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

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Interspecific competition has ecological implications for foraging strategies, microhabitat use, and activity patterns of desert rodents. Here we studied a system in which two 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. In order to test whether aggression is the driving force in this exclusion, we placed pairs of these 2 species in an experimental laboratory arena, videotaped their interactions, and later analyzed tapes for aggressive agonistic behaviors, overall activity, and ability to obtain a shared resource (mealworms). 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.

Interspecific competition is an important ecological interaction among desert rodents (Kotler and Brown 1988, Kelt et al. 1999). It 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 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*) 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,b,c; 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" (p. 116). Gutman and Dayan (2005) who repeated this study in replicated and controlled conditions found that while golden spiny mice remained primarily day active, in absence of common spiny mice they were active also 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 hours 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 of spiny mice at Ein Gedi, near the Dead Sea, where both species coexist, revealed that while 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 appear to be nocturnally adapted also in their capacity for non-shivering thermogenesis (Kronfeld-Schor et al. 2000) and in the eye structure (Kronfeld-Schor et al. 2001b). Thus Kronfeld-Schor and Dayan (2003) suggested that while 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 two 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 two 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 at 28?, as in previous studies (Freidman et al. 1997; Kronfeld-Schor et al. 2000, Zisapel et al. 1999) and a 10L:14D cycle, with standard rodent food pellets and water provided ad libitum. All mice were in good physical condition.

Observations were carried out in a cage (50 by 132 by 49 cm) with a transparent glass floor and opaque walls. A mirror was tilted underneath the cage at 45º angle, providing a bottom view of the cage and the insides of 2 overturned clay pots that were provided as shelter. Similar pots are used for shelter in the home cages of spiny mice at the research zoo. The chamber was illuminated by a 12v DC infrared light (model IP68, Tracksys, Nottingham, England) 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 (see video, Eilam et al., 2003). The video image and a time code (generated by T5010 and LTC-VITC translator T800, Telcom Research, Burlington, Canada) were recorded on a VCR. The entire system was in a darkened room with a level of illumination measured during testing of 0.0425 Lux (Gossen, Profisix Sbc, Nürnberg, Germany).

Experiments were conducted during 2 consecutive weeks (September 11-24, 2001). Mice were assigned to 12 heterospecific pairs. Mice were paired so as to minimize body mass differences between individuals of both species; while 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 ± 15 (range: 41.5 - 95.7) gr for common spiny mice and 57 ± 18 (range: 37.3 - 95.8) gr for golden spiny mice. It should be noted that while the effect of body mass difference was counterballanced in the present study by the above pairning, mean body mass in free-living populations in En-Gedi region (the origin of our captive colonies) is: common spiny mice – males 35.2 ± 0.7, females 32.0 ± 1.3; golden sping mice – males 44.1 ± 0.6, females 41.0 ± 1.1 gr (Shargal et al. 2000). Consequently, a possible competitive adavantage of golden spiny mice due to their higher body mass was mininmized in the present experimental design.

Six pairs were tested in the dark, one hour before sunrise and then tested again a week later one hour 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 also to being active during the night in absence of its congener, while 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 mice which is adapted to both day and night vision, as opposed to the common mouse which is adapted only to night vision (Kronfeld-Schor et al. 2001a,b). 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 to each side of an opaque glass divide in midchamber that prevented visual and physical contact. After 30 minutes of habituation, the glass was removed allowing the mice to establish contact and behavior was videotaped for 60 minutes. Every 10-15 minutes, the experimenter placed in the center of the arena a mealworm (*Zophobas moria*), which is a favorite food item for both species in captivity, in order to observe how they competed for the food. In order not to interfere with ongoing behavior, mealworms were placed every 10-15 minutes in the middle of the arena, when the mice were not in the area, but in their nests or interacting in one 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 by Telcom Research, Burlington, Canada). 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 = 20cm. 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 in order to describe the distribution of activity of each individual: Latency = time (sec) to cross to the other side of the arena from where mouse was habituated. Traveled distance = cumulative distance (m) traversed by each individual during the observation. Time in opposite side = cumulative time (% 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. Since the behavioral data may not be strictly independent, we used the false discovery rate method (FDR; Benjamini et al. 2001) in order to adjust *P* values for multiple comparisons within behavioral categories. Consequently, *P* values for parameters of aggressive behavior were set by FDR to 0.025, and *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 (PM: $P = 0.009$; AM: $P = 0.016$; Wilcoxon matched-pairs signed-ranks) and biting (PM: $P = 0.032$; AM: $P = 0.016$), and a higher incidence of escape was initiated by common spiny mice (PM: $P = 0.01$; AM: $P = 0.05$). However, there was no significant difference in the incidence of either taking food from the center of the arena (PM: $P = 0.82$; AM: $P = 0.28$) or food theft (PM: $P = 0.4$; AM: $P = 0.83$) see Figure 1.

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

There was no significant correlation between the differences in behaviors and body mass (see Methods for details). 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 while 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 partition was removed at the beginning of the encounter.

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 one of these species is more aggressive – it would be the common spiny mouse. Our results, however, are counter to this expectation: the golden spiny mouse is the more aggressive, whereas the common spiny mouse is certainly not “the more vigorous kindred” as previously suggested (Shkolnik 1971). While parameters that were used to measure aggressive behavior did not always reach statistical significance, for each and every pair studied in our experiments, golden spiny mice consistently traveled throughout the test chamber as if displaying more confident space use (Table 1) and consistently displayed overt aggressive behavior towards common spiny mice. Despite differences between AM and PM testing, aggression of golden spiny mice was prevalent in both early and late night testing (Figure 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,b). Thus, the time framework of our research was such that in this respect 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 patches in experimental settings, confirming that aggression is a driving force in this competitve interaction. In our study, pairs were selected to minimize the difference in body mass between individuals of the 2 species, and in consequence minimize the possible effect of body mass on the higher aggression exhibited by golden spiny mice. Moreover, there was no significant difference between the pairs in which common spiny mice were the heavier individual, 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 the two species display distinct preference community organization (predicted in models developed by Rosenzweig 1981). That being the case, aggression need not be expected. While this hypothesis may be viable at the ecological time scale, at the evolutionary time scale we have already shown that the golden spiny mouse appears to be a nocturnal species displaced into diurnality. 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 found that in laboratory settings, the common spiny mouse took over the nest of the golden spiny mouse within 24 hours, 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 *A. cahirinus* and *A. russatus* 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 *A. cahirinus* and *A. russatus* 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) in their study showed that when food was restricted in the laboratory, *A. russatus* shifts its metabolism rhythm from nocturnal to diurnal. Thus, feeding preferences and food habits, but not aggression may induce the change in activity time.

Another possible cue for the displacement of *A. russatus* from nocturnal to diurnal activity is chemical signals released by *A. cahirinus*. Exposure of naïve *A. russatus*, maintained in a light-dark cycle, to *A. cahirinus* urine and feces 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 *A. cahirinus* caused a shift of 3 h (Haim and Fluxman 1996), 2 h (Fluxman and Haim 1993) or 45 min.

(Freidman et al. 1997) in body temperature (Fluxman and Haim 1993, Freidman et al. 1997), activity (Freidman et al. 1997), and oxygen consumption (Haim and Fluxman 1996) rhythems, respectively. The authors suggested that chemical signals of *A. cahirinus* released into the common environment may play a role in the displacement of *A. russatus* 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 1987) 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 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 two alternative models, one predicting greater competitive abilities of widespread species of related species with narrow ranges, while 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 (that is, aggression) of geographically restricted species.

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

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TABLE 1. - Behaviors (mean ± SE, *n*=12) of both common and golden spiny mouse species during testing before dawn of after dusk. The adjusted P level (False Discovery Rate method, Benjamini et al., 2001) for statistical significance was set to *P* = 0.004.

	Acomys cahirinus		*ny russatus*		*P*-value	
	Before dawn	After dusk	Before dawn	After dusk	Before dawn	After dusk
Activity						
Latency (sec)	744.3±106.1	183.8±13	139±39.5	82.83±8.4	0.028	0.075
Traveled distance (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

FIGURE 1. - Mean incidence (± SE) of the different behaviors (bite, chase, escape, food theft and take food from center) after dusk (p.m.) and before dawn (a.m.) of *A. russatus* (open bars) and *A. cahirinus* (dark bars). * indicates that *P* value < 0.025 (set as significant after FDR adjustment for multiple testing).