection. Recently, McAdam and Kramer (1998) reported that squirrels and chipmunks pause frequently during locomotion and that these interruptions improve antipredator vigilance. They found that animals increased their pauses of vigilance when moving toward a condition of higher predation risk. During pauses, degus often adopted a crouching posture with the head raised in alert attitude. This position may allow degus to visually scan the surroundings, increasing their visual detection of dangerous events and hence decreasing their reaction time to flee from potential predators, as occurs in other social rodents (Blumstein, 1998). The static position adopted during pauses may also improve hearing performance in comparison

to running behavior, during which audition may be interfered by the noise generated by the movement of the animal. Our results on vigilance were also concordant with data on pauses. Degus devoted a greater fraction of their above-ground activity time to vigilance when in open areas, which parallels the vigilance behavior of other rodent species (Cassini, 1991; Leger et al., 1983). These results agree with our predictions and hence support the view that degus perceive higher predation risk in open areas. Of course, habitats may differ in several aspects beyond predation risk (e.g., food density and quality, obstructions, among others) that might affect locomotion, vigilance, and other behaviors (see Brown, 1988, Elgar, 1989). However, our study system excluded several of such factors, and consequently we suggest that flexibility in running velocity, pausing behavior, and vigilance among habitats reflect, to a large extent, adaptive antipredator responses. Although locomotion composes a small fraction of the daily time budget of degus (Kenagy et al., in press), it certainly can have a major impact on survival because it greatly affects predator escape ability (Swingland and Greenwood, 1983).

Shrub habitats may have two opposing effects on the predation risk experienced by a given prey animal. On the one hand, more complex vegetative structure might provide safer conditions against predators (e.g., Armitage, 1982) by increasing hiding cover or obstructing predator movement. On the other hand, visual and/or physical obstruction might also diminish the effectiveness of antipredator vigilance and/or escape (e.g., Schooley et al., 1995). For instance, Schooley et al. (1995) argued that Townsend's ground squirrels experience higher predation risk in shrub habitats because vegetation obstructs locomotion, making squirrels run slower during fleeing responses. Those findings are opposite to the most frequently reported effect of shrub habitats, particularly in arid environments where predation risk tends to be higher in open areas (e.g., Brown et al., 1988, Kotler et al., 1991). Because degus made intensive use of their runways, they should not have experienced increased physical obstruction in shrub habitats compared to open areas. In fact, we had observed that, upon a predatory attack, foraging degus flee toward the nearest runways and then run to the nearest burrow (see Vásquez, 1997). Observations revealed that degus consider runways a more familiar area compared to open terrain, where obstructions such as rocks, twigs, and herbs make locomotion more difficult.

Although our findings support the view that predation has been a major selective factor on movement behavior, pausing behavior may also function to gain orientation cues or increase physiological endurance. If habitat structures are used for orientation, longer pauses would be expected in areas with fewer physical landmarks (i.e., open habitats) in order to gain navigation cues (see Dyer, 1998). However, the concordant results between pauses and vigilance make the predation risk hypothesis a more parsimonious explanation. In any case, pauses may well play both roles, since in general, pauses increase the capacity to obtain different kinds of information (Dukas, 1998). In contrast, if animals move at sufficiently high velocities, thus using anaerobic energy, brief pauses may improve overall performance (e.g., Weinstein and Full, 1992, see also Pennisi, 2000). However, running velocities recorded are probably well below the maximum running speed of degus. Kenagy et al. (in press) have recently observed that degus can run up to 5.7 m/s after being released; this speed is greater than the maximum velocity expected from allometric considerations (see below). Although our data include acceleration and deceleration times and hence underestimate the maximum speed attained during a running event, it appears that degus run at submaximal speeds in their normal movements, especially if not being attacked by a predator.

Using allometric mammalian models (Garland, 1983), we calculated that the maximum speed for a 180-g degu should be 4.9 m/s (see also Jones and Lindstedt, 1993). Therefore, our field data show that spontaneous locomotion velocity of degus is below their observed and theoretical maximum, and below the maximum aerobic speed (2.4 m/s; following Garland, 1983). Consequently, intermittent running should not play an important role in endurance capacity of degus (see McAdam and Kramer, 1998, for a similar conclusion for squirrels). This assertion is further supported by empirical evidence showing that physiological recovery (accomplished through resting pauses) after bursts of maximal activity requires longer time than the activity itself (see Bennett and Ruben, 1979). However, recent findings provide new evidence for increased physiological performance due to intermittent locomotion (see Pennisi, 2000). This area certainly deserves further research.

The lack of correlation between pause duration and speed during running bursts supports our assumption that pauses and locomotion velocities can be considered as independent decisions. Pause patterns during movement episodes seem convergent with the data on vigilance during foraging activities; both increase with higher risk exposure, everything else being equal. If pauses increase with predation risk, one would expect more pauses when approaching a riskier area. We designed our study to reduce variability from this effect (see Methods). In their study on gray squirrels (*Sciurus carolinensis*) and eastern chipmunks (*Tamias striatus*), McAdam and Kramer (1998) found that both species increase their pauses when approaching situations of higher risk.

Flexibility in travel speeds supports the hypothesis that degus perceive greater predation risk in open habitats. Other rodent species also show flexibility in running speeds, although previous studies have assessed escape velocities, whereas we report spontaneous travel velocities not triggered by a noticeable stimulus. Escape speed might also vary with habitat and refuge location, suggesting that rodents exceptionally run at their maximum speed. For example, escape velocity in woodchucks (*Marmota monax*) increases with greater distances to burrow openings (Bonenfant and Kramer, 1996). In any case, submaximal travel speeds during spontaneous movements when animals are not being preyed upon may allow increments in escape velocity when attacks occur (Bonenfant and Kramer, 1996).

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