

# Different antipredator responses by *Microcavia australis* (Rodentia, Hystricognate, Caviidae) under predation risk

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## Summary

The antipredator response of rodents may depend on the species of predator and the structure of the vegetation. To investigate these effects, we compared the antipredator response of *Microcavia australis* to two predator models. We used two populations occurring at sites of the Monte desert that differ in plant structure and availability, and in predation risk. At Ñacuñán plant cover is 54.3%, the major risk of predation is from raptors. At El Leoncito plant cover is 21.9%, the predation risk is similar by raptors and carnivores. In addition we investigated whether olfactory cues for different predators may elicit different antipredator responses in absence of visual cues. This was done by presenting feces of two predators and controls in an experimental set-up. The exposed individuals reduced their activity in response to feces of both predators and not in response to the control, but they did not respond in the same way to each predator (their response to each predator was not the same). The results show that *M. australis* recognizes different predators through both sight and smell, and that the response may be influenced by vegetation structure.

*Keywords:* antipredator responses, plant structure, predation risk, rodents, sight and smell.

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## Introduction

Antipredator behavioral responses typical of rodents are: avoidance of the stimulus, reduction of locomotor activity, adoption of a static posture, vigilance, flight, hiding from predators, predator confrontation and mobbing (Owings & Coss, 1977; Curio, 1978; Eilam et al., 1999; Dielenberg et al., 2001; Shahaf & Eilam, 2003). These responses are affected by biotic factors, like plant structure and predation risk (Lima, 1987; Ebensperger & Hurtado, 2005). Vegetation is a major factor affecting rodent distribution and abundance, because it is associated with resources such as food, nesting site, protection from predators and thermoregulation (Tognelli et al., 1995). Ebensperger & Hurtado (2005) describe a differential effect of shrubs and herbaceous plants on the vigilance behavior of *Octodon degus* linked to the costs and benefits of each type of plant cover. Shrubs provide higher vertical protection than herbaceous plants, which in turn provide lateral cover but visually obstruct detection of predators and conspecifics, hindering escape. Degus adjusted the quality rather than the quantity of their vigilance activity; male and female degus allocated similarly more time to bipedal vigilance when the height of herbs was high. Therefore, predation risk would be related to the structure of vegetation (Ebensperger & Hurtado, 2005).

The role of vision and smell in detecting predators are very important. Herbivorous prey have monocular view with a wide field of vision that allows them to see around their body, giving them the opportunity of fleeing and run for safety in front of a predator (Dellman, 1993). Another sense used by rodents to locate predators besides vision is smell, for example *Microtus ochrogaster* and *Rhombomys opimus* can distinguish the odors of different predators (Ylönen, 1994; Rogovin et al., 2004). Norrdahl & Korpimäki (2000) found that, in the laboratory, *Microtus ochrogaster* responded to the smell of mustelid or other carnivore feces by avoiding the sites and reducing mobility and size of the action area. The latter antipredator response would be the reduction in size of the action area, which would limit their foraging activity (Lima, 1987; Desy & Batzli, 1989; Ylönen, 1994; Kramer & Bonenfant, 1997; Eilam et al., 1999; Norrdahl & Korpimäki, 2000; Dielenberg et al., 2001; Ebensperger & Wallen, 2002; Pusenius & Ostfeld, 2002).

*Microcavia australis* is a diurnal, burrow-inhabiting herbivore rodent, with a group social structure exhibiting low levels of aggression (Rood, 1967; Cassini, 1989; Campos, 1997). This cavy develops its behavioral patterns in the burrow area, under the cover provided by trees and/or shrubs

where predation risk is lower, and does not use areas further away from the burrow or the plant cover (Rood, 1967; Tognelli et al., 1995). The antipredator behavior is not known in *M. australis* under depredation risk. Therefore, the objective of this study was to determine different antipredator responses (vigilance, flight, and reduction of locomotor activity) under different predation risk, focusing on two populations of the Monte desert at sites (El Leoncito and Ñacuñán) that differ in plant structure and availability, and predation risk. To analyze the role of visual cues we presented the cavies with models of a raptor and of a carnivorous mammalian predator. To analyze the role of olfactory cues we presented cavies with feces of fox (*Lycalopex* sp.) or puma (*Puma concolor*, terrestrial carnivorous mammalian predator) using feces of an herbivorous mammal (European hare, *Lepus europaeus*) as a control. We hypothesize that the type of predator (aerial and/or terrestrial) and the existing vegetation affect the antipredator response by *M. australis*. We expected that individuals from the more open site (El Leoncito) would respond earlier and at a greater distance due to earlier detection of terrestrial predators. We also predict that cavies use olfactory cues to detect the presence of predators and will avoid predation by reducing mobility in response to these cues.

## Material and methods

### *Field trial*

Field experiments were carried out in two sites in the Monte desert, in Argentina. These sites differ in its climatic conditions, plant structure, and predation risk. The Man and Biosphere Reserve of Ñacuñán (34°2'S, 67°58'W; at 540 m asl) is located in the central part of the Monte desert, in the province of Mendoza. The climate is semiarid (warm-dry) and mean rainfall is approximately 330 mm, concentrated in the summer months (Cabrera, 1976). The mesquite community is the habitat preferred by *M. australis*, because of its structural complexity and the food supply it provides (Campos, 1997), plant cover is 54.3% (Taraborelli, 2006). This community is composed of three plant layers: the tree layer, dominated by *Prosopis flexuosa*, the shrub layer, and the herbaceous layer (Roig, 1971). At Ñacuñán predators are raptors (*Buteo polyosoma*, *Milvago chimango*, 23 total records) with  $0.45 \pm 0.14$  raptors/cavy (mean  $\pm$  standard error); mammalian carnivores (*Lycalopex gymnocercus*, *Galictis cuja*, *Conepatus chinga*, *Felis catus*, 7 total records) with

$0.09 \pm 0.05$  carnivores/cavy; and snakes (*Bothrops ammodytoides*, 1 record) with 0.005 snakes/cavy (Taraborelli, 2006). Other species of rodents that are present to potentially spread the predation pressure include *Ctenomys eremophilus*, *Graomys griseoflavus*, *Eligmodontia typus*, *Akodon molinae*, *Calomys musculinus*, and marsupials such as *Thylamys pallidior* (Ojeda et al., 1998; Taraborelli et al., 2003; Corbalán, 2006).

Another Monte desert site is El Leoncito National Park ( $31^{\circ}47'S$ ,  $69^{\circ}17'W$ ; 2484 m asl), located in the province of San Juan, in the Department of Calingasta, 30 km from the locality of Barreal (Márquez, 1999). The climate is arid (cold-dry), mean rainfall is below 100 mm, total winter precipitation reaches 75 mm (April–August), and occurs in the form of snow or hail; summer precipitation is lower than 10 mm (November–March) and basically pluvial (Le Houérou, 1999). Two plant layers can be observed in the Monte Phytogeographic Province, the shrub layer, where *Larrea nitida* is the dominant species, and the herbaceous layer is lower than 10 cm. Plant cover is 21.9% and there exist vast open areas (Taraborelli, 2006). At El Leoncito predators are crepuscular and nocturnal mammalian carnivores (25 total records) with  $0.21 \pm 0.05$  carnivores/cavy; e.g., *Lycalopex* sp. (records of *Lycalopex culpaeus* are the highest) and *P. concolor*; raptors (*Geranoaetus melanoleucus*, *Buteo polysoma*, *Falco femoralis*, *Falco sparverius*, *Circus cinereus*) with 24 total records in morning and afternoon hours and  $0.20 \pm 0.09$  raptors/cavy; and snakes (*Phylodryas trilineatus*, 1 record) with 0.004 snakes/cavy (Taraborelli, 2006). Other rodent species present on this site to potentially spread the predation pressure are *Phyllotis xanthopygus*, *Eligmodontia typus*, *Ctenomys mendocinus*, *Ligidium viscacia* and marsupials such as *Thylamys elegans* (Haene, 1996).

The records of predators were taken from footprints, feces, aegagropiles and from direct observations in the study area, on both sites. Predators were recorded during 7–11 days at three times of the year (February–March, April–July and September–October) for each study site from 2003 through 2005. The ratios of predators to caviés were calculated for each time of the year, and then we estimated the mean and standard error for all data. The contents of collected feces were analyzed in the laboratory under magnifying glass; species were identified by their molar teeth using keys for identifying small mammals, guidebooks, skulls in the IADIZA-CRICYT Collection and photographs (Olrog & Lucero, 1981; Pearson, 1995). For example, small

cavies compose about 44% of the diet of *Lycalopex* sp. and 45% of the diet of *P. concolor* (Taraborelli, 2006).

Individuals were captured prior to the field experiment, using Havahart and Tomahawk traps. Individuals were identified with coded metal tags (0.6 cm long), staining the hair of different body parts with gentian violet, making diverse drawings on them, for example circles, squares, vertical or horizontal lines, letters, etc. From direct observations we determined the number of individuals that could not be captured and marked.

At both sites, the presence of a terrestrial carnivorous mammalian predator (*Lycalopex gymnocercus*, grey fox; 70 cm long in total) was simulated by using a black cardboard fake fox upon four wheels similar to the methodology employed by Hoogland (1981, 1995). Also an aerial raptor was simulated (*Buteo polyosoma*, red-backed hawk; 90 cm wing span and 45 cm long) using a black cardboard silhouette experiment as described by Tinbergen (1951) and Roux et al. (2001). These were moved between burrows, with a pulley, along a transparent rope, using a fishing line retrieved by an assistant with a fishing rod from the opposite side; the fox was moved on the ground surface and the raptor at 2 m height above the ground. We support the assumption that prey animals increase their defensive response when the simulated predator moves (Tinbergen, 1951; Shahaf & Eilam, 2003). It was assumed that *M. australis* responds to a fake predator much the same as it would to a live predator. The initial location of both fake predators was approximately 40 m from the cavies group or an individual in the burrow. Experiments were shifted among groups at random (13 groups at El Leoncito and 9 at Ñacuñán) in the morning and in the afternoon (with a minimum time lapse of 30 min between experiments). For example, the carnivorous mammalian predator was simulated in group 1 in the morning, and the raptor in the afternoon or the following day. Throughout these experiments we observed different individuals, and we used only the first observation of each individual. Experiments were conducted in the season when only juvenile and adult stages are present (February–March at Ñacuñán and March–April at El Leoncito), using the methodology described by Hoogland (1981). A grid of stakes and tapes (2 m intervals) was used to estimate escape distances of cavies. At Ñacuñán, 10 trials were carried out with the fake raptor and 10 with the fake fox; at El Leoncito, 20 with the fake raptor and 26 with the fake fox. Observations were made with binoculars (8 × 40, Hoken, Wald, China) from a 2-m high observation tower located 30–50 m from the burrow being

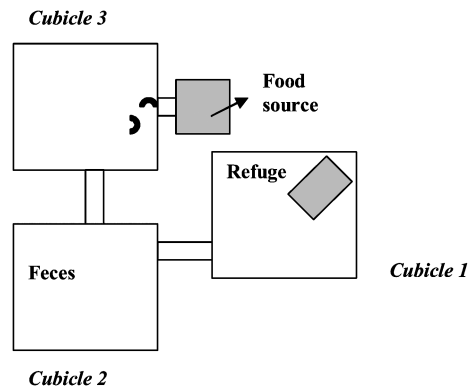
tested; a tape recorder was used for voice recording, and the experiment was video taped.

Antipredator behavior (flight, vigilance, freezing, no reaction) was recorded. These behaviors were defined as: Flight: the animal ran to its burrow and to cover as response to a threatening stimulus (Rood, 1972; Shahaf & Eilam, 2003; Taraborelli, 2006). Vigilance: alert posture, typically the animal froze with its front legs extended; the eyes directed toward the stimulus (Rood, 1972; Taraborelli, 2006). Freezing: the animal remained immobile in a sitting posture (Rood, 1972; Shahaf & Eilam, 2003). No reaction: the animal did not respond to a stimulus (Taraborelli, 2006). We recorded the duration of the response, latency time until the first antipredator response, distance between cavy or cavies and predator at the moment of the response (distance of reaction), speed of escape (distance of travel until hiding in meters/time of travel in seconds) and type of hiding place used. In addition, for the cavy or cavies, sex, life stage and company at the moment of the experiment (solitary or in group) were recorded.

#### *Experiment in captivity*

The experiment in captivity consisted in using three wood cubicles (70 × 70 × 45 cm), with a wire mesh net (2 mm) on the bottom that was covered by a layer of 5 cm of sand, and a top of wire mesh; the cubicles were interconnected by PVC tubes 30 cm long. In cubicle 1 the individual was placed inside its wooden refuge (25 × 20 × 20 cm); in cubicle 3 a closed wooden compartment was added, to be used as food source, containing apples and alfalfa pellets (Figure 1). Each individual was kept for 24 h in the cubicle system to become acclimatized to it. On the following day, wet feces of fox (fox treatment) or puma (puma treatment) or European hare (herbivorous mammal, control treatment), were incorporated into two sectors before reaching access to the food source.

The order of the individuals was random, and the sequence of treatments for each individual was random as well (for example: cavy 4b without feces, fox, hare, puma; cavy 5a fox, puma, hare, without feces). Records were taken every hour to measure both activity from animal footprints in the sand and time taken to reach the food. Cavy footprints were used as a register of activity. The activity was estimated from the percentage of sand with cavy footprints in the cubicles. After every record the sand was smoothed to find



**Figure 1.** Illustration of the experiment in captivity.

out whether the animal had actually been in the cubicles. This experiment used 5 cavies captured at Ñacuñán, all four treatments were given to each individual, and the time lapse between treatments was 2–3 weeks. Then each individual ‘rested’ for 2–3 weeks. We were not able to do the experiments with individuals from El Leoncito because they did not survive in captivity.

#### *Statistical analyses*

In analyzing the data from the field experiment, MANCOVA was used (with group size as covariable) to compare the mean distance of reaction and mean latency time among groups from both study sites and among types of predators. ANCOVA was used (with body weight of individuals as covariable) to compare the mean escape speed between individuals from both study sites and among types of predators. The  $\chi^2$  test was applied to compare the frequencies of cavies’ reaction to predators at both sites and Pearson residuals ( $r = (f \text{ observed} - f \text{ expected}) / \sqrt{f \text{ expected}}$ ) were used to find differences between said frequencies. The results of the experiment in captivity and the time individuals took to reach the food source in the different treatments were analyzed with ANOVA (single factor with blocking); the block was each individual subjected to the different treatments. Post-hoc testing (Tukey test,  $p < 0.05$ ) was used to test for differences among the variables considered; in the figures the different letters indicate differences between means. MANOVA with repeated measures in time was used to determine the existence of differences in the activity among treatments at 7 moments of the time for five individuals per treatment. When the differences resulting

from MANOVA were significant we used 'a posteriori' contrasts for multiple comparisons by the Hotelling test ( $p < 0.05$ ). The results are displayed as mean  $\pm$  standard error (SE).

## Results

### *Field trial*

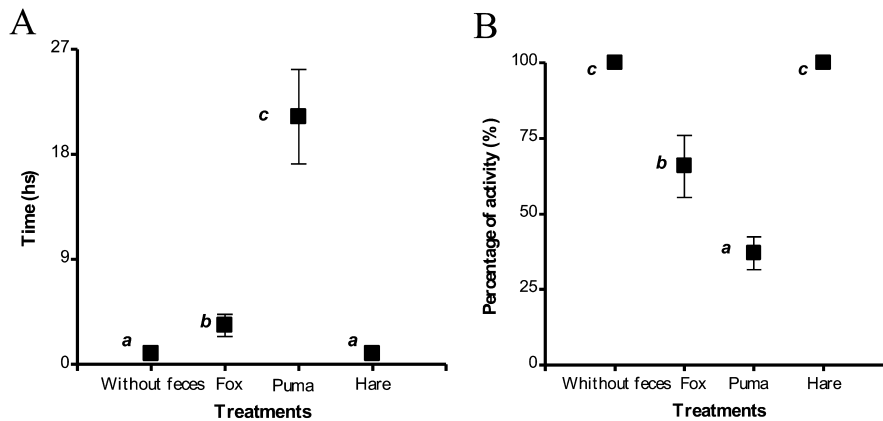
A total of 65 individuals were marked at El Leoncito and 12 individuals at Ñacuñán. From direct observations we determined the number of individuals that could not be captured and marked: 9 individuals at El Leoncito and 8 individuals at Ñacuñán. Individuals at El Leoncito reacted at greater distances from predators ( $11.4 \pm 0.4$  m) than at Ñacuñán ( $9.8 \pm 0.56$  m); Statistic of Wilks  $\lambda = 0.79$ ;  $F = 7.1$ ;  $p = 0.008$ ;  $df = 1$ ;  $N = 66$ ); latency time until the first antipredator response was higher for individuals of Ñacuñán ( $7.31 \pm 0.8$  s) than of El Leoncito ( $4.26 \pm 0.5$  s); Statistic of Wilks  $\lambda = 0.85$ ;  $F = 8.83$ ;  $p = 0.00034$ ;  $df = 2$ ;  $N = 66$ ). Differences in velocity of escape were found between individuals of both sites, though individuals of Ñacuñán ran away at higher speed ( $0.85 \pm 0.05$  m/s, El Leoncito  $0.56 \pm 0.05$  m/s;  $F = 17.4$ ;  $p = 0.0001$ ;  $df = 1$ ;  $N = 66$ ).

At Ñacuñán there were no differences in the type of reaction to the different predators, the cavies always responded by fleeing toward the burrow ( $\chi^2 = 1.001$ ;  $p = 0.701$ ;  $df = 2$ ;  $N = 20$ ). At El Leoncito the frequency of vigilance behavior when faced with the fake fox was high; and when confronted with the raptor the individuals reacted by fleeing toward the burrow and/or by hiding in galleries ( $\chi^2 = 38.741$ ;  $p < 0.0001$ ;  $df = 4$ ;  $N = 46$ ). At neither site did the cavies emit alarm calls in response to predator presentations.

### *Experiment in captivity*

Significant differences were found among treatments, individuals took longer to reach the food source when the boxes were supplied with puma and fox feces than in the control treatment (herbivorous mammal) or in the treatment without feces ( $1 \pm 0$  h). The antipredator response was more effective with puma feces than with fox feces ( $21.2 \pm 4$  and  $3.4 \pm 1$  h, respectively;  $F = 92.3$ ;  $p < 0.0001$ ;  $df = 3$ ;  $N = 25$ ; Figure 2A). The percentages of activity





**Figure 2.** (A) Mean time (h) to reach the food source in the different treatments. (B) Percentage of mean activity in the cubicles among the different treatments. Mean  $\pm$  standard error. a, b, c indicate significant differences among treatments (Tukey test  $p < 0.05$ ).

changed over time in the fox and puma treatments (Statistic of Wilks  $\lambda = 0.01$ ;  $F = 10.69$ ;  $p < 0.0001$ ;  $df = 18$ ;  $N = 25$ ). The activity in the cubicles differed significantly among treatments over time (Statistic of Wilks  $\lambda = 0.14$ ;  $F = 42.16$ ;  $p < 0.0001$ ;  $df = 3$ ;  $N = 25$ ; Figure 2B), diminishing in the presence of fox feces and even more in front of puma feces.

## Discussion

The cavies of El Leoncito reacted at a greater distance from predators and the latency time until the first antipredator response was shorter. This could be related to the presence of wide open areas where predation risk increases, and where their vision would be less impaired by shrubs and herbaceous plants. This would allow them to perceive raptors by their shadow on the ground, and to detect approach of terrestrial mammalian predators because the height of herbaceous vegetation at El Leoncito does not exceed 5 cm and the open areas are wider (80% approximately). At Ñacuñán individuals developed their behavioral patterns in the burrow area, beneath the cover provided by trees, shrubs and herbaceous plants, where shrubs and trees would give vertical protection from raptors, but herbaceous plants would obstruct visual detection of terrestrial mammalian predators and of the shadow of raptors on the ground. The number of predators at Ñacuñán was higher in

the morning hours, and the number of raptors by cavy was high (Taraborelli, 2006). Moreover, raptors are quick hunters (Roux et al., 2001) and overlap during the period of activity of caviés (Taraborelli, 2006). On this site we found that caviés responded to a threat by fleeing toward the burrow at greater speed than the individuals from the other Monte desert. Similar results were found for *Octodon degus* in the Chilean Matorral, the ability of degus to detect potential predators lowered when the herbaceous vegetation was higher, and this would enhance danger of terrestrial predators (Ebensperger & Hurtado, 2005). Degus allocated more time to vigilance and fleeing towards the burrow when the height of herbs was high (Ebensperger & Hurtado, 2005). Concerning the sense of vision in caviés, they have a quite restricted lateral monocular vision (angle of vision is  $43^\circ$ ), and their field of vision allows them to see around themselves, giving them the opportunity to flee and run for safety in front of a predator (Taraborelli, 2006).

When confronted with the fake predators, the caviés reacted with high frequencies of vigilance, and by fleeing towards the burrow and/or hiding in the galleries at both sites. Use of the refuge would increase survival of the individuals in the presence of a predator, and if the refuge were also the nesting site it would directly increase the fitness of rodents (Kramer & Bonenfant, 1997; Sundell & Ylönen, 2004). Behavioral responses typical of rodents are avoidance of the stimulus, reduction of locomotor activity, adoption of a static posture, vigilance behavior, flight and hiding from predators (Kramer & Bonenfant, 1997; Eilam et al., 1999; Dielenberg et al., 2001; Vásquez et al., 2002; Shahaf & Eilam, 2003). At neither site did the caviés emit alarm calls in response to predator presentations, but they responded with group vigilance (Taraborelli, in revision), flight toward the burrow or reduction of locomotor activity and of home range. In the presence of a weasel or a red lizard, caviés leave the burrow (P. Taraborelli, personal observation), which could be associated with the elongated body of these predators, adapted to hunting small rodents in tunnels or holes, as described for mustelids by Nordahl & Korpimäki (2000). Besides plant structure, vegetation cover and different predators, another specific factor that could have contributed to the observed results is the effect of group on antipredator responses, i.e., groups of larger size show lower levels of individual vigilance and improved efficiency in their antipredator behavior. That is to say that a predator would be detected earlier when approaching a group than a solitary individual and

could, thus, be avoided (many-eyes effect and cooperative vigilance). Despite the convincing evidence that group size plays a role in cavy vigilance (Rood, 1972; Cassini, 1989), there was no effect of grouping or cavy density on vigilance in this study. Currently, we are examining a larger data set that includes focal observations over a larger number of seasons to address this rather puzzling result, and to see whether the influence of group size on vigilance varies between sites and seasonally (Taraborelli, data not shown).

Prey species show specific adaptations that allow recognition, avoidance and defense against predators. For many mammalian species this includes sensitivity towards predator-derived odors. The typical sources of such odors include predator skin and fur, urine, feces and anal gland secretions. Avoidance of predator odors has been observed in many mammalian prey species including rats, mice, voles, deer, rabbits, gophers, hedgehogs, possums and sheep. Field and laboratory studies show that predator odors have distinctive behavioral effects which include inhibition of activity, suppression of non-defensive behaviors such as foraging, feeding and grooming, and shifts to habitats or secure locations where such odors are not present (Apfelbach et al., 2005). *M. australis* used the sense of smell to locate predators. From the results of the experiment in captivity with predator and herbivorous mammal feces, individuals were observed to take more time to reach the food source when supplied with predator feces, and puma feces had a larger effect than those of foxes. Therefore, it could be concluded that *M. australis* would be able to recognize its predators through the olfactory sense, and that this species is capable, like *Microtus ochrogaster*, of distinguishing between the scents of different mammalian carnivores (Ylönen, 1994; Norrdahl & Korpimäki, 2000), and would have the same ability as *Rhombomys opimus* to respond to these scents (Rogovin et al., 2004). A clear decline was observed in the activity of *M. australis*, which avoided the sectors with feces and reduced the activity even more in front of feces of puma than of fox, this would be another antipredator response. Predators reduce the size of the action area of their preys, limiting their foraging activity (Desy & Batzli, 1989; Ylönen, 1994; Eilam et al., 1999; Norrdahl & Korpimäki, 2000; Dielenberg et al., 2001; Borowski, 2002; Ebensperger & Wallen, 2002; Pusenius & Ostfeld, 2002). For example *Microtus socialis* avoided exposed habitats and reduced their activity in front of owls, and decreased activity and avoided sites visited by *Mustela nivalis* (carnivore) which they distinguish by the smell (Ylönen, 1994; Eilam et al., 1999). The voles display a trade-off conflict between

predator risk and foraging, if predator risk is high (Borowski, 2002). There exists a volatile substance (trimethylthiazoline) in fox feces that produces immobility and reduction of the exploratory behavior in rodents, particularly in open areas (Wallace & Rosen, 2000; Williams et al., 2005). As for felines, a mixture of odors from urine, feces, gland secretions and hair is what causes an antipredator response in rodents (Williams et al., 2005). There would, therefore, be an olfactory perception in the likely presence of a predator.

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