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CAN AGGRESSION BE THE FORCE DRIVING TEMPORAL SEPARATION BETWEEN COMPETING COMMON AND GOLDEN SPINY MICE?

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We studied a system in which 2 desert rodent species coexist through temporal partitioning. Previous research suggests that the common spiny mouse (*Acomys cahirinus*) competitively forces the golden spiny mouse (*A. russatus*) into diurnal activity, but the mechanism driving this separation is not entirely understood. To test whether aggression is the driving force in this exclusion, we analyzed interactions between pairs of these 2 species. In contrast with our working hypothesis, the golden spiny mouse was more aggressive as reflected in its significantly more frequent chasing and biting behaviors. These results suggest that aggressive interference does not explain the temporal partitioning between these species. Other factors such as foraging efficiency, antipredator avoidance, water conservation, or productivity may account for the shift of golden spiny mice into diurnal activity.

Key words: *Acomys*, aggressive behavior, interference competition, resource exploitation, spiny mice, temporal partitioning

Interspecific competition is an important ecological interaction among desert rodents (Kelt et al. 1999; Kotler and Brown 1988). Interspecific competition appears to have implications for foraging strategies, microhabitat use, activity patterns, and perhaps even community structure (Brown et al. 2000; Fox and Brown 1993; Stone et al. 1996, 2000). Microhabitat partitioning, temporal partitioning, and even competitive exclusion have been demonstrated in studies of desert rodents (Abramsky et al. 1990, 2001; Rosenzweig and Abramsky 1997). These patterns may be driven by species' differing efficiencies in exploiting different niche axes or through interference competition (Kotler and Brown 1988; Kotler et al. 1993; Ziv et al. 1993).

Competition is often considered an asymmetrical interaction (Connell 1983; Lawton and Hassell 1981; Schoener 1983), with larger-sized species favored when competition is mediated by interference (Dickman 1988; Glazier and Eckert 2002; Persson 1985; Yom-Tov and Dayan 1996). Interference competition (which "occurs when the organisms seeking a resource harm one another in the process, even if the resource is not in short supply"—Krebs 2001:82) can be assessed by studying direct agonistic behavioral interactions (Baker 1974; Meredith 1977; Wauters and Gurnell 1999), but surprisingly little such research has been carried out on desert rodents (Blaustein and Risser 1976; Bleich and Price 1995; Haim and Rozenfeld 1991; Hoover et al. 1977; Ovadia and Dohna 2003; Ovadia et al. 2005).

We studied agonistic behavioral interactions between 2 species of spiny mice, the nocturnal common spiny mouse (*Acomys cahirinus*; also known as Egyptian or Cahiro spiny mouse) and the diurnal golden spiny mouse (*A. russatus*). The 2 species coexist in rocky deserts of the Near East (Elvert et al. 1999; Kronfeld-Schor et al. 2001a, 2001b, 2001c; Shkolnik 1966, 1971). Upon removal of the common spiny mouse from the shared habitat, Shkolnik (1971) found that the golden spiny mouse turned to nocturnal activity, and suggested that the golden spiny mouse is competitively displaced by "its somewhat more vigorous kindred" (Shkolnik 1971:116). Gutman and Dayan (2005), who repeated this study in replicated and controlled conditions found that although golden spiny mice remained primarily active during the day, in the absence of common spiny mice they also were active during the night. On the other hand, common spiny mice occur allopatrically in many parts of their distributional range and nevertheless remain strictly nocturnal. Previously, Haim and Rozenfeld (1995) found that in experimental laboratory settings, after 24 h the common spiny mouse took over the nest of the golden spiny mouse, but no aggressive interactions over food or nest were observed.

A decade of research on spiny mice at Ein Gedi, near the Dead Sea, where both species coexist, revealed that although

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predation risk and climatic stress could affect activity times and foraging microhabitat use, they did not induce a shift from nocturnal to diurnal activity or vice versa (Jones et al. 2001; Kronfeld-Schor and Dayan 2003; Kronfeld-Schor et al. 2001a; Mandelik et al. 2003). Interestingly, however, golden spiny mice exhibit nocturnal temperature rhythms and immediately upon removal from the field they also exhibit nocturnal or mixed activity patterns (Kronfeld-Schor et al. 2001a). Moreover, golden spiny mice also appear to be nocturnally adapted in their capacity for nonshivering thermogenesis (Kronfeld-Schor et al. 2000) and in the eye structure (Kronfeld-Schor et al. 2001b). Thus, Kronfeld-Schor and Dayan (2003) suggested that although temporal partitioning is a viable mechanism of reducing interspecific competition, evolutionary constraints may limit the use of this diel niche axis.

Kronfeld-Schor and Dayan (1999) showed that the 2 species of spiny mice were primarily insectivorous, in particular during the summer months. Weinstein (2003) studied the spatial and temporal variations in arthropod activity and availability at Ein Gedi and found that most arthropod taxa were active either during the day or during the night. If active arthropods were likelier prey, then temporal partitioning could be a viable mechanism of coexistence between the 2 species (Kronfeld-Schor and Dayan 1999; Weinstein 2003). However, these studies could not refute the alternative hypothesis that the common spiny mouse aggressively displaces the golden spiny mouse into diurnal activity, and that this shift does not reduce resource competition between the 2 species (Kronfeld-Schor and Dayan 1999). Here we tested Shkolnik's (1966, 1971) suggestion that aggression is the force driving temporal separation of the 2 species by observing direct agonistic interactions between pairs of common and golden spiny mice during early and late night periods.

Materials and Methods

We obtained 12 golden and 12 common spiny mice, all males, from captive colonies in the I. Meier Segals Garden for Zoological Research at Tel-Aviv University, which were derived from mice that were trapped several years ago at the Ein-Gedi region, Israel. We caged conspecifics in groups of 3. Mice were acclimated >3 weeks before experimentation to an ambient temperature of 28°C, as in previous studies (Freidman et al. 1997; Kronfeld-Schor et al. 2000, Zisapel et al. 1999) and a 10:14 h light : dark cycle, with standard rodent food pellets and water provided ad libitum. Animal maintenance and treatment were in accordance with the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). All mice were in good physical condition, and were returned to the breeding colonies that are currently maintained in our research zoo.

Observations were carried out in a cage (50 × 132 × 49 cm) with a transparent glass floor and opaque walls. A mirror was tilted underneath the cage at a 45° angle, providing a bottom view of the cage and the insides of 2 overturned clay pots that were provided as shelter. Similar pots are regularly used for shelter in the home cages of spiny mice at the research zoo. The chamber was illuminated by a 12-V DC infrared light (model IP68, Tracksys, Nottingham, United Kingdom) that is invisible to mammalian eyes. An infrared-sensitive video camera (Ikegami, B/W ICD-47E, Tokyo, Japan) was placed in front of the mirror, providing a bottom view of the mice at any location in the apparatus. The video image and a time code (generated by T5010 and LTC-VITC translator T800, Telcom Research, Burlington, Ontario, Canada) were recorded on a videocassette recorder. The entire system was in a darkened room with a level of illumination as measured with a light meter (Gossen, Profisix Silicon blue cell, Nürnberg, Germany) during testing of 0.0425 lux.

Experiments were conducted over 2 consecutive weeks (11–24 September 2001). Mice were assigned to 12 heterospecific pairs. Mice were paired so as to minimize body mass differences between individuals of the 2 species in each pair; although in 8 of the pairs the golden spiny mouse was slightly heavier than the common spiny mouse, and in 4 the reverse situation occurred, the differences were not significant (paired *t*-test; $t = 1.84$, $P > 0.05$). Mean body mass of the individuals we used was 53 g ± 15 *SD* (range: 41.5–95.7 g) for common spiny mice and 57 ± 18 g (range: 37.3–95.8 g) for golden spiny mice. It should be noted that although the effect of body mass difference was counterbalanced in the present study by the above pairing, mean body mass in free-living populations in the En-Gedi region (the origin of our captive colonies) is, for common spiny mice, males 35.2 g ± 0.7 *SE* and females 32.0 ± 1.3 g; and for golden spiny mice, males 44.1 ± 0.6 g and females 41.0 ± 1.1 g (Shargal et al. 2000). Consequently, a possible competitive advantage of golden spiny mice due to their higher body mass was minimized in the present experimental design.

Six pairs were tested in the dark (under infrared light), 1 h before sunrise and then tested again a week later 1 h after sunset. The other 6 pairs were tested in a reversed order. Previous studies suggest that, at the evolutionary scale, the golden spiny mouse was competitively displaced from nocturnal activity and that it will still shift to being active during the night in absence of its congener, whereas common spiny mice are strictly nocturnal. Thus, the overlap expected between the species is during the night. Therefore, transition times between day and night are the periods of day when the 2 species are active and are most likely to interact in nature. Furthermore, experiments were preformed in the dark to avoid skewed results in favor of the golden spiny mouse, which is adapted to both day and night vision, as opposed to the common spiny mouse, which is adapted only to night vision (Kronfeld-Schor et al. 2001a, 2001b). At the beginning of each test session (90 min before sunrise or sunset), a pair of mice was transferred to the experiment room and introduced to the experimental chamber, 1 individual on each side of an opaque glass divided in midchamber that prevented visual and physical contact. After 30 min of habituation, the glass was removed allowing the mice to establish contact, and behavior was videotaped for 60 min. Every 10–15 min, the experimenter placed in the center of the arena a mealworm (*Zophobas morio*), which is a favorite food item for both species in captivity, to observe how they competed for the food. In order not to interfere with ongoing behavior, mealworms were placed in the middle of the arena every 10–15 min, when the mice were not in the area but in their nests or interacting in 1 side of the arena. The arena was washed with detergent and wiped after each testing session.

Behavior was analyzed from a slow-motion playback of the videotapes. The time code was read to a computer by a special device (T-900, Telcom Research). A custom-designed computer program allowed analysis of frequency and duration of selected behaviors. Relying on preliminary observations and behavioral elements described by Grant and Mackintosh (1963), the following behaviors were described: Chase = running after the other spiny mouse at a distance ≤20 cm. Escape = running away from the other mouse without being chased. Bite = biting the other mouse (usually followed by escape of the bitten mouse). Food capture (take food from center) = approaching the center of the arena and taking the mealworm. Food theft (take food from the other individual) = trying to steal the mealworm from the other mouse by pushing the snout near its mouth, sniffing, and then grabbing the mealworm from its mouth.

Additional parameters were measured to describe the distribution of activity of each individual: Latency = time (s) to cross to the other side of the arena from where mouse was habituated (crossing the midchamber was assessed relative to vertical line markings on the side walls). Traveled distance = cumulative distance (m) traversed by each individual during the observation. Time in opposite side = cumulative time (percent of total observation time) spent in the other side of the arena from where mouse was habituated. Preferred feeding site = incidence of food consumption in shelter, near shelter, and in the vicinity of the center.

Comparisons between the 2 species for each parameter were made using Wilcoxon matched-pairs signed-ranks test. Because the behavioral data may not be strictly independent, we used the false discovery rate method (Benjamini et al. 2001) to adjust *P* values for multiple comparisons within behavioral categories. Consequently, *P* values for parameters of aggressive behavior were set by the false discovery rate to 0.025, and the *P* value was set to 0.004 for the parameters of the distribution of activity.

RESULTS

Aggressive behavior.—Golden spiny mice displayed significantly higher incidence of chasing (Wilcoxon matched-pairs signed-ranks; evening: $P = 0.009$; morning: $P = 0.016$) and biting (evening: $P = 0.032$; morning: $P = 0.016$), and a higher incidence of escape was initiated by common spiny mice (evening: $P = 0.01$; morning: $P = 0.05$). However, no significant difference was found in the incidence of either taking food from the center of the arena (evening: $P = 0.82$; morning: $P = 0.28$) or food theft (evening: $P = 0.4$; morning: $P = 0.83$; Fig. 1).

Activity.—Aggressive behavior was consistent with the spatial distribution of activity. Golden spiny mice traversed longer distances (evening: $P = 0.0022$; morning: $P = 0.059$) and had a shorter latency to cross the center to the common spiny mouse's side (evening: $P = 0.075$; morning: $P = 0.028$), yet, of these only evening distances were significantly longer in golden spiny mice. No difference was found in the proportion of time that individuals of each species spent in the 2 sides of the chamber (evening: $P = 0.06$; morning: $P = 0.21$). No significant difference was found in preferred feeding site (in shelter: evening: $P = 0.01$; morning: $P = 0.34$; near shelter: evening: $P = 0.23$; morning: $P = 0.81$; center: evening: $P = 0.28$; morning: $P = 0.028$), although golden spiny mice seemed less restricted in feeding sites and ate in the vicinity of the center, near their shelter, or inside it. In contrast, common spiny mice mainly ate inside or near the shelter (Table 1).

No significant correlation was found between the differences in behaviors and body mass. Aggressive behavior of golden spiny mice was consistently observed in both the 4 pairs in which the common spiny mouse was slightly heavier than the golden spiny mouse and the 8 pairs in which the golden spiny mouse was slightly heavier. It should be noted that although the acclimation period was not videotaped, we noticed that upon being introduced to the apparatus, both spiny mice explored the arena for few minutes, and then hid in their shelters (overturned clay pots), where we found them when the partition was removed at the beginning of the encounter.

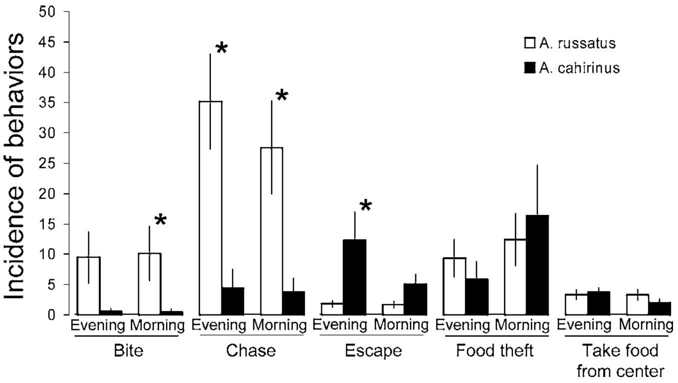

FIG. 1.—Mean incidence (± *SE*) of the different behaviors (bite, chase, escape, food theft, and take food from center) after dusk (evening) and before dawn (morning) of paired *Acomys russatus* (open bars) and *A. cahirinus* (dark bars). Asterisk indicates $P < 0.025$ (set as significant after false discovery rate adjustment for multiple testing).

DISCUSSION

In a field manipulation experiment, Shkolnik (1966, 1971) found that the golden spiny mouse shifts to diurnal activity as a result of interspecific competition with the common spiny mouse (see also Gutman and Dayan 2005). Accordingly, it could be expected that if 1 of these species is more aggressive, it would be the common spiny mouse. However, our results are counter to this expectation: the golden spiny mouse was the more aggressive, whereas the common spiny mouse was certainly not the more vigorous kindred as previously suggested (Shkolnik 1971). Although parameters that were used to measure aggressive behavior did not always reach statistical significance, for each pair studied in our experiments, golden spiny mice were consistently less confined in their space use and travel throughout the test chamber (Table 1) and consistently displayed overt aggressive behavior toward common spiny mice.

Despite differences between morning and evening testing, aggression of golden spiny mice was prevalent in both (Fig. 1). It should be noted that all our experiments were conducted during the dark time of transition between day and night, when the 2 species are active and are most likely to interact in nature (Kronfeld-Schor et al. 2001a, 2001b). Thus, the time frame of our research was such that it provided a sound simulation of the potential for aggressive interactions in the field (Shkolnik 1971).

Generally, in mammals, individuals of the larger species are stronger and more aggressive, and this provides an edge in competitive interference interactions. For example, in a different desert community, Ziv et al. (1993) demonstrated that the larger *Gerbillus pyramidum* is active during the earlier hours of the night, when seed density is higher, and aggressively displaces the smaller *G. allenbyi* to later hours of the night. Ovadia and Dohna (2003) and Ovadia et al. (2005) videotaped direct agonistic interactions between gerbils on foraging

Table 1.—Behaviors ($\bar{X} \pm SE$, $n = 12$) of common and golden spiny mice during testing in the morning, before dawn, and in the evening, after dusk. Asterisk indicates significant difference between species at adjusted *P* level (false discovery rate method—Benjamini et al. 2001), which was set to $P = 0.004$.

	Common spiny mice		Golden spiny mice		*P* value	
	Morning	Evening	Morning	Evening	Morning	Evening
Behavior						
Latency to move (s)	744.3 ± 106.1	183.8 ± 13	139 ± 39.5	82.83 ± 8.4	0.028	0.075
Distance traveled (m)	189.5 ± 12.7	216.6 ± 11.4	264.29 ± 13.9	352.3 ± 18.8	0.059	0.0022*
Time in other individual's side (%)	34.2 ± 1.9	61.47 ± 1.6	49.6 ± 1.61	49.1 ± 0.9	0.21	0.06
Preferred eating site (incidence)						
In shelter	5.9 ± 0.6	6.6 ± 0.5	4.7 ± 0.7	1.1 ± 0.1	0.34	0.01
Near shelter	4.5 ± 0.6	8.7 ± 1.5	4.7 ± 0.4	1.8 ± 0.2	0.81	0.23
Center	0.4 ± 0.1	0.9 ± 0.2	2.4 ± 0.2	1.4 ± 0.2	0.028	0.28

patches in experimental settings, confirming that aggression is a driving force in this competitive interaction. In our study, pairs were selected to minimize the difference in body mass between individuals of the 2 species, and in consequence to minimize the possible effect of body mass on the greater level of aggression exhibited by golden spiny mice. Moreover, no significant difference was found between the pairs in which common spiny mice were the heavier individuals, and those in which the reverse situation occurred. In all, therefore, the present results were not directly dependent on body mass.

Our results suggest that interference competition does not drive golden spiny mice into diurnal activity, in contrast with Shkolnik's (1971) hypothesis. Based on our enclosure experiments, where golden spiny mice still exploited the diurnal niche more than the night even in absence of common spiny mice (Gutman and Dayan 2005), it could be argued that, as suggested for distinct habitat preferences (Rosenzweig 1981), the 2 species have different and distinct preferences for activity time. That being the case, aggression need not be expected. Although this hypothesis may be viable at the ecological timescale, at the evolutionary timescale we have already shown that, based on its vision and temperature regulation, the golden spiny mouse appears to be a nocturnal species displaced into diurnality (Kronfeld-Schor and Dayan 2003). Perhaps its diurnal adaptations now override its nocturnal ancestry, still obvious in various aspects of its physiology and morphology (see ''Introduction'').

Alternatively, our results may reflect a short-term interaction under specific laboratory conditions that do not necessarily reflect the situation in natural habitats. Previous research has found that in laboratory settings, the common spiny mouse took over the nest of the golden spiny mouse within 24 h, but no aggressive interactions over a food dish were observed (Haim and Rozenfeld 1995). Thus, it could be suggested that the aggression of golden spiny mice is short-termed and ceases in the longer run. Additional studies that commence at the introduction of individuals to the same environment, and extend to a longer period of study, may shed further light on this issue.

Analyses of feeding preferences and food habits show that spiny mice subsist on vegetation, seeds, and invertebrates (Degen et al. 1986; Kronfeld-Schor and Dayan 1999). The arthropod component of common and golden spiny mice diets was 7% and 24%, respectively, in winter compared with 90% and 66%, respectively, in summer (Kronfeld-Schor and Dayan 1999). Because the arthropod prey of common and golden spiny mice are likely to show diurnal patterns in availability (Weinstein 2003), temporal partitioning could well promote resource partitioning and coexistence, particularly in summer. So the shift in activity time may be resource (food) mediated. In fact, Merkt and Taylor (1994) showed that when food was restricted in the laboratory, the golden spiny mouse shifts its metabolism rhythm from nocturnal to diurnal. Thus, feeding preferences and food habits, but not aggression, may induce the change in activity time.

Other possible cues for the displacement of golden spiny mice from nocturnal to diurnal activity are chemical signals released by common spiny mice. Exposure of naïve golden spiny mice, maintained on a light–dark cycle, to urine and feces of common spiny mice caused a phase advance of 6.8 h in the time of the beginning of activity, so the mice displayed a pattern of relative diurnal activity (Haim and Rozenfeld 1993). In other experiments, exposure to golden spiny mice caused a shift of 3 h (Haim and Fluxman 1996), 2 h (Fluxman and Haim 1993), or 45 min (Freidman et al. 1997) in rhythms of body temperature (Fluxman and Haim 1993; Freidman et al. 1997), activity (Freidman et al. 1997), and oxygen consumption (Haim and Fluxman 1996), respectively. The authors suggested that chemical signals of common spiny mice released into the common environment may play a role in the displacement of golden spiny mice from nocturnal activity.

We found that golden spiny mice are consistently (but not always significantly) more aggressive than common spiny mice, and this is surprising considering that common spiny mice displace golden spiny mice from their optimal activity pattern (Shkolnik 1971). The common spiny mouse is geographically the more widespread of the 2 species (Mendelssohn and Yom-Tov 1999) and exploits a wider range of habitats (Jones et al. 2001; Shargal et al. 2000). Our results are expected in various models of coexistence, with the larger species (in this case, the golden spiny mouse) the more restricted in range and habitat use and the more dominant behaviorally over the wide-ranging species (Glazier and Eckert 2002). Glazier and Eckert (2002) tested 2 alternative models, one predicting widespread species have greater competitive abilities than related species with narrow ranges, whereas the other predicts the opposite pattern. Their measure for competitive ability was aggressive agonistic behavior as reported in the literature surveyed, and their results support a model of greater competitive ability (i.e., aggression) of geographically restricted species.

In sum, examination of our present data does not support interference (aggressive) competition as the driving force in the competitive interaction between these 2 species. Other mechanisms, such as exploitative competition, may drive temporal partitioning and coexistence in this rocky desert rodent system.

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