

COEXISTENCE OF TEMPORALLY PARTITIONED SPINY MICE: ROLES OF HABITAT STRUCTURE AND FORAGING BEHAVIOR

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Abstract. Two coexisting species of spiny mice in rocky deserts in Israel temporally partition activity in opposite parts of the diel cycle. *Acomys cahirinus* is nocturnal and *A. russatus* is diurnal, although it becomes nocturnal if its congener is experimentally removed, suggesting that the temporal partitioning is driven by interspecific competition. Such extreme temporal partitioning within the diel cycle has not previously been recorded elsewhere among mammals. Using artificial food patches, we studied microhabitat use and foraging efficiencies under seasonally variable predator regimes and physiological pressures to assess the roles that habitat structure and foraging behavior might play in coexistence. The two species showed trade-offs in foraging efficiency leading to different strategies of microhabitat use that may help promote coexistence. *A. cahirinus* is a “cream skimmer,” a relatively inefficient forager that gives up at relatively high giving-up densities, and a habitat generalist; whereas *A. russatus* is a habitat specialist, perhaps compensating for this restricted niche by foraging very efficiently to low giving-up densities. Seasonal shifts in foraging microhabitat suggest that the response to predation risk from snakes in summer overrides and opposes the effects of physiological costs and risk from owls and diurnal raptors, leading to increased predatory risk and foraging microhabitat overlap in summer. Temporal partitioning of the food resource may compensate for decreased partitioning of the habitat resource in summer. Provision of cover was more important than escape distance in determining habitat and microhabitat use. Boulder fields in rocky deserts provide a physical structure that is more complex and provides more continuous cover than is available in open deserts, where most research on community structure of desert rodents has been carried out. We propose that this physical structure of rocky deserts, in conjunction with the desert adaptations of *A. russatus*, may enable the extreme temporal partitioning to opposite parts of the diel cycle and, therefore, contributes to coexistence in this community.

Key words: *Acomys*; coexistence; foraging; giving-up densities; habitat structure; microhabitat partitioning; predation risk; predator enhancement; rocky deserts; rodent communities; spiny mice; temporal partitioning.

INTRODUCTION

Niche differentiation in heterogeneous environments has long been considered a major mechanism of coexistence among competing species in ecological communities (e.g., MacArthur and Levins 1967, May and MacArthur 1972, Schoener 1974, 1986, Kotler and Brown 1999). Species separation along niche axes, usually involving several dimensions such as habitat, food, and time, should result in decreased overlap in resource use, which may reduce competition and enhance coexistence. One model for studying species coexistence (Brown 1988) applies optimal foraging theory (Emlen 1966, MacArthur and Pianka 1966) to concepts of niche partitioning (MacArthur 1958, Schoener 1974). In this trade-off theory, each species has a part of each niche axis on which it is superior to its competitors (Brown 1989). Coexistence is allowed when each species by itself leaves sufficiently profitable conditions on one

or more niche axes for other species to experience positive fitness (Kotler and Brown 1999).

The majority of ecological studies dealing with coexisting competitors view habitat or microhabitat partitioning to be a primary mechanism of coexistence (e.g., Dickman et al. 1983, Price 1986, Rosenzweig 1987, Kotler and Brown 1988, Abramsky et al. 1990b, Brown et al. 1994, Morris 1996). Classical theories propose that coexistence may operate through microhabitat choice (Rosenzweig 1987, Morris 1996), and there are several models to explain this. Under the trade-off theory, coexistence in a habitat and microhabitat mosaic is possible if there are foraging trade-offs between species, either behavioral or evolutionary (morphological or physiological), in the efficiency with which resources can be converted to new biomass (Brown et al. 1994, Vincent et al. 1996), in relative ability to avoid predation (e.g., Kotler 1984, Brown et al. 1988, Lima and Dill 1990), or in both. Under this scenario, by virtue of their behavioral, morphological, or physiological traits, different species tend to perform better in different habitats, differing in foraging efficiency on different substrates, including food encoun-

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ter efficiency, handling time, or conversion efficiency (Brown 1996, Vincent et al. 1996), or in ability to avoid predation.

Dietary partitioning among guilds of granivorous or predatory species typically occurs on a predator size/food size axis, with larger species tending to select larger average seed or prey size (e.g., Brown and Lieberman 1973, Dayan and Simberloff 1994, Jones 1997, Jones and Barmuta 1998). For this to function as a mechanism of coexistence, each species must differ in their ability to handle or digest different foods (Kotler and Brown 1999).

Theoretically, temporal segregation can reduce the per capita impact of one forager on the prey available to the other species, thereby facilitating coexistence. Mechanisms include different activity times for different prey species and rapid turnover of the shared food resource within the period involved in the temporal segregation (Schoener 1974). The hypothesis of temporal partitioning of rapidly renewable resources has recently gained support from studies of granivorous rodents foraging on shifting dune systems where winds uncover and redistribute seeds on a daily basis (Kotler et al. 1993, 1994, Ziv et al. 1993). However, the few studies dealing with predators have failed to confirm that temporal differences in activity result in the taking of prey that are differentially available during different hours of the day (reviewed by Schoener 1986).

Two decades of thorough and insightful research on the community ecology of desert rodents has contributed substantially to our understanding of and the development of theory about the role of ecological interactions and environmental heterogeneity in structuring animal communities. Studies of coexistence among desert rodents have focused on habitat and microhabitat partitioning on spatially variable resources, differences in foraging efficiency, food particle selection, and aggressive interference among open desert rodents (e.g., Price 1986, Bowers et al. 1987, Brown 1987, 1989, 1996, Kotler and Brown 1988, 1999, Abramsky et al. 1990b, Brown et al. 1994, 1999, Dayan and Simberloff 1994, Hughes et al. 1994, Rosenzweig and Abramsky 1997). Temporal partitioning within the nocturnal phase of the diel cycle has recently received attention (Kotler et al. 1993, 1994, Ziv et al. 1993).

However, nearly all studies of desert rodents have been conducted on granivorous rodent communities that dwell in sandy (or loess) deserts, just one of two major desert types. Little is known about rodents in rocky deserts, a physical environment that differs in structure dramatically from sandy deserts in ways that may substantially influence how predation risk is manifested and, hence, have implications for habitat use and coexistence of the rodent community. While sandy deserts range in structure from unstable sand devoid of vegetation to quite well-vegetated areas of stabilized soil (Rosenzweig and Abramsky 1985), the type of shelter that they provide for rodents is essentially iso-

lated shrubs in an expanse of open space (Brown et al. 1988). Rocky deserts also incorporate a range of structures, from small cobbles embedded in a hard soil crust grading to giant boulder fields at the base of cliffs. While the cobble habitats provide little cover for rodents, the boulder fields provide a structurally more complex and more continuous sheltered habitat than is available in sandy deserts. Prior to this research, only two studies had included rocky desert rodents: one on density-dependent habitat selection among sandy and rocky desert rodents, which included both cobble and boulder sites (Rosenzweig and Abramsky 1985), and one on mechanisms of coexistence among avian and mammalian desert granivores that included cobble habitat (Kotler and Brown 1999).

In the rocky deserts of southern Israel exists a very interesting model system with which to examine the roles of the physical structure of the environment, climatological forces, and interspecific interactions in coexistence. Two species of omnivorous spiny mice (Genus *Acomys*; Family Muridae), both specialized lithophiles, coexist in the boulder fields, and adjacent cobble habitat of this rocky desert. Most interestingly, they exhibit extreme temporal partitioning between congeners, to opposite parts of the diel cycle, which is otherwise extremely rare among mammals. This temporal partitioning has been shown to result from interspecific competition (Shkolnik 1971) and is especially interesting because the species displaced into a diurnal activity mode does so in a hot desert where daytime summer temperatures can exceed 40°C. Another consequence of the temporal partitioning is that the two species experience different predator regimes. So here we have the interplay between physical structure of the habitat, foraging behavior, dietary partitioning, temporal partitioning, climatological forces and consequent physiological pressures, and predation pressures, in a rocky desert. This paper represents a part of the first major study to address community structure of rocky desert rodents.

Our specific aim in this paper is to assess the roles that the rocky desert habitat structure and foraging behavior might play in coexistence of these two species of temporally partitioned spiny mice. To this end, we used artificial food patches to study microhabitat use and foraging efficiencies. We set up experimental comparisons to address the following questions: (1) Are there differences in microhabitat use and foraging efficiencies that might function as mechanisms of coexistence between these two competitors? To answer this, we compared foraging microhabitat preferences and foraging behavior of the diurnal *A. russatus* and nocturnal *A. cahirinus* in winter and summer. (2) How does seasonal variation in predator regimes influence species' differences in foraging habitat use and foraging efficiencies and, therefore, coexistence? We compared foraging microhabitat preferences and efficiencies between summer, when snakes were active, and

winter, when snakes were absent. (3) How does seasonal variation in physiological costs of foraging activity influence species' differences in foraging habitat use and foraging efficiencies and, therefore, coexistence? We compared foraging behavior of *A. russatus* between summer (high light levels, high daytime and mild nighttime temperatures) and winter (lower light levels, mild daytime and low nighttime temperatures) in all-day experiments and in just the cool hours of the day (early morning and late afternoon), thus factoring out the high costs of *A. russatus* being active in the middle of the summer day.

THE STUDY SYSTEM

Acomys russatus and *A. cahirinus* are similar in morphology, gross habitat requirements (Shargal 1997), and diet (Degen et al. 1986, Kronfeld and Dayan 1999) but exhibit extreme temporal partitioning. The common spiny mouse, *Acomys cahirinus*, is active during the night, and the golden spiny mouse, *Acomys russatus*, is diurnal. A key study showed that if the nocturnal species, *A. cahirinus*, is experimentally removed from the shared habitat, *A. russatus* shifts its activity time and becomes nocturnal (Shkolnik 1971). Shkolnik (1971) ascribed this phenomenon to the Gaussian principle of competitive exclusion and suggested that *A. russatus* is driven into a diurnal activity mode by its "somewhat more vigorous" (albeit smaller) congener. That *A. russatus* shifts back to nocturnal activity in the absence of *A. cahirinus* implies that the two species compete, and that the fitness cost of diurnal activity for *A. russatus* is higher than the cost of being nocturnally active in the absence of *A. cahirinus*. This fitness cost may be physiological (coping with different temperature and light conditions), ecological (predation pressure), result from evolutionary constraint (Kronfeld-Schor et al. 2000a), or be a combination of all.

How are the likely mechanisms of coexistence operating? For temporal partitioning to be effective in promoting coexistence requires that food resources are renewable or that prey species are active at different times of the diel cycle. Analysis of feeding preferences and food habits show that spiny mice subsist on vegetation, seeds, and invertebrates (Degen et al. 1986, Kronfeld and Dayan 1999), seasonally including snails (Abramsky et al. 1990a, 1992). Vegetation and seeds are unlikely to be renewed frequently in the hard soil environment of rocky deserts and so do not provide the opportunity for temporal partitioning. Both species are much more predatory during spring and summer. 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 and Dayan 1999). Because the arthropod prey of *A. cahirinus* and *A. russatus* are likely to show diurnal patterns in availability, temporal partitioning could well promote resource partitioning and coexis-

tence. This is yet to be confirmed, though, as specific identification of the arthropod prey has not yet been possible.

An alternative hypothesis is that *A. russatus* is aggressively excluded into diurnal activity by *A. cahirinus*. *A. russatus* is able to withstand diurnal conditions by virtue of its desert adaptations, such as high thermal tolerance, extremely low field metabolic rate, and low water requirements (Shkolnik 1966, Degen et al. 1986, Kam and Degen 1991, 1993, Merkt 1991), but the shift does not significantly reduce resource overlap between the two species (Kronfeld and Dayan 1999), or it may do so only during the summer months while in winter the two species overlap significantly in a largely vegetarian diet. Kronfeld and Dayan (1999) argue that food and not shelter sites is the factor limiting population densities of both species at Ein Gedi, our study site in Israel. In this scenario, an alternative mechanism of coexistence, possibly based on habitat partitioning, must be operating. The spiny mice overlap in their gross habitat requirements, although *A. russatus* uses the boulder microhabitats almost exclusively whereas *A. cahirinus* uses open areas as well (Shargal 1997).

The two species of mice are subject to different physiological pressures and predators, by virtue of their activity patterns at opposite parts of the diel cycle. Physiological heat stress during summer in hot deserts is considerable, so most small mammals are nocturnally active, spending the day in burrows and other shelters that provide a favorable microclimate (Schmidt-Nielsen 1964, Shkolnik 1988). In the Judaeen Desert, the combined effects of hot daytime temperatures in summer (average daily maximum is 38°C) and a low average annual rainfall (80 mm, Jaffe 1988) may make daytime activity in the open very inhospitable for a mouse. A recent physiological study using the doubly labeled water technique supports this contention (Kronfeld-Schor et al. 2001). This study, however, also suggests a higher energetic cost to nocturnal activity of *A. cahirinus* during winter, which probably reflects the cost of thermoregulating during cold winter nights (Kronfeld-Schor et al. 2001).

Spiny mice are preyed upon by Blanford's foxes (*Vulpes cana*, although they form only a small part of the fox's diet, Geffen et al. 1992), owls (Hume's Tawny Owl, *Strix butleri*, Mandelik 1999), snakes (saw-scaled viper, *Echis coloratus*), and probably also diurnal raptors (Common Kestrel, *Falco tinnunculus*). Indirect evidence for the evolutionary importance of predation are spines on spiny mouse rumps, a histological mechanism for tail loss (both are more marked in *A. russatus*, Shargal et al. 1999), relative immunity to the venom of the saw-scaled viper *Echis coloratus* (so far studied only in *A. cahirinus*, Weissenberg et al. 1997), and a reduction of foraging by *A. cahirinus* in open areas in response to moonlight (Mandelik 1999).

Risk of predation by avian and mammalian predators is a threat year-round, particularly in open areas, as

structurally complex microhabitats interfere with aerial attacks on prey (Kotler et al. 1988, Longland and Price 1991). However, physiological stress, whether heat or cold, is seasonal, as is risk of predation by vipers, which are inactive in winter. Physiological stress will be a factor primarily in open areas on summer days (heat) for *A. russatus* and possibly on winter nights (cold) for *A. cahirinus*. Predation by vipers will be a threat primarily under boulders during the day (where these nocturnal sit-and-wait predators rest curled up), and during the night, both under and between boulders and in open areas, habitats where the snakes are either lying still or actively moving at night (Mendelsohn 1965; Hadas Hawlena, unpublished data).

METHODS

The technique

We measured giving-up densities (GUDs) in artificial food patches to provide information on habitat and microhabitat use and foraging efficiencies, particularly in relation to physiological and predation pressures as perceived by the mice. This technique, developed by Brown (1988), assumes that a forager is behaving optimally and that the density of food remaining in the patch when it gives up foraging should correspond to a harvest rate (H) at which the energetic gain from foraging just balances the metabolic cost of foraging (C), the cost of the risk of predation in foraging in that patch (P), and the missed opportunity cost (MOC) of not foraging elsewhere or indulging in other life maintenance or social activities that have a fitness component. Thus, the quitting harvest rate satisfies $H = C + P + \text{MOC}$. To these components, Kotler and Brown (1988) and Bouskila (1995) add the cost of interference competition. GUDs, besides being a measure of quitting harvest rate, are also a measure of foraging efficiency, the extent to which an individual can profitably harvest resources at very low resource abundances (Brown 1988, 1989). Our use of a standard artificial food patch maintained similar metabolic costs of foraging associated with digging for food at each artificial patch and similar missed opportunity costs from not foraging in other artificial food patches across species, seasons, and experiments. However, metabolic costs of foraging can vary between species owing to anatomical and physiological differences. It can also vary between seasons as climatological and therefore, physiological conditions for foraging varied separately for the nocturnal and diurnal species. There also would be seasonal and species differences in the missed opportunity costs associated with both foraging in natural food patches and changing social factors such as reproduction.

Our artificial food patches consisted of aluminum trays ($30 \times 20 \times 4$ cm, a size that fitted easily under boulders) containing 2 L of finely sifted local soil, which preserved clear mouse footprints, and 2 g of

crushed and sieved sunflower seed (1–2 mm diameter) mixed thoroughly together. Preliminary trials, in which captive and free-ranging *A. cahirinus* and *A. russatus* were presented with a choice of food types (sunflower, millet, commercial cat food, commercial rat pellets, red and brown lentils, barley, rice, split green peas, white and borlotti beans, sesame seeds, and buckwheat), revealed that of the highly preferred foods (sunflower, cat food, and rat pellets), sunflower was the easiest to crush to a uniform size and clean of soil debris. Also during preliminary trials, we measured giving-up densities over a wide range of initial seed densities (0.5–6 g). Within a microhabitat, giving-up densities were independent of initial density (M. Jones, personal observations), thereby satisfying the assumptions of the giving-up density technique that the mice were using a quitting harvest rule and that the results are not distorted from the mice becoming satiated or finding the trays too late in the day (Brown 1989). Frames constructed from heavy wire and fine-filament fish netting kept birds out of the trays during the day. Mice reached the trays easily by biting through one strand in the net, but to ensure that any consequent foraging costs were equal across species and treatments, frames (with mouse holes in the netting repaired morning and night) were used both day and night and in all microhabitats. Frames for uncovered sites measured $40 \times 60 \times 30$ cm, a minimum size that effectively excluded birds from reaching the trays, whereas those for under-boulder sites (crevices) were necessarily smaller ($30 \times 40 \times 20$ cm).

Compared with rodents from sandy deserts, spiny mice do not have much opportunity to dig for seed in the compacted soils and cramped space of their natural habitat. During the four weeks of preliminary trials, we habituated the mice to the experimental setup, both to digging freely in the trays for sunflower seed and to the location of each tray. Each experiment was preceded by three days or nights of pre-baiting to ensure that the trays had been discovered before the experiment commenced.

Trays were set out at dawn or dusk and the remaining seed collected at dusk or dawn, respectively. At the end of each experimental period we identified (to genus) and recorded footprints in the trays and quickly covered the trays so that there would be no foraging by the nontarget species after it turned dark or light, as the case may be (e.g., from *A. russatus* when clearing the previous night's experiment). Because it took time to sieve the trays that had been foraged (usually between 5 and 15 trays), we split this time evenly between light and dark so as to take time equally off the natural foraging period of either species. That is, if it took 40 min to sieve the trays, we started sieving 20 min before, and finished 20 min after dawn or dusk, respectively. For the same reason, we alternated the starting point for the sieving at opposite ends of the study site on a 24-h basis. The trays were then sieved and the re-

maining seed from trays that had been foraged by *Acomys* spp. collected and weighed. Trays, including those foraged by other rodents or birds, were then replenished with preweighed aliquots of seed and set up for the next day or night. All trays that had not been visited were sieved and replenished with new seed every second day.

We conducted experiments lasting all day and all night for five consecutive days in winter and three consecutive days in summer to compare the foraging habitat preferences and efficiencies of *A. russatus* and *A. cahirinus* at different periods of the diel and seasonal cycles when different predators are active. In addition, we carried out an experiment in which the trays were opened for only 2 h each in the early morning and late afternoon, when sun angles were low and it was cooler and less bright. We set up the experiment at dawn; then, after recording foraging by different species from footprints in each tray, covered the trays with mouse-proof lids 2 h after dawn. We removed the lids 2 h before dusk later in the same day and then recorded foraging and collected the seed at dusk. This "cool hours experiment" was repeated for 3 d each in winter and summer.

Study area

We conducted the experiments simultaneously at two replicate sites, the Field School site, and the Kibbutz site, in the Ein Gedi Nature Reserve, on the steeply sloping escarpment of the Judean Desert near the Dead Sea in Israel (31°28' N, 35°23' E, 300–325 m below sea level). Mouse populations at the two sites were independent for the duration of the study as they were separated by 2 km and two deep canyons (Elvert et al. 1999, Shargal et al. 2000). We selected two linear sections of a discrete habitat boundary formed by the edge of a scree of large boulders (boulder habitat, B) at the foot of cliffs and the open slope or shelf (open habitat, O) below, characterized by small rocks (cobbles) with isolated larger rocks. Within each of the two main habitats, two microhabitats were defined representing different degrees of shelter or distance from shelter and presumably different levels of risk from predation. The resultant four microhabitats represented a gradient in features of habitat structure that relate to shelter from predators and climate.

The boulder habitat comprised jumbled rocks up to 2 m in diameter and provided continuous shelter for the mice in the interstices under and between the boulders. Seed trays in the under boulder (UB) microhabitat were placed completely under boulders, in interstices large enough that a mouse could comfortably forage in the tray, but not large enough to permit a fox, owl, or kestrel to pounce easily. The under boulder seed tray sites had sheltered access to the continuous boulder field. Between boulder (BB) tray sites were within 2 m of the continuous boulder field. A mouse foraging

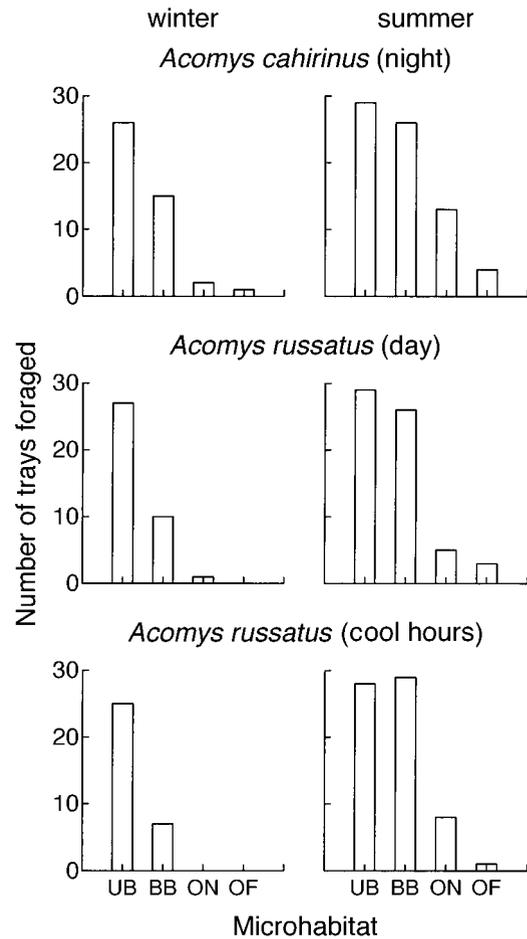


FIG. 1. The number of trays foraged in each microhabitat by *Acomys cahirinus* (trays open all night) and *Acomys russatus* (trays open all day or in the early morning and late afternoon cool hours only) in winter and summer. Total number of trays available = 40. Microhabitats: UB, under boulder; BB, between boulder; ON, open near; OF, open far.

in a between boulder tray had no overhead cover, but could run in at least three directions to reach shelter.

The open habitat comprised numerous small rocks on the surface of the ground and isolated boulders, which were generally in full contact with the ground surface and offered no refuge. To reach shelter from the open habitat, mice had to run back to the boulder field in one direction only. The two microhabitats where seed trays were placed were thus defined by escape distance: open near (ON) was 2.5 m from the edge of the continuous boulder field and open far (OF) was 5 m from shelter.

Seed tray stations were arranged such that the trays in the two microhabitats within each major habitat type (boulder or open) were placed 2.5 m apart. These pairs of trays in the two major habitat types were situated 10 m apart because the transition from continuous boulder field to open habitat was gradual rather than abrupt. Thus, each station comprised a total of four seed trays,

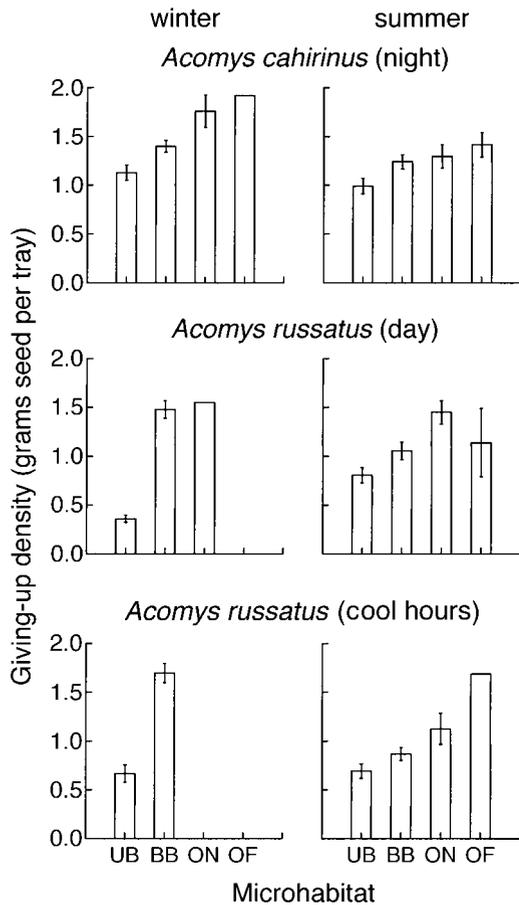


FIG. 2. Giving-up densities (means \pm 1 SE) in each microhabitat for *Acomys cahirinus* (trays open all night) and *Acomys russatus* (trays open all day or in the early morning and late afternoon [cool hours only]) in winter and summer. Zero values mean that no trays were foraged in those microhabitats. Abbreviations are as in Fig. 1.

one in each of the four microhabitats, providing a choice of foraging sites for the mice. Five stations were placed at each study site, a total of 40 trays per night ($n = 20$ at each site; 10 in each microhabitat). Within a site, stations were placed 30 m apart, a distance based on daily movements known from trapping records (Shargal 1997) that was designed to minimize the possibility of the same individuals feeding in more than one station.

The overwhelming majority of small mammals in the rocky habitats at Ein Gedi are spiny mice (Shargal 1997). Other nocturnal rodents included the larger *Sekeetamys calurus*, and the smaller, very scarce and also nocturnal *Gerbillus dasyurus*. Foraging in trays by either species (and by birds) could be easily distinguished from *Acomys* by the size of their footprints. The quantity of food provided in a previous trapping study (Shargal et al. 2000) was greater than that provided by the seed trays; yet this quantity did not precipitate a shift in activity times of *A. russatus* (Kronfeld 1998), so

such a shift was not expected in our present study. Therefore, we could safely assume that *A. cahirinus* were responsible for the *Acomys* footprints in the trays from nocturnal foraging and that *A. russatus* were responsible for the diurnal foraging.

Statistical analyses

We derived two types of data from the field study: the number of trays foraged in a given microhabitat and the giving-up densities in those trays. The number of trays where mouse footprints or digging activity were recorded provides an indication of the extent of foraging in that microhabitat or situation. These data are confounded, however, with population size. More mice of one species, at one site or in one season, mean that it is more likely that a tray in a given habitat will be found by a mouse. Population size of *A. russatus* was greater than *A. cahirinus* at both Field School and Kibbutz sites (Elvert et al. 1999, Shargal et al. 2000) and may change seasonally, in particular increasing in the summer breeding season. Accordingly, comparisons of the number of trays visited between, but not within, seasons and species may reflect relative population size. To account for this, we analyzed the per capita tray foraging rate between the species, using population data for the Kibbutz (Shargal et al. 2000) and Field School (Elvert et al. 1999) sites, respectively. We analyzed differences in the number of trays foraged using a contingency table approach. Initially, we tested for differences among groups of trays, sites, and nights using one-way chi-square tests across each habitat and microhabitat. The main effects (species, seasons, and microhabitats) were analyzed using multiway frequency analyses and log-linear modeling (Version 7.0, SYSTAT 1997). All first order effects (number of trays foraged, species, season, and microhabitat) were fixed in the model; only second and higher order effects that included the interaction of the dependent variable (number of trays foraged) with the independent variables were of interest (Tabachnik and Fidell 1989). One four-way analysis (species, season, microhabitat, and number of trays foraged) and three three-way analyses (season, microhabitat, and number of trays foraged for the day- and the night-long experiments for *A. cahirinus* and *A. russatus*, respectively, and the cool hours experiment for *A. russatus*) were conducted. Results for the separate three-way models for each species are presented as well as for the four-way model, both for comparison with the cool hours experiment (*A. russatus*) and because there are biologically interesting but statistically nonsignificant patterns in microhabitat use that are otherwise masked.

Giving-up densities, represented by the mass of seed left in the tray, provided us with information about the foraging decisions of the mice once they had commenced foraging in a tray. Giving-up densities should be independent of the number of mice (one or more than one) that have visited a tray as foraging decisions

for each individual depend on the harvest rate in the tray at the time (Brown 1988). Initially, we used Mann-Whitney U tests or Kruskal-Wallis tests to check for differences among groups of trays, sites, and nights across each habitat and microhabitat for each species. Nonparametric statistics were used because the data were not normally distributed, even after logarithmic or square-root transformations, and in *A. cahirinus*, variances were heteroscedastic among microhabitats. We performed a three-way ANOVA on rank-transformed means of GUDs to test for differences, including possible interactions, between species, seasons, and microhabitats (Conover and Iman 1981, Brown et al. 1994). For this analysis, data for the open near and open far microhabitats were combined as sample sizes in both categories were too small in winter. The one open habitat category was then compared with the two boulder microhabitats. We justified keeping the boulder microhabitats separate as the preliminary analyses had shown that the significant differences among microhabitats were between the boulder and open habitats, and between the under boulder and between boulder microhabitats with less difference between the two open microhabitats.

RESULTS

In our initial checks for foraging differences among sites, groups of trays, and dates, we found no differences in the number of trays foraged for either species (all $P > 0.05$) or in the GUDs among sites or dates. There were some differences in GUDs among groups of trays in the winter experiments. We found differences among groups of trays in the UB microhabitat for *A. cahirinus* ($n = 46$, $G = 20.54$, $df = 9$, $P = 0.015$) and in the BB microhabitat for *A. russatus* ($n = 16$, $G = 10.17$, $df = 4$, $P = 0.038$). These differences may relate to variation in the structure of the boulder habitat near its margin with the open habitat. Despite our efforts to select tray sites that satisfied a defined set of criteria, at least one group of trays in a section of the boulder field had less cover and connectedness to the continuous boulder field than other areas. Differences in the UB microhabitat for *A. cahirinus* may also reflect differences in the level of artificial illumination from the Ein Gedi settlement that reaches each line (Mandelik 1999). As this variation represents the habitat as actually experienced by the mice, we pooled the data for groups of trays as well as those for sites and dates.

Acomys cahirinus and *A. russatus* showed a strong gradient in foraging behavior in summer and winter. Both species foraged most in the UB microhabitat and less in the open microhabitat, with *A. cahirinus* foraging least in the OF microhabitat (Figs. 1 and 2). Both species foraged the most trays (microhabitat-by-number-of-trays foraged term in the four-way model, and in three-way analyses for *A. cahirinus* and *A. russatus*, Table 1) to the lowest giving-up densities (microhabitat

term, Table 2) in the UB microhabitat within the boulder field, followed by the BB microhabitat, the ON microhabitat and with the least trays foraged to the highest GUD in the OF microhabitats in the open habitat (Figs. 1 and 2). The standardized log-linear parameter estimates (Table 1) indicate that the foraging microhabitats most important in determining the relative strength of the effects were first, under boulders, and second, the two open microhabitats (effects with the largest standardized parameters are the most important in influencing the expected frequency of a cell, Tabachnik and Fidell 1989). These patterns also held for *A. russatus* in both seasons even when the trays were open only in the cool hours of the day (microhabitat-by-number-of-trays foraged term in the three-way model of cool hours experiment, Table 1, Fig. 1; microhabitat term, Table 2, Fig. 2).

Both species foraged a similar number of trays in each of the microhabitats (no species-by-microhabitat term in the four-way model, Table 1; Fig. 1), although there was a trend for *A. cahirinus* to forage more trays in the less protected microhabitats (BB, ON, and OF in winter and ON and OF in summer) than *A. russatus* (Fig. 1). *Acomys russatus* was present in much higher density than *A. cahirinus* at both sites, yet a similar number of trays were foraged by each species (Table 3). This gave rise to a significantly greater number of trays foraged per capita by *A. cahirinus* (separate variances; $t = 10.689$, $df = 2$, $P = 0.051$), indeed almost twice that of *A. russatus* (Table 3). There was no difference between sites in the number of trays foraged per capita (separate variances; $t = -0.104$, $df = 2$, $P = 0.927$). There were seasonal differences for both species in the number of trays foraged (four-way and three-way analyses for both species, all-day experiments, Table 1). Both species foraged more trays in all microhabitats in summer than in the winter (Fig. 1). Seasonal differences in the number of trays foraged were not consistent across microhabitats (season-by-microhabitat term, four-way analysis, Table 1) probably because of the greater seasonal change in foraging in the between boulder microhabitat in *A. russatus* (season-by-microhabitat term in three-way analysis, Table 1), but not *A. cahirinus* (season-by-microhabitat term in three-way analysis, Table 1; Fig. 1).

Acomys russatus showed similar seasonal patterns in the number of trays foraged whether the trays were open all day or just in the four cooler hours (Fig. 1). More trays were foraged in the more open microhabitats in summer than in winter (season-by-number-of-trays foraged term in *A. russatus* cool-hours analysis, Table 1) and the pattern of foraging across microhabitats was different between summer and winter (season-by-microhabitat term in *A. russatus* cool-hours analysis, Table 1) for the same reasons as outlined above.

There was a difference between species in giving-up densities (Table 2; Fig. 2) that was not consistent across microhabitats (species-by-microhabitat inter-

TABLE 1. Summary of the hierarchical log-linear models of between-seasons comparisons of the number of trays foraged across microhabitats (all-day and cool-hours experiments) by *Acomys cahirinus* and *A. russatus*.

Analysis	Significant terms	G score			Standardized log-linear parameter estimates (λ /SE [λ]) for each microhabitat and season
		G	df	P	
Four-way analysis	microhabitat \times number of trays foraged	301.7	21	<0.001	tray foraged: 9.846 (UB), 4.441 (BB), -6.248 (ON), -8.669 (OF); signs reversed for tray not foraged.
	season \times number of trays foraged	59.03	19	<0.001	tray foraged: -6.269 (winter), 6.269 (summer); signs reversed for tray not foraged.
	season \times microhabitat	34.38	21	0.033	winter: 4.284 (UB), 2.270 (BB), -3.027 (ON), -3.846 (OF); signs reversed for summer.
<i>A. cahirinus</i>	microhabitat \times number of trays foraged	130.90	6	<0.001	tray foraged: 6.597 (UB), 3.299 (BB), -4.038 (ON), -6.448 (OF); signs reversed for tray not foraged.
	season \times number of trays foraged	23.22	4	<0.001	tray foraged: -4.251 (winter), 4.251 (summer); sign reversed for tray not foraged.
	season \times microhabitat	11.86	6	0.0651	winter: 2.716 (UB), 1.600 (BB), -1.794 (ON), -2.590 (OF); signs reversed for summer.
<i>A. russatus</i>	microhabitat \times number of trays foraged	160.01	6	<0.001	tray foraged: 7.317 (UB), 3.062 (BB), -4.816 (ON), -5.796 (OF); signs reversed for tray not foraged.
	season \times number of trays foraged	31.70	4	<0.001	tray foraged: -4.653 (winter), 4.653 (summer); signs reversed for tray not foraged.
	season \times microhabitat	18.26	6	0.006	winter: 3.416 (UB), 1.626 (BB), -2.574 (ON), -2.921 (OF); signs reversed for summer.
<i>A. russatus</i> (cool hours)	microhabitat \times number of trays foraged	177.62	6	<0.001	tray foraged: 7.284 (UB), 4.093 (BB), -3.500 (ON), -4.909 (OF); signs reversed for tray not foraged.
	season \times number of trays foraged	54.59	4	<0.001	tray foraged: -5.072 (winter), 5.072 (summer); signs reversed for tray not foraged.
	season \times microhabitat	34.32	6	<0.001	winter: 3.993 (UB), 2.253 (BB), -3.083 (ON), -3.707 (OF); signs reversed for summer.

Notes: The standardized log-linear parameter estimates are provided for each combination of the terms in the model. Total for four-way analysis, $N = 480$; *A. cahirinus*, $N = 240$; *A. russatus*, $N = 240$; cool hours, $N = 240$.

action term, Table 2). There also were seasonal differences in GUDs, which were consistent across species (season-by-species interaction term) but not across microhabitats (season-by-microhabitat interaction term, Table 2). The three-way interaction between season,

species, and microhabitat also was statistically significant (Table 2).

In general, *A. russatus* foraged the more sheltered microhabitats to a lower GUD and the less sheltered microhabitats to a higher GUD than did *A. cahirinus*

TABLE 2. Comparisons of giving-up densities between species, seasons, and microhabitats based on a three-way ANOVA on the rank-transformed means.

Source	SS	df	MS	F	P
Season	19 790.887	1	19 790.887	8.108	0.005
Species	13 975.418	1	13 975.418	5.726	0.018
Microhabitat	193 685.070	2	96 842.535	39.676	<0.001
Season \times Species	1 920.679	1	1 920.679	0.787	0.376
Season \times Microhabitat	32 525.219	2	16 262.609	6.663	0.002
Species \times Microhabitat	38 175.638	2	19 087.819	7.820	0.001
Season \times Species \times Microhabitat	35 529.962	2	17 764.981	7.278	0.001
Error	502 806.433	206	2 440.808		

TABLE 3. Per capita tray-foraging rates for *Acomys russatus* and *A. cahirinus* at both sites.

Species	Density (mice/ha)		Total no. trays foraged		Per capita tray foraging rate	
	FS	KB	FS	KB	FS	KB
<i>A. cahirinus</i>	20	19	57	59	2.85	3.11
<i>A. russatus</i>	36.5	28	58	43	1.59	1.54

Notes: Mouse densities are Jolly-Seber population estimates from Elvert et al. (1999) for the Field School site (FS) and Shargal et al. (2000) for the Kibbutz site (KB).

(Fig. 2). All three significant interactions resulted from seasonal differences in foraging patterns across microhabitats in *A. russatus* but not in *A. cahirinus*. *A. russatus* foraged the under boulder microhabitat to a much lower GUD and the between boulder microhabitat to a much higher GUD in winter than in summer. *A. cahirinus* maintained the pattern of a gradual decrease in foraging from the under boulder to the open far microhabitats in both seasons, although the decrease in GUDs in summer was more marked in the increasingly open microhabitats (Fig. 2).

When the trays were left open only in the cooler hours of the day, *A. russatus* demonstrated a seasonal shift in foraging (Table 4) that also was not consistent across microhabitats (season-by-microhabitat interaction term, Table 4), similar to the all-day experiments (Fig. 2).

DISCUSSION

Acomys cahirinus and *A. russatus* both showed a year-round graded preference for foraging habitats and microhabitats that provided the most overhead cover and small spaces in which to hide. Of the two ways in which habitats and microhabitats vary, the provision of cover rather than escape distance seemed to be the more important for both species of mice. This was indicated by the greater differences in foraging (both the number of trays foraged and giving-up density) between both the boulder and open habitats, and the under and between boulder microhabitats, which differed in proximity to cover, than among the two open microhabitats, which varied in escape distance to cover. These preferences are consistent with what is expected if the mice perceive a predation risk from raptorial predators such as owls, as has been shown for *A. cahirinus* (Mandelik 1999).

In spite of these apparent similarities in foraging microhabitats, *Acomys cahirinus* and *A. russatus* appeared to follow two different strategies in habitat use and foraging behavior. *A. cahirinus* was more general in its habitat use, using a broader range of microhabitats, including the safest and most climatically favorable microhabitat (UB), but also all of the increasingly risky and exposed microhabitats (BB, ON, OF, respectively). *A. cahirinus* was a relatively inefficient forager though, a "cream skimmer" (sensu Brown et al. 1994), giving up foraging early when harvest rates were still quite high and food patches relatively rich. Cream-skimmer species usually compensate for their inefficient foraging ability by traveling faster to visit more patches, by using dormancy to ride out periods of low resource availability, or by gaining a competitive advantage at rich food resources through aggressive interference competition (reviewed in Brown et al. 1994). *A. cahirinus* appeared to use the first strategy, as well as possibly the last. Despite *A. russatus* populations being larger than those of *A. cahirinus* at both sites, both species visited a similar number of trays. *A. cahirinus* thus visited more trays per capita than *A. russatus*, suggesting that this cream skimmer did indeed travel faster to visit more patches.

A. russatus was more of a habitat specialist, largely restricting its foraging activity to the boulder habitat and showing a strong preference for staying under boulders within this habitat. However, *A. russatus* foraged trays to a much lower GUD under boulders compared with the lowest GUDs that *A. cahirinus* attained in any habitat. Lower GUDs have been viewed by previous researchers as reflecting higher foraging efficiencies (e.g., Brown et al. 1997). Based on assumptions discussed by Brown (1997) and not on testing for other measures of efficiency for these specific species, it appears that *A. russatus* was a very efficient forager within its restricted habitat niche. No data are presently available on conversion efficiencies in these species, and handling times of sunflower seeds were minimal, but perhaps the larger size of *A. russatus* means that it is better at digging and therefore has a higher encounter efficiency than *A. cahirinus* (sensu Vincent et al. 1996). The ability to forage efficiently may enable *A. russatus* to restrict its activity to the safest habitats and also may enable it to persist in sympatry with *A. cahirinus*.

In answer to our first question, our data suggest that

TABLE 4. Comparisons of giving-up densities between seasons and microhabitats for *Acomys russatus* in the cool-hours experiment using a two-way ANOVA on the rank-transformed means.

Source	SS	df	MS	F	P
Season	5 602.653	1	5 602.653	9.116	0.003
Microhabitat	17 507.547	1	17 507.547	28.487	<0.001
Season × Microhabitat	6 625.889	1	6 625.889	10.781	0.001
Error	52 240.102	85	614.589		

coexistence between the two *Acomys* species may be promoted by trade-offs in their efficiencies of foraging leading to different strategies of microhabitat use. The trade-off may result in *A. cahirinus* using microhabitats where the risk of predation (from raptorial predators such as owls or kestrels) and physiological costs are higher than those used by *A. russatus*. An alternative explanation is that these costs may be higher during the day. Comparison of foraging efficiencies and microhabitat use between diurnal and nocturnal populations of *A. russatus*, or perhaps direct measurements of foraging efficiencies of the mice and relative hunting efficiencies of owls and kestrels, may enable us to test this further.

Both species of spiny mice shifted their foraging activity toward more open habitats in summer compared with winter. As *Echis coloratus*, the major snake predator of *Acomys* at Ein Gedi, prefers boulder habitats when active during the warmer months (Mendelssohn 1965), this shift toward open habitats in summer is compatible with a strong avoidance response to the presence of snakes. Seasonal differences in ambient temperature (which may affect metabolic costs of foraging) also were considered, but our results suggest that snakes are the predominant reason for the changes in foraging between seasons. When we factored out the major component of the higher metabolic costs of foraging during the day in summer by opening the trays only in the cool hours of the day, the seasonal shift in foraging patterns of *A. russatus* was similar to that when the trays were open all day. Previous studies (Shkolnik 1966, Kronfeld-Schor et al. 2000a) have shown that during the hot summer, *A. russatus* have two activity peaks, in the morning and in the afternoon, that correspond with the time of our cool-hours experiment, so this result may not be surprising. Quite possibly, the cool-hours experiment captured much of the total foraging during this hot season.

That *A. russatus* was recorded foraging in the open habitat only once in winter, when heat loads and light intensity were moderate, but was recorded 17 times in summer, even in the middle of the day (direct observation) when metabolic costs were at their greatest, suggests that their aversion response to the presence of snakes overrides the desire to reduce metabolic costs and water loss. Regardless of snakes in the boulder field, though, the mice should not forage in the open if the costs of predation or thermoregulation are sufficiently high as to render foraging there unprofitable. Foraging could become profitable in the more open microhabitats if the presence of snakes in the boulder fields reduces the overall amount of food gathered per capita. This situation would increase the marginal value of energy and, therefore, reduce the predation and physiological costs for a given amount of exposure, provided food availability and dispersion remained the same. Breeding activity, which increases energetic demands and which occurs in summer in both species

(Shargal et al. 2000), also would increase the marginal value of energy and the profitability of foraging in the open.

The dramatic response of spiny mice to snakes was exemplified by the presence of a snake for two days and a night between two of the trays in the boulder habitat. During the day, the snake moved under a boulder near the under boulder tray and the mice (*A. russatus*) foraged in the between boulder but not in the UB tray. At night, the snake moved out and lay near the BB tray. The mice (*A. cahirinus*) foraged in the UB tray 2.5 m away but not in the BB tray near the snake.

While both species of mice avoided the boulder microhabitats where the snakes were active in summer, the two species showed different foraging responses to vipers which reflected their respective foraging efficiencies and strategies of microhabitat use. First, because of their baseline microhabitat preferences, this seasonal shift in foraging to more open microhabitats affected *A. russatus* in the between boulder and the open microhabitats, and *A. cahirinus* mostly in the open microhabitats. Second, *A. russatus*, with its more restricted habitat use, exhibited a seasonal reversal in foraging patterns within the boulder field microhabitats. GUDs were higher in the UB microhabitat than in the BB microhabitat on summer days when snakes were lying under boulders, compared with the very low GUDs under boulders in the absence of snakes in winter. This reversal in foraging response was not shown by *A. cahirinus*, which is active in a wider range of habitats. *E. coloratus* is nocturnally active, like *A. cahirinus*, and can be found away from cover at night, between boulders or, occasionally, in the open habitat (H. Hawlena, *personal communication*, M. Jones, *personal observations*). The nocturnal movements of the snakes, particularly in the boulder microhabitats, may explain the dramatic increase by *A. cahirinus* in use of the open habitat, but only a smaller increase in use of the boulder habitat, in summer compared with winter, when *A. cahirinus* foraged mostly in the boulder field. We were unable to factor out possible costs of thermoregulating during the cold winter nights in the open areas, so it is possible that a physiological factor works in conjunction with the effect of snakes. It is also possible that the greater diversity and density of diurnal raptors overwintering in Israel, including at Ein Gedi, compared with summer populations, works in conjunction with snakes to accentuate seasonal differences in use of the open microhabitats for *A. russatus*.

To address our second and third questions, the responses by both species of mice to seasonal differences in predator regimes (predation risk from snakes in summer but not in winter) appeared to override the opposing effects of physiological costs of summer activity in the open and the effects of predation risk from raptorial predators (owls and kestrels). The consequent shift in foraging strategy between winter and summer implies that during summer, when foraging efficiencies

(GUDs) in the boulder habitat are more similar, ecological overlap between the two species may increase. During summer, though, both species shift to a much more insectivorous diet (Kronfeld and Dayan 1999). If the arthropod species available during the day and night are different, the extreme temporal partitioning may provide the potential for partitioning of food resources. This shift toward insectivory may compensate for the greater overlap in use of foraging microhabitat during the summer months.

The reversal in ranking of microhabitats in the presence of snakes in summer in spite of predation risk from owls and kestrels and favorable microclimate suggests that the mice may experience risk-enhancing effects from these multiple predators. From the predator viewpoint this has been called predator facilitation (Charnov et al. 1976, Korpimäki 1987, Kotler et al. 1992, Sih et al. 1998). Indirect effects of multiple predators on the behavior of prey species have been demonstrated in both aquatic invertebrate and vertebrate systems (Charnov et al. 1976, Rahel and Stein 1988, Soluk and Collins 1988, Sih et al. 1998), including desert rodents and their predators (Charnov et al. 1976, Kotler et al. 1992). They occur when avoidance of one predator results in exposure to a greater risk from the other. For *Acomys*, avoiding snakes in the boulder field in summer means exposing themselves to a greater risk of predation from owls (Mandelik 1999) or raptors in the open, and also possibly, for *A. russatus*, accepting a greater metabolic cost from being exposed to more extreme environmental conditions. Whether the opposing effects of raptorial and reptilian predators on microhabitat selection in *Acomys* result in increased rates of predation or in increased metabolic costs of foraging can only be determined with controlled experiments.

A similar response has been reported in nocturnal gerbils and heteromyids in open deserts. Gerbils and kangaroo rats face a conflict between use of open microhabitat where risk from owls is high and bush microhabitat where snakes lie in ambush (Kotler et al. 1992, Bouskila 1995). The rodents avoided the open entirely in the presence of owls or high illumination, which facilitates owl hunting, but increased their exposure to owls in the presence of snakes, which lie in ambush in the sheltered, bush habitat. The more complex cover offered by the jumble of boulders and interstices in the rocky desert at Ein Gedi, compared with cover available in open deserts, may increase the risk from snakes to rodents in rocky deserts. There is far more opportunity for a mouse to happen upon a concealed snake in a boulder field than under a bush. The differences in physical structure between open and rocky deserts may have other influences on rodent community dynamics as well.

The boulder field component of rocky deserts, in which spiny mice live, provides a structurally more complex and more continuous sheltered habitat than is

available even in well vegetated open or sandy deserts. In an open or sandy desert, the sheltered habitat consists of isolated shrubs in an expanse of open space (Brown et al. 1988). In the course of a night's foraging, rodents in open deserts need to cross open spaces, where they are at higher risk from raptorial predators, between patches of cover. By contrast, in rocky desert terrain the boulder habitat provides a spatially intricate microhabitat with continuous overhead cover. Both species of spiny mice prefer to forage within the continuous sheltered habitat. Trips into the open habitat are discrete events so the risk from raptorial predators, whether nocturnal owls or diurnal kestrels, is more intermittent and more avoidable. We propose that the structurally complex and continuous nature of the rocky desert boulder habitat, in synergism with the superior physiological adaptations to deserts of *A. russatus* (Shkolnik 1966, Degen et al. 1986, Kam and Degen 1991, 1993, Merkt 1991), may provide the opportunity for diurnal activity by *A. russatus* that may not exist in other types of deserts. This is supported by the importance of cover rather than escape distance in determining habitat and microhabitat preferences. The habitat template of rocky deserts may thus enable the unique and extreme temporal partitioning between spiny mice to opposite parts of the diel cycle and contribute to coexistence in this community.

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LITERATURE CITED

- Abramsky, Z., H. Alfiá, M. Schachak, and S. Brand. 1990a. Predation by rodents and the distribution and abundance of the snail *Trochoidea seetzenii* in the Central Negev Desert of Israel. *Oikos* **59**:225-234.
- Abramsky, Z., M. L. Rosenzweig, B. Pinshow, J. S. Brown, B. Kotler, and W. A. Mitchell. 1990b. Habitat selection: an experimental field test with two gerbil species. *Ecology* **71**:2358-2369.
- Abramsky, Z., M. Schachak, A. Subach, S. Brand, and H. Alfiá. 1992. Predator-prey relationships: rodent-snail interactions in the Central Negev Desert of Israel. *Oikos* **65**: 128-133.
- Bouskila, A. 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* **76**:165-178.
- Bowers, M. A., D. B. Thompson, and J. H. Brown. 1987. Foraging and microhabitat use in desert rodents: the role of a dominant competitor. *Oecologia* (Berlin) **72**:77-82.
- Brown, J. H. 1987. Variation in desert rodent guilds: patterns, processes, and scales. Pages 185-203 in J. H. R. Gee and P. S. Giller, editors. *Organization of communities: past and present*. Blackwell Scientific, Oxford, UK.
- Brown, J. H., and G. A. Lieberman. 1973. Resource utili-

- zation and coexistence of seed-eating desert rodents in sand-dune habitat. *Ecology* **54**:788–797.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioural Ecology and Sociobiology* **22**:37–47.
- Brown, J. S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. *Ecological Monographs* **59**:1–20.
- Brown, J. S. 1996. Coevolution and community organisation in three habitats. *Oikos* **75**:193–206.
- Brown, J. S., B. P. Kotler, and W. A. Mitchell. 1994. Foraging theory, patch use, and the structure of a Negev Desert granivore community. *Ecology* **75**:2286–2300.
- Brown, J. S., B. P. Kotler, and W. A. Mitchell. 1997. Competition between birds and mammals: a comparison of giving-up densities between crested larks and gerbils. *Evolutionary Ecology* **11**:757–771.
- Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia (Berlin)* **76**:408–415.
- Brown, J., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* **80**:385–399.
- Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. *American Naturalist* **110**:247–259.
- Conover, W. J., and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistician* **35**:124–129.
- Dayan, T., and D. Simberloff. 1994. Morphological relationships among coexisting heteromyids: an incisive dental character. *American Naturalist* **143**:462–477.
- Degen, A. A., M. Kam, A. Hazan, and K. A. Nagy. 1986. Energy expenditure and water flux in three sympatric desert rodents. *Journal of Animal Ecology* **55**:421–429.
- Dickman, C. R., K. Green, P. L. Carron, D. C. D. Happold, and W. S. Osborne. 1983. Coexistence, convergence and competition among *Antechinus* (Marsupialia) in the Australian high country. *Proceedings of the Ecological Society of Australia* **12**:79–99.
- Elvert, R., N. Kronfeld, T. Dayan, A. Haim, N. Zisapel, and G. Heldmaier. 1999. Telemetric field studies of body temperature and activity rhythms of *Acomys russatus* and *Acomys cahirinus* in the Judean Desert of Israel. *Oecologia (Berlin)* **119**:484–492.
- Emlen, J. M. 1966. The role of time and energy in food preferences. *American Naturalist* **100**:611–617.
- Geffen, E., R. Hefner, D. W. Macdonald, and M. Ucko. 1992. Diet and foraging behavior of Blanford's foxes, *Vulpes cana*, in Israel. *Journal of Mammalogy* **73**:395–402.
- Hughes, J. J., D. Ward, and M. R. Perrin. 1994. Predation risk and competition affect habitat selection and activity of Namib Desert gerbils. *Ecology* **75**:1397–1405.
- Jaffe, S. 1988. Climate of Israel. Pages 79–94 in Y. Yom-Tov and E. Tchernov, editors. *The zoogeography of Israel*. Dr. W. Junk, Dordrecht, The Hague, The Netherlands.
- Jones, M. E. 1997. Character displacement in Australian dasyurid carnivores: size relationships and prey size patterns. *Ecology* **78**:2569–2587.
- Jones, M. E., and L. A. Barmuta. 1998. Diet overlap and abundance of sympatric dasyurid carnivores: a hypothesis of competition? *Journal of Animal Ecology* **67**:410–421.
- Kam, M., and A. A. Degen. 1991. Diet selection and energy and water budgets of the common spiny mouse *Acomys cahirinus*. *Journal of Zoology, London* **225**:285–292.
- Kam, M., and A. A. Degen. 1993. Effect of dietary preformed water on energy and water budgets of two sympatric desert rodents, *Acomys russatus* and *Acomys cahirinus*. *Journal of Zoology, London* **231**:51–59.
- Korpimäki, E. 1987. Dietary shifts, niche relationships and reproductive output of coexisting kestrels and long-eared owls. *Oecologia* **74**:277–285.
- Kotler, B. 1984. Risk of predation and the structure of desert rodent communities. *Ecology* **65**:689–701.
- Kotler, B. P., Y. Ayal, and A. Subach. 1994. Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. *Oecologia (Berlin)* **100**:391–396.
- Kotler, B. P., L. Blaustein, and J. S. Brown. 1992. Predator facilitation: the combined effects of snakes and owls on the foraging behavior of gerbils. *Annales Zoologici Fennici* **29**:199–206.
- Kotler, B. P., and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* **19**:281–307.
- Kotler, B. P., and J. S. Brown. 1999. Mechanisms of coexistence of optimal foragers as determinants of the local abundances and distributions of desert granivores. *Journal of Mammalogy* **80**:361–374.
- Kotler, B. P., J. S. Brown, R. J. Smith, and W. O. Wirtz II. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. *Oikos* **53**:145–152.
- Kotler, B. P., J. S. Brown, and A. Subach. 1993. Mechanisms of species coexistence of optimal foragers: temporal partitioning of two species of sand dune gerbils. *Oikos* **67**:548–556.
- Kronfeld, N. 1998. Coexistence among desert spiny mice: ecological, physiological and biochemical aspects. Dissertation. (In Hebrew, English summary.) Tel Aviv University, Tel Aviv, Israel.
- Kronfeld, N., and T. Dayan. 1999. The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species. *Oecologia (Berlin)* **121**:123–128.
- Kronfeld-Schor, N., A. Haim, T. Dayan, N. Zisapel, M. Klingenspor, and G. Heldmaier. 2000a. Seasonal thermogenic acclimation of diurnally and nocturnally active desert spiny mice. *Physiological and Biochemical Zoology* **73**:37–44.
- Kronfeld-Schor, N., E. Shargal, A. Haim, T. Dayan, N. Zisapel, and G. Heldmaier. 2001. Temporal partitioning among diurnally and nocturnally active desert spiny mice: energy and water turnover costs. *Journal of Thermal Biology* **26**:139–142.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**:619–640.
- Longland, W. S., and M. V. Price. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology* **72**:2261–2273.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**:499–519.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence and divergence of co-existing species. *American Naturalist* **101**:377–385.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* **100**:603–609.
- Mandelik, Y. 1999. Foraging microhabitat use and foraging efficiencies of the common spiny mouse, *Acomys cahirinus*. Thesis. (In Hebrew, English summary.) Tel Aviv University, Tel Aviv, Israel.
- May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences* **71**:3230–3233.
- Mendelssohn, H. 1965. On the biology of the venomous snakes of Israel. *Israel Journal of Zoology* **14**:185–212.
- Merkt, J. R. 1991. Switching down metabolism: an adaptation to food shortage in the desert. Dissertation. Harvard University, Cambridge, Massachusetts, USA.
- Morris, D. W. 1996. Coexistence of specialist and generalist rodents via habitat selection. *Ecology* **77**:2352–2364.

- Price, M. V. 1986. Structure of desert rodent communities: a critical review of questions and approaches. *American Zoologist* **26**:39–49.
- Rahel, F. J., and R. A. Stein. 1988. Complex predator–prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. *Oecologia* (Berlin) **75**:94–98.
- Rosenzweig, M. L. 1987. Community organisation from the point of view of habitat selectors. Pages 469–489 in J. H. R. Gee and P. S. Giller, editors. *Organisation of communities: past and present*. Blackwell Scientific, Oxford, UK.
- Rosenzweig, M. L., and Z. Abramsky. 1985. Detecting density-dependent habitat selection. *American Naturalist* **126**:405–417.
- Rosenzweig, M. L., and Z. Abramsky. 1997. Two gerbils of the Negev: a long term investigation of optimal habitat selection and its consequences. *Evolutionary Ecology* **11**:733–756.
- Schmidt-Nielsen, K. 1964. *Desert animals: physiological problems of heat and water*. Clarendon Press, Oxford, UK.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* **185**:27–39.
- Schoener, T. W. 1986. Resource partitioning. Pages 91–126 in J. Kikkawa and D. J. Anderson, editors. *Community ecology: pattern and process*. Blackwell, Melbourne, Australia.
- Shargal, E. 1997. Population biology and ecophysiology of coexisting *Acomys cahirinus* and *Acomys russatus*. Thesis. (In Hebrew, English summary.) Tel Aviv University, Tel Aviv, Israel.
- Shargal, E., N. Kronfeld-Schor, and T. Dayan. 2000. Population biology and spatial relationships of coexisting spiny mice of the genus *Acomys*. *Journal of Mammalogy* **81**:1046–1052.
- Shargal, E., L. Rath-Wolfson, N. Kronfeld, and T. Dayan. 1999. Ecological and histological aspects of tail-loss in spiny mice (Rodentia: Muridae, *Acomys*) with a review of its occurrence in rodents. *Journal of Zoology*, London **249**:187–193.
- Shkolnik, A. 1966. Studies in the comparative biology of Israel's two species of spiny mice (genus *Acomys*). Dissertation. (In Hebrew, English summary.) Hebrew University, Jerusalem, Israel.
- Shkolnik, A. 1971. Diurnal activity in a small desert rodent. *International Journal of Biometeorology* **15**:115–120.
- Shkolnik, A. 1988. Physiological adaptation to the environment: the Israeli experience. Pages 487–496 in Y. Yom-Tov and E. Tchernov, editors. *The zoogeography of Israel*. Dr. W. Junk, Dordrecht, The Hague, The Netherlands.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* **13**:350–355.
- Soluk, D. A., and N. C. Collins. 1988. Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. *Oikos* **52**:94–100.
- SYSTAT. 1997. SYSTAT 7.0: new statistics. SPSS, Chicago, Illinois, USA.
- Tabachnik, B. G., and L. S. Fidell. 1989. *Using multivariate statistics*. Second edition. Harper and Row, New York, USA.
- Vincent, T. L. S., D. Scheel, J. S. Brown, and T. L. Vincent. 1996. Trade-offs and coexistence in consumer-resource models: it all depends on what and where you eat. *American Naturalist* **148**:1038–1058.
- Weissenberg, S., A. Bouskila, and T. Dayan. 1997. Resistance of the common spiny mouse (*Acomys cahirinus*) to the strikes of the Palestine saw-scaled viper (*Echis coloratus*). *Israel Journal of Zoology* **43**:119.
- Ziv, Y., Z. Abramsky, B. P. Kotler, and A. Subach. 1993. Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos* **66**:237–246.