

EFFECT OF CONGENERIC CHEMICAL SIGNALS OF DIFFERENT AGES ON FORAGING RESPONSE AND FOOD CHOICE IN THE FIELD BY GOLDEN SPINY MICE (*Acomys russatus*)

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Abstract—The common spiny mice *Acomys dimidiatus* and golden spiny mice *Acomys russatus* coexist in the extreme warm and dry parts of the Rift Valley in Israel. However, they are temporally segregated in that the former is nocturnal, whereas the latter is diurnal. Daily rhythms of physiological and behavioral variables in *A. russatus* responded to semiochemical signals released by *A. dimidiatus* (in the urine and feces). Both species feed upon the same food items but at different times of the 24-hr cycle. The main aim of the present study was to test under field conditions the foraging response of *A. russatus* to odors of different ages released by *A. dimidiatus*. Various feeding and behavioral variables were compared in three groups of *A. russatus*. The results show that fresh semiochemical signals released by *A. dimidiatus* decrease the feeding efficiency and increase the rate of smelling from a distance in *A. russatus*. These results support the idea that temporal segregation between the two coexisting species is at least partly through semiochemicals present in the urine and feces.

Key Words—Heterospecific chemical signals, feeding behavior, urine and feces, *Acomys*, spiny mouse, arid environment.

INTRODUCTION

The coexistence of spiny mice of the genus *Acomys*, the common spiny mouse *A. dimidiatus* (Harrison and Bates, 1991) and the golden spiny mouse *A. russatus*, has been shown to be through exclusion of the latter from nocturnal activity by the former (Shkolnik, 1971). Attempts have been made in the last decade to understand the mechanisms for such temporal segregation. Under laboratory conditions when *A. russatus* is kept separately from *A. dimidiatus*, it manifests body temperatures and oxygen consumption daily rhythms typical of nocturnal species (Rubal et al., 1992). Body temperature and oxygen consumption daily rhythms of *A. russatus*, exposed to indirect chemical signals released by *A. dimidiatus*, showed a phase shift of approximately 2 hr compared with controls (Fluxman and Haim, 1993; Haim and Fluxman, 1996). However, when studying the response of the daily activity rhythms of *A. russatus* to direct contact with urine and feces released by *A. dimidiatus*, a shift of approximately 7 hr into diurnal activity was observed (Haim and Rozenfeld, 1993). From these studies and others, it was concluded that semiochemicals released from the urine and feces of *A. dimidiatus* are important in maintaining the temporal segregation between the two species.

Furthermore, the hypothesis that the nest site (resting place) could be a source of competition between the congeners was tested under laboratory conditions (Haim and Rozenfeld, 1995). The results supported the hypothesis, and it was also noted that *A. russatus* keeps its resting place only by being active during the daytime when *A. dimidiatus* is inactive. Recently, Van Aarde and Haim (1999) have shown that semiochemical signals released by *A. dimidiatus* may affect aspects of reproduction in *A. russatus*.

Both species utilize the same diet (Shkolnik, 1966), but it is eaten at different times of the 24-hr cycle. However, food is probably the source of competition between the two species. From this, we asked the following question: do semiochemicals of different age released by *A. dimidiatus* have an effect on feeding behavior of *A. russatus*? We recorded feeding behavior of *A. russatus* in the field in relation to the size and quality of food items. We studied the change in frequency of feeding sessions and of behavioral acts in response to semiochemicals released by *A. dimidiatus*.

METHODS AND MATERIALS

Study Area. Field observations were carried out at the foot of Masada cliff, 3 km from the Dead Sea shores in the Jehudean desert, which is a part of the Rift Valley, in Israel. The study area was located close to the ruins of a Roman camp, at about 340 m below sea level. The climate is extremely dry and hot. The average annual precipitation is 47 mm with large year-to-year fluctuations. The mean minimum temperature, recorded in January, was 11°C, whereas the mean

maximum temperature, recorded in July, reached 39°C (Jaffe, 1988). Petri dishes containing different food items were used (see below). The dishes were set close to walls made of rough stones, 2 m wide at their base and 1.2 m high. The walls were built some 2000 years ago and are inhabited by different rodent species; however, the dominant species in the area are the spiny mice *A. russatus* and *A. dimidiatus* (Dobly et al., 1999). Along these walls, garbage has accumulated, some of which is presumably consumed by the mice inhabiting the walls. In order to observe marked individuals, *A. russatus* were trapped before the current study (Dobly et al., 1999) and individually marked with an animal-marking crayon (Raidi-Raider, Ottenbach, Germany).

Feeding Observations. Clean Petri dishes (liquid dish-washing soap, water, and then ethanol 70%) were set on a white piece of filter paper (28 × 23 cm). Each dish contained five different items: (1) an intact grilled peanut ($N = 1$); (2) half a peanut seed ($N = 5$); (3) corn seeds ($N = 10$); (4) wheat seeds ($N = 15$); and (5) oat flakes ($N = 15$). The position of the different food items in the Petri dishes as well as mass and energy contents are presented in Figure 1. Two Petri dishes were positioned at a distance of 1.5 m from each other in each session, which lasted 1 hr. A total of 28 sessions were performed.

Preliminary observations indicated that mice were not disturbed by the observer (Dobly et al., 1999). Direct visual observations were carried out from an exposed spot at a distance of 3 m from 8:45 to 16:00 hr. We chose daytime in order to observe *A. russatus*. Different behavioral variables were recorded (see Dobly et al., 1999): emerging from shelter, watching, approaching a Petri dish, smelling from

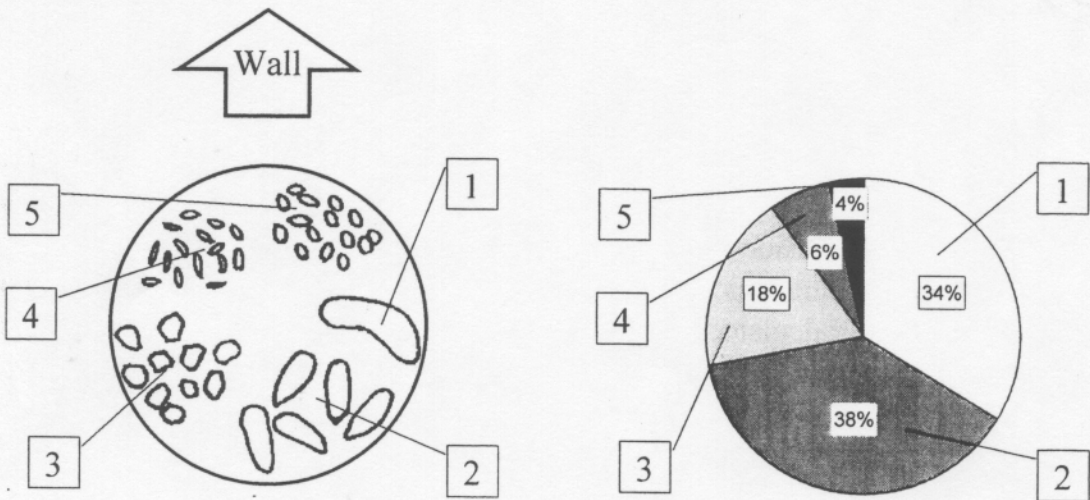


FIG. 1. Presentation and composition of dietary items offered in each Petri dish used as an artificial feeding site. The types, numbers, energy contents, and total weights were as follows: (1) intact grilled peanut (ca. 2 seeds, 1 × 14,000 cal, 2 g), (2) half a peanut seed (5 × 3200 cal, 2.5 g), (3) corn seeds (10 × 750 cal, 1.6 g), (4) wheat seeds (15 × 175 cal, 0.65 g), and (5) oats (15 × 100 cal, 0.35 g). The total energy percentages are given in the pie chart.

a distance, and close sniffing. When more than one mouse was active, behavioral patterns were recorded by using a video camera (Sony Hi8 CCD-TRV70E). Data were analyzed frame by frame. At the end of each session, the food items left over were counted and the Petri dishes cleaned. We also used the number of food items touched, i.e., the number of food categories with at least one item eaten. The energy values of the different food items were determined by using a bomb calorimeter (Semimicro Calorimeter 1425, Parr).

Exposure to Heterospecific Odors. In 15 of 28 sessions, the observed mice were exposed to a type of odor obtained from *A. dimidiatus*. Toilet paper and feces, obtained from traps in which *A. dimidiatus* were successfully trapped, were used as a source of the heterospecific odors. All the collected odorous items were kept in a sealed plastic bag. In eight cases, *A. russatus* were offered, in each session and in each dish, a combination of fresh urine (on one piece of toilet paper) with three fecal pellets collected on the same day (we used three pellets according to the average number available per day). In seven cases, only three fecal pellets were used for testing the response of *A. russatus* to feces alone, 24 hr after collection. Paper was put below the Petri dishes, and the feces were put close to the dishes on the side of the wall. Therefore, three different groups were studied: (1) control (no odor), (2) heterospecific feces only, collected one day before exposure (old odor) and (3) fresh heterospecific urine and feces (fresh odor). We did not compare heterospecific odor to homospecific odor as other laboratory and field studies have shown that only heterospecific odor has a repellent effect on *A. russatus* (Haim and Rozenfeld, 1993; A. Haim and E. Baert, unpublished data). Beyond this identified effect of homospecific versus heterospecific odors, our main purpose was to test the unknown difference between fresh and old heterospecific odor.

Data Analyses. Results are presented as frequency, percentage, mean \pm standard deviation, or median with range. In order to establish differences among studied groups, the following statistical tests were used: chi-square test, Mann-Whitney *U* test, and Kruskal-Wallis one-way ANOVA. All were one-tailed due to the hypothesis of a negative influence of heterospecific odor on feeding. To test the food preference inside one treatment, we used two-tailed Friedman two-way ANOVA. To determine which pairs were the sources of the detected difference in ANOVA tests, we calculated the critical difference necessary for significance in each compared pair.

RESULTS

A total of eight golden spiny mice (five females and three males) were marked and observed. At least one mouse appeared in 22 of the 28 sessions. The six sessions with no mouse were from groups with old [two of seven (29%)] or fresh [four of eight (50%)] odors. This distribution of appearance among the three groups is different (chi-square test, $P < 0.01$, Table 1). Similarly, in all sessions with at

TABLE 1. FEEDING BEHAVIOR OF *Acomys russatus* UNDER THREE ODOR TREATMENTS OF ARTIFICIAL FEEDING SITES

Measurement	Types of heterospecific odors ^a			Statistical tests
	None	Old	Fresh	
Number of sessions with mice	100% (13/13)	71% (5/7)	50% (4/8)	$P < 0.01$, chi-square test
Number of mice per session	1.54 (SD = 0.97) (20/13)	1.71 (SD = 1.70) (12/7)	0.88 (SD = 1.13) (7/8)	$P = 0.045$ between none and fresh odor, Mann-Whitney <i>U</i> test
Median latency to appear (min, sec)	20'27" [2'20"-52'45"] (<i>N</i> = 20)	15'05" [2'00"-53'00"] (<i>N</i> = 12)	29'45" [1'50"-47'15"] (<i>N</i> = 7)	NS, Kruskal-Wallis one-way ANOVA, <i>df</i> = 2
Median latency to eat (min, sec)	1'10" [0'05"-38'25"] (<i>N</i> = 19)	1'10" [0'10"-8'30"] (<i>N</i> = 9)	1'07" [0'25"-04'40"] (<i>N</i> = 4)	NS, Kruskal-Wallis one-way ANOVA, <i>df</i> = 2
Relative frequency of smelling from a distance	13.3% (<i>N</i> = 14)	14.5% (<i>N</i> = 8)	28.0% (<i>N</i> = 6)	$P = 0.041$, Kruskal-Wallis one-way ANOVA, <i>df</i> = 2
Relative frequency of close sniffing	11.1% (<i>N</i> = 14)	13.4% (<i>N</i> = 8)	9.2% (<i>N</i> = 6)	NS, Kruskal-Wallis one-way ANOVA, <i>df</i> = 2
Percentage and number of mice that ate	95% (19/20) 1.46 (SD = 0.88)	75% (9/12) 1.29 (SD = 1.11)	57% (4/7) 0.50 (SD = 0.76)	$P = 0.017$ between none and fresh odor, Mann-Whitney <i>U</i> test
Mean food touched (out of 10)	3.5 (SD = 2.7) (<i>N</i> = 13)	2.6 (SD = 2.6) (<i>N</i> = 7)	1.1 (SD = 1.8) (<i>N</i> = 8)	$P = 0.031$, Kruskal-Wallis one-way ANOVA, <i>df</i> = 2

^aNone: no odor (control), old: one-day-old heterospecific feces; fresh: fresh heterospecific urine and feces. Range of median is given in square brackets, SD = standard deviation.

least one animal observed, there were, on average, more individuals per session in the control group than in the fresh odor group; the old odor group was intermediate (Mann-Whitney U test, $N = 21$, $P = 0.045$, Table 1).

No significant difference was noted among the three groups in regards to the median time to appear or to eat (Table 1). Moreover, in three cases (two controls and one old odor, 15% and 14%, respectively), an *A. dimidiatus* was detected; all of them appeared only once and took either an entire or half a peanut in a single trip lasting less than 10 sec.

Not all observed *A. russatus* ate from the Petri dish. Table 1 shows, for the three groups studied, the number of mice that ate food, as well as the number of food types that were touched by mice. Mice from the control group ate more frequently than mice confronted with fresh odor (95% vs 57%, Mann-Whitney U test, $N = 27$, $P = 0.017$). Similarly, with regard to number of food types touched, a significant difference was noted only between control mice and those exposed to fresh odor (Kruskal-Wallis one-way ANOVA, $df = 2$, $N = 28$, $P = 0.031$, Table 1).

Mice of all groups preferred the larger items with a high-energy content per gram. The item most often taken on a first visit was the whole peanut, and then the half peanuts. In total, a larger amount of grilled intact peanuts was eaten than oats, corn, or wheat seeds (Friedman two-way ANOVA, $df = 4$, $N = 28$, $P = 0.017$). The energy context of the five food types is presented in Figure 2. The relationship then became clearer. The energy value of whole peanuts eaten is higher than that of corn, wheat, or oats (Friedman two-way ANOVA, $df = 4$, $N = 28$, $P = 0.008$).

The analysis of behavioral patterns revealed that mice exposed to fresh odor showed more smelling from a distance than control mice (Kruskal-Wallis one-way ANOVA, $df = 2$, $N = 28$, $P = 0.041$, Table 1). However, no difference was detected either in close sniffing or in any other recorded behavior (e.g., while the maximum number of mice approaching a Petri dish decreased among the three treatments, the medians were not different: no odor: 2.5 (range 1–30), old: 2.5 (1–19) fresh: 3.0 (1–10), Kruskal-Wallis one-way ANOVA, $df = 2$, $N = 28$, NS).

DISCUSSION

Food and energy consumption in *A. russatus* have been studied under short and long photoperiod regimes (Haim et al., 1994). Under acclimation to a short day, *A. russatus* consumed significantly more food compared with acclimation to a long day. The energetic demands of *A. russatus* are low in relation to its body mass, compared with mesic species. Field metabolic rates (FMR) were compared between the two *Acomys* species by using the doubly labeled water technique (Degen, 1994). Daily metabolic rates of *A. russatus* were 27% lower than those for a similar sized *A. dimidiatus*. The energy content of the items offered in

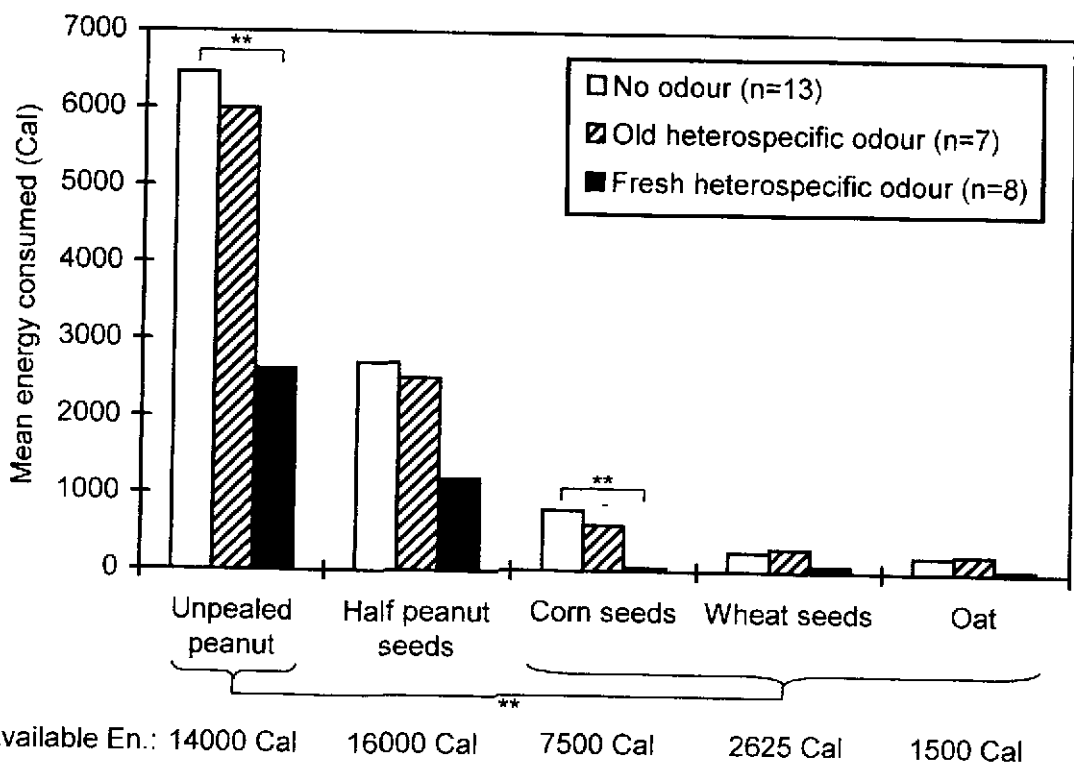


FIG. 2. Mean energy taken from the five food types by the mice under three different treatments. The total energy available is given below each food type (Available En.). Two-tailed Friedman two-way ANOVA, one-tailed Kruskal-Wallis one-way ANOVA, and one-tailed Mann-Whitney U tests were used ($*P < 0.05$, $**P < 0.025$).

the Petri dish exceeded the energy demands, even during the winter season when experiments were carried out.

Our results show that *A. russatus* selected the largest food item (intact peanut), which contained the highest energetic value. Such selection would be advantageous to a diurnal animal by minimizing the time spent foraging and reducing vulnerability to predation or overheating. These requirements are consistent with the high number of distant smelling bouts and the small number of close sniffing bouts recorded in the presence of fresh odor. The results of food selection support the conclusion of Kerley and Erasmus (1991) that rodent preference for seeds is related to the net rate of energy intake provided by the seed.

However, our results revealed a significant decrease in food and energy intake as a result of exposure to fresh urine and feces released by *A. dimidiatus*. In a laboratory study, *A. russatus* marked its food with an oral secretion (Rozenfeld et al., 1994). Oral marking by *A. russatus* may serve to mask the original odor of *A. dimidiatus*. The number of sessions in which mice appeared upon exposure to fresh heterospecific odor and the number of mice per session were significantly lower compared with control sessions. This suggests that odor can act from a distance. However, it seems that under dry desert conditions, odor sources are

not so effective. Therefore, we conclude that, at least partly, scent marking of the habitat by *A. dimidiatus* contributes to the temporal segregation of the two species. As *A. russatus* does not accumulate food in its resting place, the marking of food items supports the hypothesis that such marking has a heterospecific role (Rozenfeld et al., 1994).

From the results of this and previous studies, we conclude that heterospecific odors released in the urine and/or feces of *A. dimidiatus* have an effect on the behavior of *A. russatus*. Activity in *A. dimidiatus* is confined to the early hours of the dark phase (Shkolnik, 1966). Hence, we assume that odors released at night during the activity period of *A. dimidiatus* decline with time, so that when *A. russatus* is active, the odor effect is of little significance.

As the temporal segregation between the two species is maintained, at least partly, by chemicals released by *A. dimidiatus* (Haim and Rozenfeld, 1993), we assume that this depends on fresh urine and feces. The chemicals involved appear to be volatile. Semiochemicals produced in the urine and feces of *A. dimidiatus* can bring about competitive exclusion of *A. russatus* from nocturnal activity and can be used to exclude them from access to food and habitat resources. The isolation of the chemical component of this signal will be important for future studies, involving the segregation of coexisting species.

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