



SYMPOSIUM

Interspecific Competition and Torpor in Golden Spiny Mice: Two Sides of the Energy-Acquisition Coin

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Synopsis We studied the occurrence of torpor in golden spiny mice in a hot rocky desert near the Dead Sea. In this rodent assemblage, a congener, the nocturnal common spiny mouse, competitively excluded the golden spiny mouse from the nocturnal part of the diel cycle and forced it into diurnal activity; this temporal partitioning allows the two species to partition their prey populations, particularly in summer when the diet of the two species is comprised mainly of arthropods, and largely overlap. We studied the effect of the presence of the common spiny mice at two resource levels (natural food availability and food added *ad libitum*) on populations of golden spiny mice in four large outdoor enclosures: two with common spiny mice removed and two enclosures with populations of both species. We hypothesized that with interspecific competition and/or reduced resources, golden spiny mice will increase their use of torpor. As we expected, supplemented food reduced the total time spent torpid. In summer, when the different activity periods of the two species results in prey species partitioning, removal of the congener did not affect torpor in the golden spiny mouse. However, in winter, when insect populations are low and the two species of mice overlap in a largely vegetarian diet, removal of the common spiny mouse reduced torpor in golden spiny mice, whether food was supplemented or not. This result suggests that torpor, a mechanism that allows small mammals to sustain periods of low availability of resources or high energetic requirements, may also help them to tolerate periods of enhanced interspecific competition. This may be a significant short-term mechanism that reduces competition and hence increases fitness, in particular of individuals of the subordinate species whose accessibility to resources may be limited.

Introduction

When two coexisting species require the same limiting resources of energy, competition occurs (Simberloff and Dayan 1991; Begon et al. 2005). When the energy demands of mammals are not met, they enter a state of torpor and so reduce energy demands (Geiser 2004; Heldmaier et al. 2004). High levels of competition that result in reduced levels of resource must therefore induce torpor, and use of torpor must reduce the level of interspecific competition; thus, torpor and competition appear to be two sides of the same energy-acquisition coin.

Resource competition has been implicated in microevolutionary change (e.g., Losos 1994), in shifts along niche axes (Kronfeld-Schor and Dayan 2003,

2008), and in assembling and structuring ecological communities (Tilman 2004). Resource partitioning is assumed to be the chief mechanism of coexistence between competitors; specializing in different microhabitat use, different spectra of resources, or different activity times, reduces overlap in use of resources and allows competitors to coexist. If species are unable to partition resources—they cannot coexist and the subordinate competitor will be lost from the ecological community (Tilman 1982).

These mechanisms of coexistence function by reducing the amount of overlap in use of energy resources among individuals of competing species (Schoener 1974). The same result can be achieved temporarily through an alternative

mechanism—entering torpor during times of intense competition, thereby reducing the amount of energy needed.

Torpor is a state of metabolic depression extensively studied in the context of surviving adverse environmental conditions such as extreme temperatures or limited availability of food or water. During torpor, mammals decrease their body temperature and expenditure of energy. These variations in body temperatures are considered adaptive (e.g., Humphries et al. 2003; Cooper et al. 2005; Ehrhardt et al. 2005; Kortner and Geiser 2009; Angilletta et al. 2010). They allow mammals to survive periods when the intake of energy is limited, relative to the requirements for it. This can occur either because of high-energy demands in extreme temperatures or because of limiting resources; when resources are limiting, competition occurs. In fact, in the laboratory, the use of torpor was shown to increase with increasing cost of foraging (Schubert et al. 2008, 2010), as would be the case when interspecific competition for resources occurs. Increased foraging costs may also result from interspecific interference competition, and therefore also driving the use of torpor.

In spite of what should be an obvious link, the role of torpor in biotic interactions (other than predation) was rarely addressed, although it was suggested, e.g., by Bieber and Ruf (2009) and Riek et al. (2011). We studied the relationship between resource levels, resource competition, and torpor in a rocky desert rodent, the golden spiny mouse (*Acomys russatus*), in order to gain insight into how interspecific competition and resource levels affect the use of torpor as a mechanism to reduce the demand for energy. We focused on a research system in which the nocturnal common spiny mouse (*Acomys cahirinus*) and the diurnally active golden spiny mouse coexist (Elvert et al. 1999; Shargal et al. 2000). Experimental research suggest that the golden spiny mouse had been competitively forced into diurnal activity by the common spiny mouse (Shkolnik 1966, 1971; Gutman and Dayan 2005). Various physiological and morphological characteristics of the golden spiny mouse support this hypothesis (Kronfeld-Schor et al. 2000, 2001a, 2001b, 2001c; Kronfeld-Schor and Dayan 2003, 2008; Cohen and Kronfeld-Schor 2006; Levy et al. 2007; Cohen et al. 2009, 2010).

These two omnivorous species overlap in diet (Kronfeld and Dayan 1998; Kronfeld-Schor and Dayan 1999); in summer, when arthropod abundance peaks (Vonshak et al. 2009), they become primarily insectivorous (Kronfeld-Schor and Dayan

1999). Since arthropod prey species also exhibit temporal activity patterns (Vonshak et al. 2009), temporal partitioning reduces resource overlap and thus reduces interspecific competition (Kronfeld-Schor and Dayan 1999). In winter, the two species exhibit a more herbivorous diet and thus have greater overlap in use of food resources (Kronfeld-Schor and Dayan 1999); however, they can compensate by foraging in different microhabitats and thereby coexist (Jones et al. 2001). Coexistence between the two species appears to be resource-based rather than interference-based (Gutman and Dayan 2005; Pinter-Wollman et al. 2006).

Limited availability of food induces torpor in golden spiny mice (Ehrhardt et al. 2005; Gutman et al. 2006). In a previous study, we found that when kept alone in large outdoor experimental enclosures, golden spiny mice decreased the amount of time spent torpid when provided by food *ad libitum* (Levy et al. 2011). Thus, we have an excellent model system in which resource limitation affects both interspecific competition and use of torpor. How does interspecific competition then affect the use of torpor?

Under semi-natural conditions, we studied the effect of interspecific competition at two resource levels on torpor. In two large field enclosures, golden spiny mice were kept alone (removal experiment) while in two others they were kept with their competitor—the common spiny mouse. Specifically we asked:

- (1) how do resource levels (natural field levels versus food supplied *ad libitum*) affect the total time spent in torpor by individuals in the presence of, and in the absence of the competitor, in winter and in summer? and
- (2) how does total time spent in torpor vary between summer and winter in golden spiny mouse populations when both species are present and in populations when golden spiny mice are kept alone?

It is widely accepted that interspecific competition results in reduced fitness, more so in the subordinate species (Hogstedt 1980). Decreasing energy expenditure through torpor, may contribute to coexistence if food is the limiting factor. In the case of interspecific competition for resources, it is expected that individuals, in particular those of the subordinate species, will use torpor. Thus, we hypothesize that with interspecific competition and/or reduced resources, individual golden spiny mice will increase their use of torpor.

Materials and methods

Experimental protocol

Experiments were conducted in the summer of 2003 (August and early September) and in the winter of 2004 (January and February) in four field enclosures. Body temperature (T_b) of golden spiny mice was measured under semi-natural conditions in summer and in winter. Sunflower seeds were added *ad libitum* to the enclosures for 7 days, followed by 10 days with natural availability of food.

Experimental enclosures

We conducted our field experiment at the Ein Gedi nature reserve, in the Judean Desert, near the Dead Sea (31° 28' N, 35° 23' E, 300 m below sea level) in four established 1000 m² enclosures. The enclosures were constructed of 10-mm wire mesh buried 3 cm into the ground and standing 70 cm high. Thus, the natural predators (foxes, snakes, owls, and diurnal raptors) and prey (mostly arthropods) of spiny mice could enter and exit the enclosures freely. Two enclosures contained individuals from both species while the other two enclosures contained golden spiny mice only. In each enclosure, the mice were descendants of eight individuals that were trapped in the area in 2001 (for details, see Gutman and Dayan 2005) and bred in the enclosures, and therefore they were in the presence of absence of competition for several generations. The population in each enclosure was continuously regulated over the years, by releasing or removing individuals to other enclosures, and from time to time, wild-caught individuals were added to the enclosures to avoid inbreeding. Population densities were kept at about double the natural population densities (Shargal et al. 2000). The sex ratio of the population within the enclosures was also monitored and was managed at 1:1. For identification, each individual was implanted with a PIT tag (Passive Integrated Transponder, product of Destron-Fearing).

Two enclosures contained 16 mice, 8 mice per enclosure ($n=4$ of each species). Transmitters (~2 g, Sirtrack LTD, New Zealand) were implanted in the abdominal cavity (for surgical details, see Simberloff and Dayan 1991; Levy et al. 2007, 2011) of these golden spiny mice ($n=4$ in each enclosure, two males and two females) at each season. Of these, we successfully monitored six mice during summer and three mice during winter under conditions both of *ad libitum* food and natural availability of food.

The other two enclosures contained 16 ($n=8$ in each enclosure) and 15 ($n=8$ or $n=7$ in each enclosure) golden spiny mice during summer and

winter, respectively. Transmitters were implanted in 12 golden spiny mice (2 males and 4 females in each of 2 enclosures) during summer and in 13 golden spiny mice during winter (6 males and 7 females with $n=6$ and $n=7$ in the two enclosures). Of these, we successfully monitored nine individuals during summer and eight individuals during winter under conditions both of *ad libitum* food and natural availability of food.

We placed three artificial foraging patches in each enclosure, plastic trays (30 × 20 × 4 cm) containing 2 L of finely sifted local soil. During the *ad libitum* session, we placed a large amount of peeled sunflower seeds on each tray, and replenished the pile every few days, so that food was plentiful during the entire experiment. During the other session, no food was placed in the trays. Since spiny mice do not hoard food (Shkolnik 1966), we assume that the latter conditions simulated natural availability of food. Frames constructed of heavy wire and fine-filament fish netting excluded birds from the trays during the day (details in Jones and Dayan 2000). Mice reached the trays easily by biting through one strand in the net.

Monitoring T_b and ambient temperature

Each implanted radio-transmitter uses a unique frequency, which enables individual identification. The transmitter uses a comparison circuit against which to reference the pulse period being determined by the temperature. We used a RX-900 scanner-receiver (Televilt LTD) connected to two dipole antennas for data logging. The receiver scanned each frequency for a period of 45 s, and whenever a signal was received, the time, frequency, pulse parameters, active antenna, and signal strength were logged. Hence, data for each transmitter were logged once every 20 min. Before implantation, transmitters were calibrated in a water bath to the nearest 0.1°C using a precision mercury thermometer. We converted the pulse period to a temperature using the calibration curves produced by using five different temperatures.

Ambient temperature (T_a) was measured to the nearest 0.5°C every 30 min using a data logger thermometer (iButton ds1921 thermochrom). The thermometer was placed in one enclosure under boulders in the shade, representing the microhabitat used the most by spiny mice.

Data analysis

We recorded over 200,000 T_b readings at each season. In order to analyze such numerous data efficiently, we developed a computer program that

computes T_b according to the transmitter-specific calibration curve, and enters the records into an SQL database (see R code in Levy et al. 2011). In order to identify biologically unreasonable T_b readings that should be ignored during data analysis, we included a filter algorithm in the program: If a reading differed from the previous and subsequent readings of the same individual by more than 7°C , it was omitted. We calculated individual mean T_b at each 20-min interval during each treatment. Measurements of T_a were also inserted into the database. We also calculated mean daily rhythms of T_a for each season (at 30-min intervals), and the average T_b for each T_a was recorded.

For analysis of bouts of torpor, we defined the torpor T_b threshold as calculated by Willis (2007); this changes with T_a . The threshold T_b for torpor was $34.6^\circ\text{C} \pm 0.5^\circ\text{C}$ (mean \pm SD) and $34.0^\circ\text{C} \pm 0.4^\circ\text{C}$ during summer and winter, respectively. For each individual, we calculated the total time torpid per day for each season. In previous studies we found that that acclimation to the different availability of food in this system occurred after 3 days of treatment, and therefore for the calculations of torpor under conditions of natural availability of food, we omitted the first 3 days of the session (Levy et al. 2011).

Statistical analysis

Mixed Effects modeling was used because it appropriately acknowledges correlations in the outcome matrix that result from repeated observations of individuals. We analyzed data using the R statistical programming language (version 2.11.1; R Development Core Team, 2010), using the lme function from the nlme package (version 3.1–96, Pinheiro et al. 2009) with individuals' identity as the random factor. We started each model with the full model. Then we identified the optimal residual variance structure (Zuur et al. 2010). Model selection of the optimal residual variance structure was based on the Akaike Information Criterion, AIC, which measures goodness of fit and model complexity (Burnham and Anderson 1998). We examined the effect of season, food availability, and competition on the use of torpor by golden spiny mice. All calculations were made at the individual level, and then averaged for the figures.

Results are presented as mean or estimate \pm SD.

Results

Increased availability of food resulted in a decrease in the use of torpor in both seasons. The average

time/day each golden spiny mouse spent torpid was 575 ± 70 min longer under natural availability of food compared with *ad libitum* food (natural availability of food: $df=193$, $t=8.11$, $P<0.001$) in the presence of, and absence of, common spiny mice (Figs. 1 and 2). In the absence of their competitor, golden spiny mice used torpor more often during summer than during winter; under *ad libitum* food, mice spent less time torpid during winter by 42 ± 39 min than during summer, and under natural availability of food, they spent 301 ± 72 min ($P<0.01$) less time torpid during winter than they did during summer [winter effect: -119 ± 44 , $df=193$, $t=-2.71$, $P<0.01$; no competitor \times winter effect: 77 ± 58 , $df=193$, $t=1.32$, $P=0.19$; natural availability of food \times winter \times no competition effect: 511 ± 120 , $df=193$, $t=-4.24$, $P<0.001$ (min)] (Figs. 1 and 2).

The presence of common spiny mice had no influence on use of torpor when food was added, either during summer or during winter [no competitor effect: 13 ± 49 , $df=17$, $t=0.26$, $P=0.79$; no competitor \times winter effect: 77 ± 58 , $df=193$, $t=1.32$, $P=0.19$ (min)] (Figs. 1 and 3). Under natural availability of food, the presence of a competitor resulted in an increase (by 246 ± 94 min) in the use of torpor during winter, but not during summer (natural availability of food \times winter: $df=193$, $t=2.61$, $P<0.01$; natural availability of food \times no competitor effect: 57 ± 84 , $df=193$, $t=0.68$, $P=0.50$) (Figs. 1–3). As a result, use of torpor in the presence of a competitor was higher by 125 ± 100 min during winter than during summer.

Discussion

Golden spiny mice kept in the presence of, and in absence of common spiny mice were affected by the availability of energy; food supplementation reduced the total time spent torpid. This result implies that in times of scarce resources, golden spiny mice can cope by reducing the amount of energy they spend (Levy et al. 2011).

When kept alone and without food supplementation, golden spiny mice spent more time torpid in summer than in winter, suggesting that torpor allowed them to save not only energy but also water (Levy et al. 2011). When food was supplemented *ad libitum*, thus removing the stress of limited energy, golden spiny mice still spent more time torpid in summer than in winter, both in the presence and absence of common spiny mice (although in both enclosures the absolute time spent torpid was much lower than it was without food

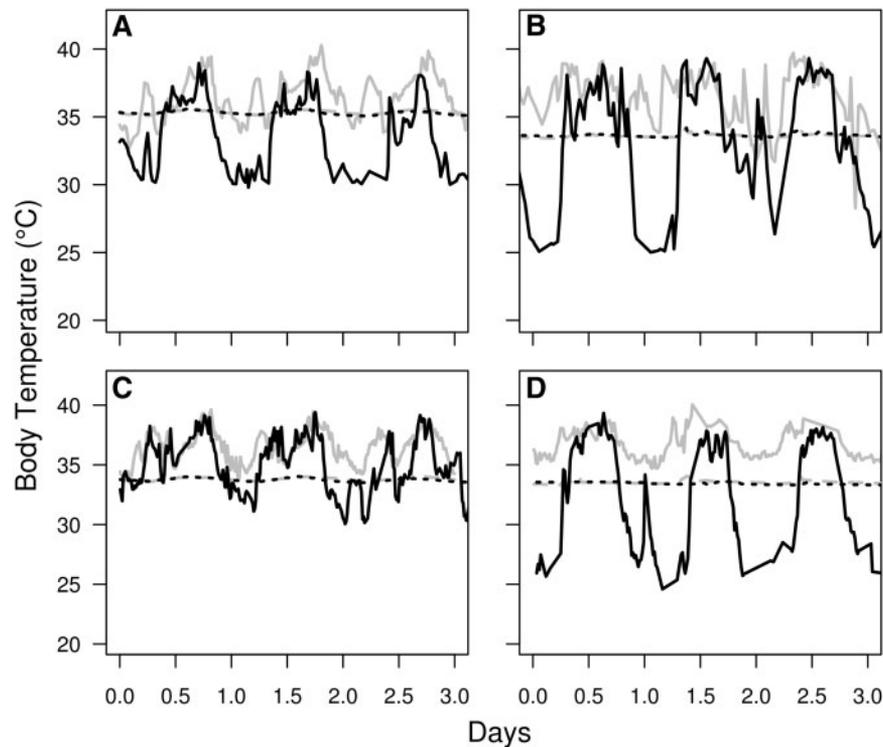


Fig. 1 T_b rhythms of two golden spiny mouse individuals, kept in the absence (**A**—summer, **B**—winter) or in the presence (**C**—summer, **D**—winter) of common spiny mice during the *ad libitum* (gray), and natural availability of food (black). Dashed lines represent the calculated torpor thresholds during the *ad libitum* (gray), and natural availability of food (black).

supplementation). When food is supplemented, depression of resources by the common spiny mouse ceases to be significant, so the pattern of torpor that occurs in the presence of common spiny mice does not differ from that in the enclosures where the golden spiny mice are kept alone. Supplementing food clearly increased the availability of energy, so torpor was no longer as crucial as a means of conserving energy; however, in summer its function also must be to save water (see above). Hence, even when food was supplemented, the mice spent more time torpid in summer than in winter.

When kept in the presence of common spiny mice and with natural availability of food, we find a reversed pattern, with golden spiny mice spending more time torpid in winter than in summer. Can interspecific competition explain this conflicting pattern?

During summer, availability of arthropods is high and both species are largely insectivorous; therefore, temporal partitioning reduces overlap in the use of resources because different taxa of arthropods are active at different parts of the diel cycle (Kronfeld-Schor and Dayan 1999; Vonshak et al. 2009). It is perhaps not surprising that during summer the presence or absence of the competing congener does not

affect torpor in golden spiny mice, whether or not food is supplemented.

During winter, however, the availability of arthropods drops, overlap in resources increases, and thus competition for resources is expected to become more intense. Consequently, the two species exhibit increased trade-offs in microhabitats used for foraging (Jones et al. 2001), although significant overlap remains. Accordingly, during winter the presence of common spiny mice increases the time spent by golden spiny mice in torpor, under natural availability of food. Consequently the total time spent torpid in winter is greater than in summer when common spiny mice are present and when food is not supplemented, because interspecific competition over resources is more significant in winter than in summer due to increased overlap of resources.

The ability to use adaptive thermoregulation and to undergo torpor, a mechanism for coping with high-energy requirements and low availability of energy, as well as need for the conservation of water (Shkolnik and Borut 1969; Kronfeld-Schor et al. 2000, 2001a, 2001b), may well be significant also for promoting coexistence between the golden spiny mouse and its congener.

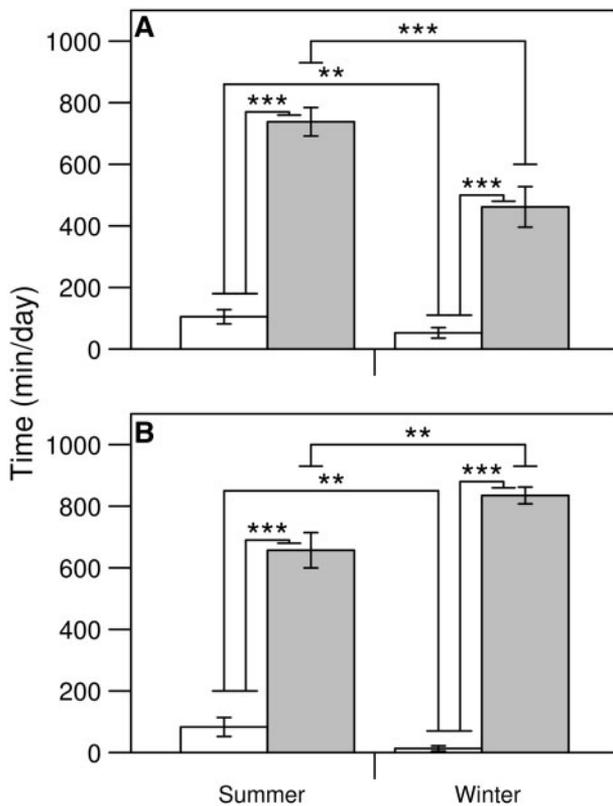


Fig. 2 Effect of season on daily (mean \pm SE) time spent in torpor by golden spiny mice in the absence of (A) common spiny mice (summer, $n=9$; winter, $n=8$), and in the presence of (B) common spiny mice (summer, $n=6$; winter, $n=3$) under *ad libitum* food (open bars) and under natural availability of food (filled bars). ** $P < 0.01$; *** $P < 0.001$

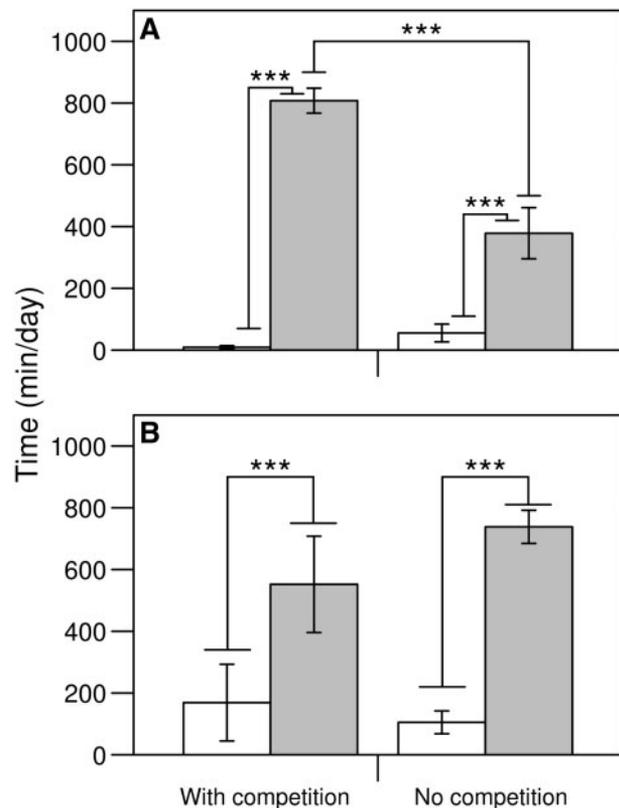


Fig. 3 The influence of competition on daily (mean \pm SE) time torpid by golden spiny mice during winter (A) in the presence ($n=3$) and absence ($n=8$) of common spiny mice, and during summer (B) in the presence of ($n=6$), and in the absence of ($n=9$) common spiny mice under *ad libitum* (open bars) and natural food availability (filled bars). *** $P < 0.001$

Interspecific competition impacts the population dynamics of competing species (e.g., Zeineddine and Jansen 2005; Kimura and Chiba 2010), drives microevolutionary change (Dayan and Simberloff 2005), and may affect the composition and structure of communities (e.g., Bowers and Brown 1982; Stone and Roberts 1991; Parra et al. 1999). These outcomes of competition occur at different temporal scales, with the most rapid response expected in population dynamics, with both mortality and fecundity affected by the availability of resources (Begon et al. 2005). However, even population dynamics do not usually manifest a rapid enough response to short-term excursions from mean energy availability or energy requirements. These excursions from the mean can result either from fluctuations in availability of resources (because of prey population dynamics, for example) or fluctuations in climatic conditions, and hence of the energy requirements for thermoregulation. In small mammals, torpor is a mechanism that can allow individuals to sustain temporary periods of increasing gap between the requirements for energy

and its availability (Geiser and Turbill 2009). Torpor must thus dampen short-term fluctuations in competition for resources in a variable environment.

The risk of predation can also affect accessibility of resources, by reducing the time spent foraging and possibly also by reducing accessibility to microhabitat suitable for foraging. Risk of predation was repeatedly found to play a major role in desert communities (Brown et al. 1988; Kotler et al. 1994; Jones and Dayan 2000) and plays a significant ecological and evolutionary role in this spiny mouse assemblage (Weissenberg et al. 1997; Shargal et al. 1999; Jones and Dayan 2000; Jones et al. 2001). It was recently suggested that torpor also must play a significant role in allowing small mammals to sustain times of increased risk of predation (Bieber and Ruf 2009; Riek et al. 2011), but never has been tested. We suggest that it also may play a similar role in our spiny mouse system. This, however, remains to be studied.

Availability of resources in desert environments exhibits strong and largely unpredictable fluctuations in space and time. Therefore torpor, clearly a

significant physiological response in spiny mice, is most likely a common mechanism that allows small mammals to cope with sporadic gaps between the availability of resources and the requirements for energy. Therefore, torpor impacts both, the levels of interspecific competition and the effect of competition on the fitness of individuals.

In summary, both competition and torpor in small mammals are related to availability and/or accessibility of resources; competition drives the use of torpor while torpor must allow species to sustain periods of resource shortages that may be competitively induced, and thus function as an additional mechanism mitigating competitive interactions.

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