

Two strategies for coping with food shortage in desert golden spiny mice

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Abstract

Desert rodents face periods of food shortage and use different strategies for coping with it, including changes in activity level. Golden spiny mice (*Acomys russatus*) inhabit rock crevasses and do not dig burrows nor store food. When kept under 50% food restriction most, but not all, golden spiny mice defend their body mass by physiological means. We tested the hypothesis that these rodents use two different behavioral strategies, i.e., increasing activity level and searching for food or decreasing activity level and conserving energy to cope with food shortage. Twelve golden spiny mice were fed *ad libitum* for 14 days, followed by 40 days of 50% food restriction, and 14 days of refeeding. Body mass, food consumption and general activity were monitored. Seven mice significantly reduced activity level, concentrating their activity around feeding time, lowering energy expenditure and thus keeping their body mass constant (“resistant”), while five (“non-resistant”) significantly increased activity level (possibly searching for food) and thus energy expenditure, thereby losing mass rapidly (more than 25% of body mass). The non-resistant golden spiny mice were active throughout many hours of the day, with high variability both between and among individuals. The use of two strategies to cope with food shortage as found in the golden spiny mice may be of evolutionary advantage, since it allows a more flexible reaction to food restriction at the population level.

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1. Introduction

Desert environments are characterized by unpredictable food availability, and animals may face periods of food shortage. In rodents, different strategies for coping with food shortage have been described, including the use of torpor (e.g., [1–6]), food hoarding (e.g., [5–11]), and increasing foraging activity or migration (e.g., [12]).

The term “torpor” is generally used for a variety of states in which metabolic rate, during a part of the circadian cycle, falls below its normal resting level, permitting body temperature to approach ambient temperature, and thus saving the metabolic cost of thermoregulation [13]. The other strategies involve a change in activity level: keeping activity level low, or even lowering it under food restriction serves as a mechanism for conserving energy (as employed by e.g., chipmunks [*Eutamias minimus*], ground squirrels [*Citellus townsendi*], dormice [*Glis glis*], [12], deer

mice [*Peromyscus*], [14]). On the other hand, increased activity level was found in several rodent species under food restriction (e.g., rats [*Rattus norvegicus*], hamsters [*Mesocricetus auratus*] and guinea pigs [*Cavia porcellus*], [12], house mice [*Mus musculus*], [14]), a behavior that was termed starvation-induced hyperactivity (SIH). SIH is usually studied using running wheels, but was described also in the absence of a running wheel (e.g., [3,15–18]). It was suggested that the increased activity during food restriction represents an increase in foraging or migratory behavior, which may increase the chances of survival in a free-living animal [12,15,19–22].

The interspecific variation in the response to food restriction described above has been ascribed to natural selection operating on the different species, against the background of their habitat, diet, physiology etc. (reviewed by [22,23]). For example, Cornish and Mrosovsky [12] suggested that hibernators that become obese before the hibernation period are relatively unmotivated by food restriction, and will not increase (or indeed decrease) their activity level during food restriction.

The golden spiny mouse (*Acomys russatus*) which inhabits rocky deserts in Jordan, Sinai (Egypt), and the south of Israel

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[24] inhabits rock crevasses, does not dig burrows and does not store food [25], possibly because its diet is comprised mainly of arthropods [26], which cannot be stored. A recent study showed that arthropods abundance in the golden spiny mice natural habitat fluctuates at the daily and seasonally levels, and their abundance is relatively low in winter [27,28]. Therefore, we assume that these rodents are exposed to food shortage periods. It was previously shown that under 50% food restriction, most golden spiny mice, which we called “resistant”, reduce their metabolic rates in order to balance their body mass for a prolonged period of time, using torpor or a torpor-like state [6,29]. We also found that two out of the 12 food-restricted golden spiny mice showed a different response to food restriction: they lost weight at a higher rate than the others, and in order to prevent death from starvation, we terminated the food restriction period for these two individuals at an earlier stage. We called these mice “non-resistant” [6]. Such interindividual variability was not reported by Ehrhardt et al. [29], who reported an increase in activity level, with high variability ($127 \pm 44\%$) as a result of food restriction. However, a similar observation was documented by Rubal [30], in which two out of six golden spiny mice lost weight and did not survive a 60% food restriction. The two individuals that did not balance their body mass in Gutman et al. [6], did not reduce but even increased (albeit not significantly) their average daily metabolic rates (ADMR), in contrast to the other individuals, although they did reduce their core body temperature [6]. We assumed that the high ADMR observed in these individuals, even though they employed torpor like the resistant golden spiny mice, could have resulted from increased general activity during the activity phase. In the current experiment we looked at the possibility that golden spiny mice use two different strategies, i.e., increasing or decreasing activity level, combined with the use of torpor, to cope with food shortage.

2. Methods

2.1. Animals and housing

A breeding colony of golden spiny mice originally trapped near the Dead Sea, Israel, is kept at the Meier I. Segals Garden for Zoological Research at Tel Aviv University (permit number 2003/16295). Twenty-one days before the experiment started, we randomly chose twelve mature (1–2 years old) golden spiny mice (six males and six females, average body mass 59.08 ± 2.56 g) from our colony. The mice were individually housed in $38 \times 24 \times 13$ cm plastic cages, under controlled laboratory conditions of 12:12 LD, and ambient temperature of 30 ± 1 °C (lower critical temperature of their thermal neutral zone) [31]. Water and rodent chow (Koffolk serial no. 19510) were provided *ad libitum*, or as specified in the experimental protocol.

2.2. Experimental protocol

The experiment started with 14 days of *ad libitum* feeding, followed by 39 days of food restriction (as in [6]) and 14 days of refeeding. Body weight and activity were monitored. During the

food restriction period, a weighed daily individual portion (50% of the individual measured average *ad libitum* daily consumption) was given around 10 min after dark period onset, when oxygen consumption, core body temperature and heart rate peaked under *ad libitum* food availability (see [6]). Based on a previous work on food restriction in golden spiny mice [30], where two out of the six individuals tested died from starvation after losing ca. 30% of their body mass, we decided to terminate food restriction if an individual would lose more than 25% of its average body mass at *ad libitum*. At the end of the food restriction period, we assigned the mice into two groups, according to Gutman et al. [6]: the first group (resistant) consisted of mice that were able to achieve a new constant body mass, defined as an insignificant effect ($P > 0.05$) of days at food restriction on five body mass measurements, 2–3 days apart. The second group (non-resistant) included all the individuals that continued to lose weight.

2.3. Body mass, food consumption and energy intake

Body mass was measured at least twice a week using an electronic scales (Sartorius, ± 0.1 g, or Sekel, ± 0.01 g). Individual *ad libitum* food intake was measured by giving a weighed (Sekel, ± 0.01 g) amount of commercial pellets. Orts and feces were collected after 48 or 72 h, dried to a constant mass at 60 °C, and weighed. Energy content of the pellets (19.3 ± 0.05 kJ g $^{-1}$) was measured using a bomb calorimeter (Gallenkamp), which was calibrated by ascending mass of benzoic acid (Analar, 26.45 kJ g $^{-1}$). Based on Grodzinski and Wunder [32] we assumed that metabolized energy intake (MEI) was 98% of the digested energy. Digestibility in golden spiny mice does not change significantly between *ad libitum* and food restriction ($85.33 \pm 0.57\%$, [6]). Therefore, following Gutman et al. [6], metabolized energy intake (MEI) was estimated to be 83.62% of the golden spiny mice gross energy intake.

2.4. General activity

Although wheel running is routinely used as a simple measure for activity monitoring in rodents, in the recent years several publications on different species (e.g., [20,33,34]), including golden spiny mice [35], have shown that wheel running may have an effect on activity rhythms. Therefore, we chose to monitor general activity using a custom-made system composed of infrared detectors (Intrusion detector model MH10, Crow group, Israel) that were placed above each cage and connected to a PC. Data were collected continuously using Workbench software (Strawberry Tree Inc.), at 6-min intervals.

2.5. Statistics

Daily activity level is presented in relation to individual average *ad libitum* activity. Activity rhythm is presented as percentage of the individual total daily activity level. Effect of food restriction on activity level was analyzed on arcsine-transformed data. Statistical analysis was performed using

STATISTICA 6 (StatsSoft, Inc., USA). Repeated measures ANOVA was used to detect and compare the effect of food restriction and refeeding on the different parameters measured (within factor, days at food restriction or at refeeding; between factor, type of golden spiny mice). Significant ANOVAs were followed by Fisher's least significant difference (LSD) post-hoc test. Significance level was defined as $P<0.05$. *T*-tests and paired *t*-tests were used to compare body mass between and within types of golden spiny mice at and between end points of diet regimes, respectively. Double plotted actograms were generated using Clocklab software (Actimetrics, USA).

3. Results

3.1. Body mass

Food restriction had a significant effect on golden spiny mice body mass ($P<0.001$, Fig. 1A). Seven (three females and four males) of the 12 golden spiny mice (resistant) adjusted their energy expenditure to their energy intake during food restriction, and were able to keep their body mass constant (at $94.2\pm0.4\%$ of their *ad libitum* body mass) during the last 2 weeks of food restriction ($P>0.05$, 5 consecutive measurements, 2–3 days apart as from the 25th day at food restriction, Fig. 1A). The other five mice (non-resistant, three females and two males) kept losing weight, and their body mass was

significantly lower than that of resistant golden spiny mice during the food restriction period ($P<0.05$, Fig. 1A). Of the five non-resistant mice, two mice lost more than 25% of their body mass after 21 days at food restriction, and were therefore refed. Two other mice lost more than 25% of their body mass after 39 days, and the fifth mouse, was at less than 85% of its averaged *ad libitum* body mass at the end of food restriction, and showing no sign of stabilization. Therefore, we included it in the non-resistant group.

Comparing body masses of the two groups during *ad libitum* food availability, no significant difference was found (LSD post hoc analysis of initial body mass, $P>0.05$, Fig. 1A). Nevertheless, a significant interaction was found between the effect of food restriction on body mass and animal type ($P<0.05$, Fig. 1A). Fisher LSD post hoc analysis revealed that at the end of food restriction, body mass of non-resistant golden spiny mice was significantly lower than that of resistant golden spiny mice ($P<0.05$).

During the 14 days of refeeding, both groups of golden spiny mice gained body mass ($P<0.001$) without any sign of stabilization (Fig. 1A). Body mass of resistant spiny mice was significantly higher ($P<0.01$) during the entire refeeding period (lack of a significant interaction, $P>0.05$, Fig. 1A). After 14 days of refeeding, resistant golden spiny mice reached a significantly higher body mass than their average body mass at *ad libitum*, ($113.83\pm2.08\%$, paired *t*-test, $P<0.001$, Fig. 1A), while body mass of the non-resistant group was similar to their average body mass at *ad libitum* ($102.28\pm4.27\%$, paired *t*-test, $P>0.05$, Fig. 1A). Thus, at the end of the experiment, resistant golden spiny mice were significantly heavier than the non-resistant animals (*t*-test, $P<0.05$, Fig. 1A).

3.2. Food consumption and energy intake

No significant difference between average *ad libitum* food consumption of the two groups was found (resistant: $2.60\pm0.12\text{ g}\cdot\text{day}^{-1}$, non resistant: $2.49\pm0.54\text{ g}\cdot\text{day}^{-1}$, $P>0.05$, *t*-test). Metabolized energy intake of the resistant golden spiny mice was $40.16\pm1.97\text{ kJ day}^{-1}$, and that of the non-resistant, $40.58\pm3.94\text{ kJ day}^{-1}$.

During *ad libitum* feeding in both groups, and during the last 2 weeks of food restriction in the resistant group, all mice maintained a constant body mass ($P>0.05$, Fig. 1A). Therefore, we can assume that during these periods their energy expenditure matched energy intake (assuming body composition did not change during that period, as measured using DEXA, [6]). Since energy intake during food restriction was 50% of *ad libitum* consumption, it can be concluded that energy expenditure of the resistant golden spiny mice during the last 2 weeks at food restriction had reduced by 50%, reaching $20.08\pm0.98\text{ kJ day}^{-1}$ (Fig. 2A). During that time, the non-resistant animals kept losing body mass at a constant average rate of 0.47 g day^{-1} (linear regression; $R^2=0.97$, $P<0.001$, Fig. 1A). As previously found by us and others, golden spiny mice use fat stores as an additional energy source during food restriction [6,29]. Therefore, energy expenditure of the non-resistant mice can be calculated as the sum of MEI and energy gained from oxidizing body fat (39.36 kJ g^{-1} , [36]), i.e., $20.08+$

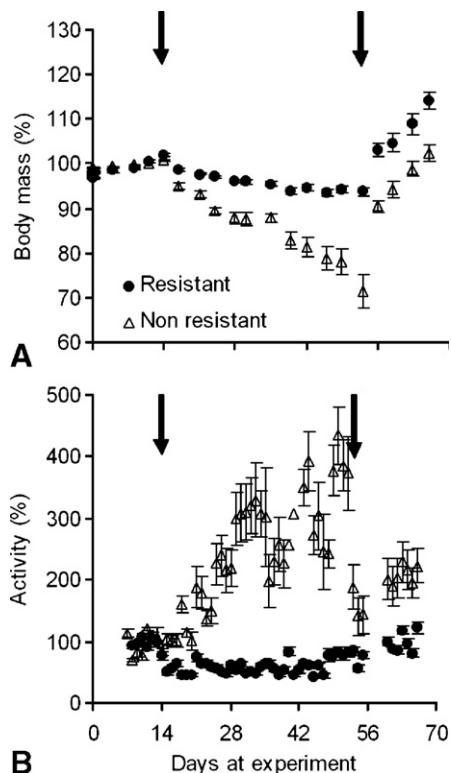


Fig. 1. Changes in body mass (A) and activity level (B) during *ad libitum* feeding, 50% food restriction (between black arrows) and refeeding, in resistant (circles, $n=7$) and non-resistant (triangles, $n=5$) golden spiny mice. Data (average \pm S.E.) are presented as percentage of individual average body mass (A) or activity (B) at *ad libitum*.

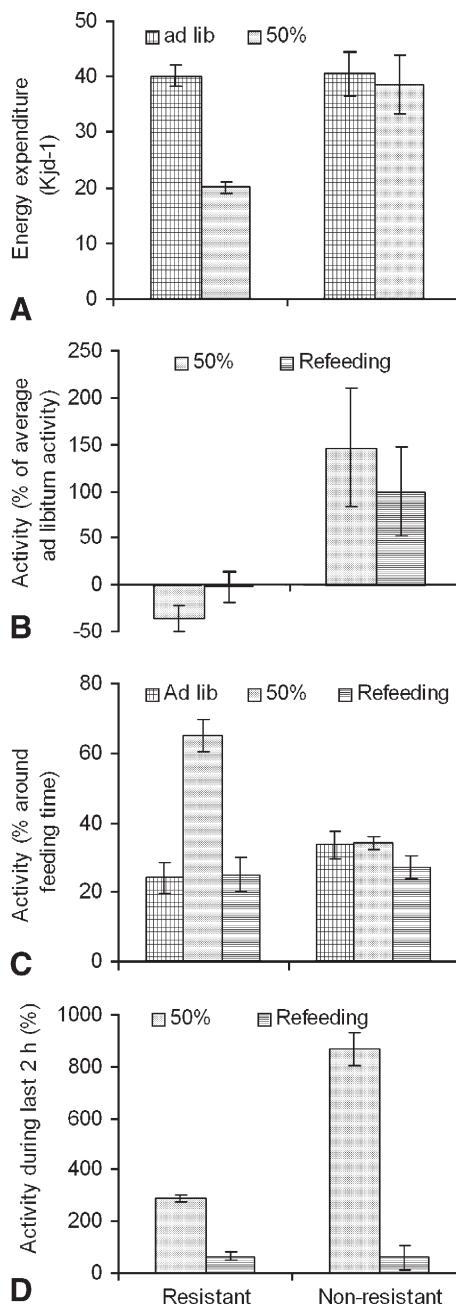


Fig. 2. Changes in daily energy expenditure (A), body mass (B), activity level (C), activity around feeding time (± 2 h around feeding time during food restriction: ca. 10 min after light offset) and during the 2 h preceding feeding time (D) during *ad libitum* feeding, 50% food restriction and refeeding, in resistant ($n=7$) and non-resistant ($n=5$) golden spiny mice. Data (average \pm S.E.) are presented in kJ day^{-1} (A), percentage of individual activity at *ad libitum* (B), percentage of individual daily activity (C) and percentage of individual average activity at *ad libitum* (D).

$0.47 \times 39.36 = 38.6 \pm 5.14 \text{ kJ} \cdot \text{day}^{-1}$, which is not significantly different from *ad libitum* energy expenditure ($P>0.05$, Fig. 2A).

3.3. General activity

Food restriction had a significant effect on golden spiny mice activity ($P<0.001$, Figs. 1B and 2B), and there was a significant interaction between food restriction and group ($P<0.001$, Figs.

1B and 2B): Resistant golden spiny mice significantly reduced their general activity (post-hoc analysis, $P<0.05$, from the first day of food restriction, Fig. 1B) while non-resistant mice significantly increased their general activity level (post-hoc analysis, $P<0.05$, from day 13 of food restriction, Fig. 1B). At that time point (day 13), activity level of resistant animals was minimal, reaching $47.98 \pm 3.91\%$ of their average activity at *ad libitum*, while activity level of the non-resistant animals was $213.62 \pm 36.68\%$ above their average *ad libitum* activity (Fig. 1B). During the last 2 weeks of food restriction, resistant golden spiny mice activity level was $65.38 \pm 5.18\%$ of *ad libitum*, while activity level of non-resistant golden spiny mice was over 400% of their *ad libitum* average activity level (Fig. 1B).

During the last week of refeeding, activity levels of resistant golden spiny mice returned to average *ad libitum* activity level (post hoc analysis, $P>0.05$, Figs. 1A and 2A), while that of the non-resistant animals was significantly higher than their average *ad libitum* activity level (post hoc analysis, $P<0.05$, Figs. 1A and 2B).

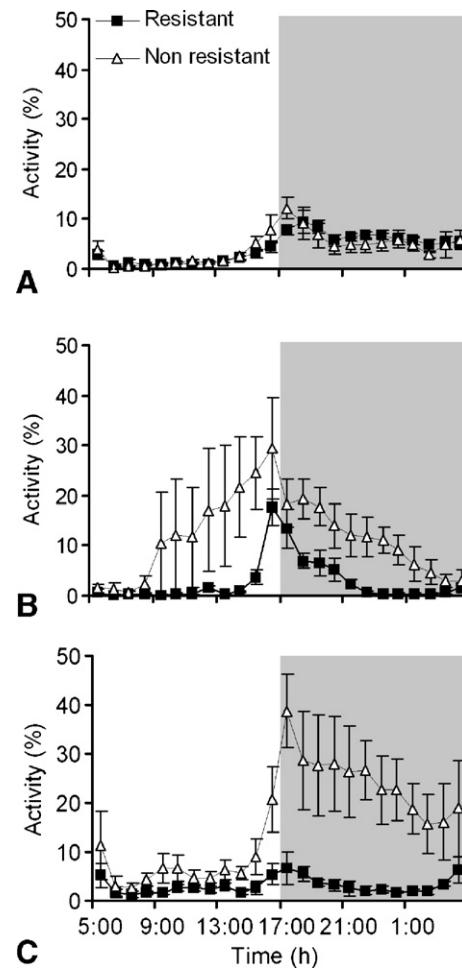


Fig. 3. Daily activity rhythms during *ad libitum* feeding (A), last 2 weeks of 50% food restriction (B) and refeeding (C) in resistant (squares, $n=7$) and non-resistant (triangles, $n=5$) golden spiny mice. Data (average \pm S.E.) are presented as percentage of individual daily activity level during *ad libitum* feeding. Lights off between 17:00 h and 05:00 h (gray area). Individual daily portion (50% of the individual average *ad libitum* daily consumption) was given about 10 min after lights offset.

3.4. Activity rhythms

During *ad libitum* feeding, there were no noticeable differences in activity rhythms between the two groups of animals: both were nocturnally active (Figs. 3A and 4A–F). We also analyzed the percentage of activity concentrated around food delivery time (± 2 h around feeding time during food restriction, which was about 10 min after dark period onset). There were no significant differences in percentage of activity concentrated around feeding time between the two groups during *ad libitum* feeding ($P>0.05$, Figs. 2C, 3A and 4). However, food restriction had a significant effect on percentage of activity around feeding time ($P<0.01$) and there was a significant interaction with group of golden spiny mice

($P<0.01$, Figs. 2C and 3B): during food restriction, resistant mice concentrated $65.18\pm4.63\%$ of their activity around feeding time as opposed to 24.28 ± 4.44 during *ad libitum* feeding (post-hoc analysis $P<0.05$, Figs. 2B–C and 4A–F). Percentage of activity around feeding time of non-resistant mice did not change significantly during food restriction (33.45 ± 4.20 during *ad libitum* feeding vs. $34.15\pm1.95\%$ throughout food restriction, post-hoc analysis $P>0.05$; Figs. 2C and 3B). Furthermore, during food restriction, non-resistant golden spiny mice were active during many hours of the day (Figs. 3B and 4D–F), with high inter-individual variability (Figs. 3B and 4D–F), while resistant animals displayed a typical activity pattern, concentrating activity around feeding time (Figs. 3B and 4A–C). Food anticipatory behavior (increase arousal and activity during the

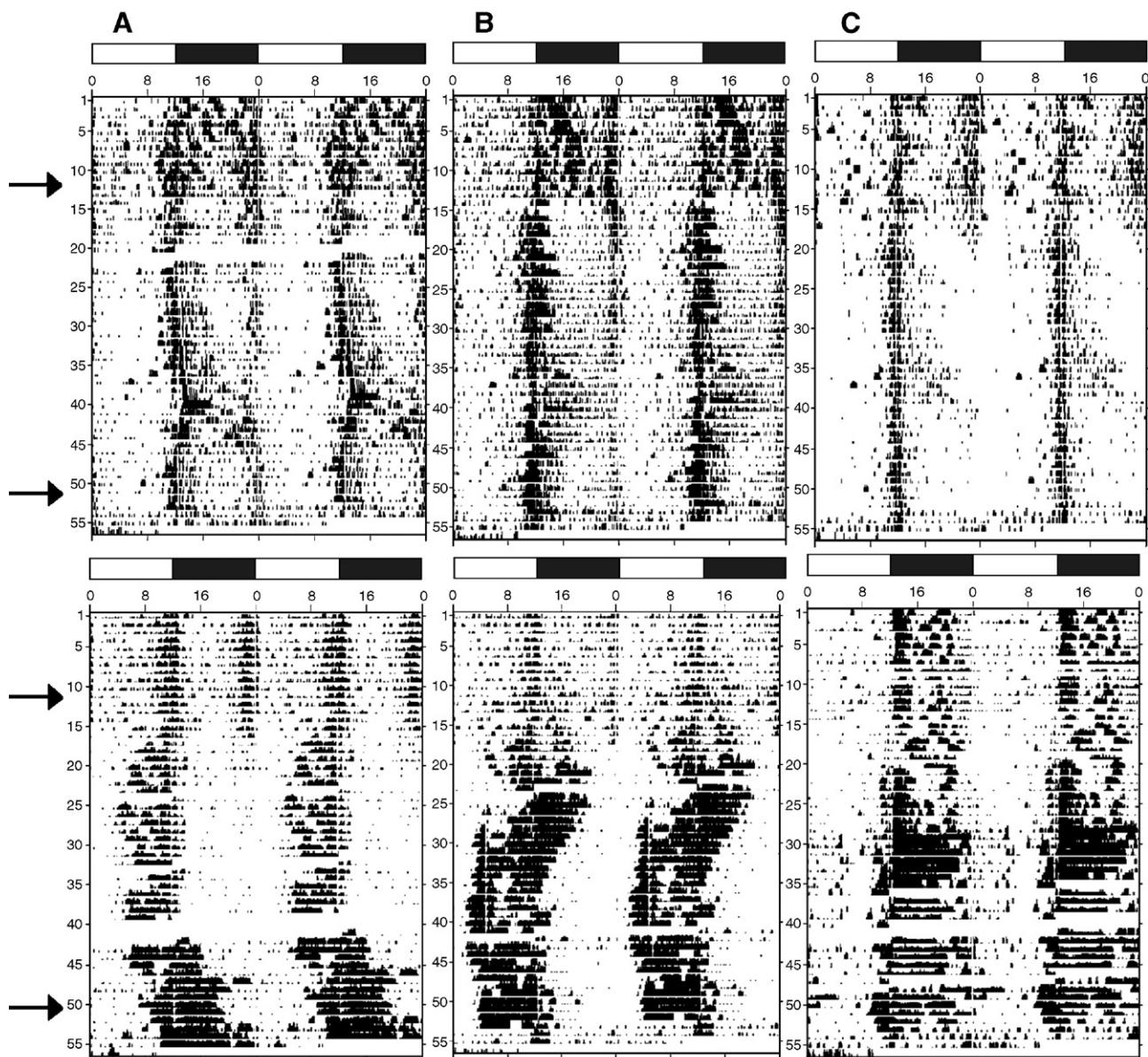


Fig. 4. Double daily plots of activity levels of three representative resistant golden spiny mice (upper line, A–C) and three representative non-resistant golden spiny mice (lower line, D–F) during *ad libitum* feeding, 50% food restriction (between black arrows) and refeeding. Xaxis represents zeitgeber time. Dark bars at the top of the plots represent the dark hours. During food restriction, individual daily portion (50% of the individual average *ad libitum* daily consumption) was given about 10 min after lights offset.

hours immediately preceding feeding time) [37] was displayed by both types of golden spiny mice: in both, maximal activity level under food restriction was observed during the hours immediately preceding feeding time. Furthermore, in the non-resistant animals, activity level during these hours increased by 870%, while average daily activity level increased by 150%. In the resistant animals activity level during these hours increased by 289%, while average daily activity level decreased by 36% (Figs. 2D and 3A–B).

During refeeding, even though activity levels were significantly different from *ad libitum* activity levels, activity patterns of both groups were similar to *ad libitum* patterns: percentage of activity around feeding time was not significantly different from *ad libitum* (post-hoc analysis, $P>0.05$, Fig. 2C) and both groups displayed a nocturnal activity rhythm similar to activity rhythms during *ad libitum* (Fig. 3C).

The high inter-individual variability of activity pattern during food restriction in the non-resistant mice resulted at least in part from spontaneous shifts in their activity pattern (Fig. 4D–F). For example, one individual (Fig. 4D) shifted its activity from nocturnal to diurnal a few days after the beginning of food restriction, and spontaneously returned to nocturnal activity a few days before the end of the food restriction period (Fig. 4D). Another individual (Fig. 4E), displayed a different pattern: at the beginning of food restriction it concentrated its activity in the dark hours, and after about 10 days of food restriction shifted into a more diurnal pattern (Fig. 4E).

4. Discussion

During food restriction, seven out of the twelve individuals tested reduced their activity levels, and presumably entered a daily torpor, a strategy employed by golden spiny mice [6,29] and numerous other species during food shortage periods (e.g., [5,15,38]; reviewed by [13]). The capability of this species to enter torpor may contribute to its survival in its unpredictable desert habitat by enabling energy and water conservation during transient food shortage periods.

General activity level of the other five individuals increased in response to food restriction, as was previously documented in several other species (e.g., lemurs, [3], Djungarian hamsters, [15], mice, [17]). This increase may resemble starvation-induced hyperactivity, observed in numerous and diverse species in the presence of a running wheel (reviewed by [19,20,22]). The observed increase in general activity levels may represent an increase in foraging behavior, or in travel or migration behavior to a new habitat in the free-ranging animal, an interpretation suggested for increased wheel running in response to food restriction [12,19–21] and for general activity in Djungarian hamsters [15]. There was no difference between males and females in the response to food restriction, and both showed both responses. Therefore we do not separate the results or the discussion by sex.

These results suggest that within the golden spiny mouse population, two strategies for coping with food shortage exist: some individuals counter the lower energy intake by lowering energy expenditure, entering daily torpor, reducing activity

level, and waiting for better times; while other individuals increase activity level, attempting to increase energy intake by increasing foraging or by migrating to a better habitat. It is currently unclear whether the individual spiny mouse can alternate between the two strategies, or if each individual uses one strategy only, if the different strategies represent phenotypic plasticity or are genetically determined, or what the factors or mechanisms that maintain the polymorphic reaction are. These issues deserve further study.

In rats, body mass must fall to some relatively fixed critical level before activity substantially increases [39], and there is a correlation between pre-deprivation body mass and days to peak activity [40]. The behavioral changes in activity levels, reflecting the search for food, are triggered by the utilization of body protein vs. lipid stores [39]. We found no significant difference in activity levels or body masses of the two groups before food restriction, and no correlation between body mass or body mass loss and the increase in activity level. Therefore, we conclude that the different responses to food shortage that we observed do not result from the same phenomenon. Furthermore, since all individuals used in the current study (as well as in 6) originated from our laboratory colony raised under *ad libitum* food supply for several generations, these different responses to food shortage do not result from prior acclimatization to different conditions, or from gestational programming [41]. Another possible trigger for the use of the different strategies may involve plasma leptin levels: it was found that in rats, leptin suppresses semi-starvation induced hyperactivity, and that hypooleptinemic patients rank their motor restlessness higher than upon attainment of their maximal leptin level during inpatient treatment [21]. Therefore, it was suggested that hypooleptinemia, as a result of food restriction, may represent the initial trigger for the increased activity levels in human patients with anorexia nervosa and in food-restricted rats [21,22]. It is possible that the development of the two strategies for coping with food shortage in golden spiny mice are related to plasma leptin levels, i.e., that the non-resistant golden spiny mice have lower leptin levels than the resistant golden spiny mice, and that these low levels are required, or even trigger, the increase in activity levels. We are currently testing this hypothesis.

The use of two strategies to cope with hostile environmental conditions was previously described in Djungarian hamsters (*Phodopus sungorus*, [15]), and in grey mouse lemurs (*Microcebus murinus*, [3]), where animals may be able to use different tactics, alternating foraging and entering periods of inactivity associated with daily torpor bouts induced by starvation. Such individual variation may have an ecological advantage, since it allows a flexible response of the population towards fluctuations in food availability, especially in desert habitats, where food availability fluctuates unpredictably in space and time.

The energy available for an individual is the sum of energy consumed as food plus the energy stored within the body. Energy expenditure of golden spiny mice was calculated from their individual food intake, and the individual decrease in body mass. Since the resistant golden spiny mice maintained their

body mass constant (after the initial decrease), we conclude that during the 50% food restriction, the decrease in their activity level and the presumed use of torpor led to 50% decrease in energy expenditure, as we had previously documented by measuring oxygen consumption in this species [6]. Energy expenditure of golden spiny mice that increased their activity level remained constant, as we had previously documented [6]. This constant energy expenditure probably resulted from the use of daily torpor during the rest periods combined with increased activity during the activity period. Hence, the energy conserved by the use of torpor was used for increasing activity level.

During food restriction, resistant golden spiny mice concentrated their activity in the beginning of the dark period (when daily food portion was given) and displayed food anticipatory behavior; the non-resistant golden spiny mice also displayed food anticipatory behavior, but their activity rhythm was highly variable, both among and between individuals. The golden spiny mice are well known for their ability to switch activity time, and be either nocturnally or diurnally active (e.g., [42]). This is rather uncommon: nocturnal and diurnal activities are accompanied by physiological, behavioral and anatomical adaptations. Therefore, transitions between nocturnal and diurnal lifestyles are relatively rare ([43–45]; reviewed by [46]). In their natural habitat, the golden spiny mice change their activity pattern as a result of environmental conditions: interspecific competition with the common spiny mouse [47,48] or thermoregulation [49]. Recent evidence suggests that the interspecific competition is at least partly resource mediated, with food as the limiting factor [50]. The two competing spiny mice species are primarily insectivorous [26]. Different arthropod taxa in the spiny mice habitat were found to be active during day or night, suggesting that temporal partitioning could indeed be a mechanism of coexistence between the two species [27,28]. It is possible that when we food-restricted the animals, they switched activity times in order to increase the chances to find higher food availability. Food availability manipulations on golden spiny mice in controlled experimental enclosures in their natural habitat showed that when food (rodent chow) was added, they changed activity patterns, suggesting that resource level may indeed be a proximate cue for activity preferences of these rodents [50].

During refeeding, both groups of golden spiny mice gained body mass without any sign of stabilization. Body mass of the resistant group was significantly higher than their average *ad libitum* body mass, while that of the non-resistant group was not significantly different from their *ad libitum* body mass. Both groups adjusted their activity levels to the change in food availability: resistant animals increased their activity level, and returned to their average *ad libitum* activity level, while the non-resistant animals reduced activity level, however, it still remained significantly higher than their average *ad libitum* activity level, supporting the hypothesis that the changes in activity levels of both groups have developed in order to cope with temporal food shortage.

In summary, desert rodents face periods of food shortage and use different strategies for coping with it, including changes in activity level. In this study we have shown that golden spiny mice use two different behavioral strategies, i.e., increasing activity

level possibly in order to search for food at the expense of energy usage, thus losing mass rapidly (non-resistant), or conserving energy by decreasing activity level, adjusting energy expenditure to energy intake and maintaining body mass constant (resistant). The use of two strategies may be of evolutionary advantage, since it allows a more flexible reaction to food restriction at the population level.

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