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LETTER

Foraging sequence, energy intake and torpor: an individual-based field study of energy balancing in desert golden spiny mice

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Abstract

We studied the relationship between sequence of foraging, energy acquired and use of torpor as an energy-balancing strategy in diurnally active desert golden spiny mice. We hypothesised that individuals that arrive earlier to forage will get higher returns and consequently spend less time torpid. If that is the case, then early foragers can be viewed as more successful; if the same individuals arrive repeatedly early, they are likely to have higher fitness under conditions of resource limitation. For the first time, we show a relationship between foraging sequence and amount of resources removed, with individuals that arrive later to a foraging patch tending to receive lower energetic returns and to spend more time torpid. Torpor bears not only benefits but also significant costs, so these individuals pay a price both in lower energy intake and in extended periods of torpor, in what may well be a positive feedback loop.

Keywords

adaptive thermoregulation, costs, energy balance, field study, fitness, food intake, foraging, golden spiny mice, individual, torpor.

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INTRODUCTION

Living organisms depend on energy for maintenance, growth and reproduction. Therefore, foraging, the process of energy acquisition by animals, is subject of much empirical and theoretical work, which has already provided significant scientific insight and theory (Stephens & Krebs 1986; Stephens *et al.* 2007). Much empirical foraging research was carried out on small mammals at the population level, yet we know that there are important fitness-relevant interindividual differences in foraging abilities. It is assumed that individuals that are efficient foragers will have higher fitness and hence be selected for (Stephens & Krebs 1986; Stephens *et al.* 2007). Conversely, fitness of individuals that are not able to meet their energy demands is adversely affected to the point of death. This is particularly significant for endotherms, whose energy requirements are relatively high. Therefore, endotherm species have evolved to cope with periods of low resource availability by controlled reduction in body temperatures (T_b) (hibernation and daily torpor); under these conditions, hibernation and tordpor increase individual fitness and survival (e.g. Geiser & Turbill 2009; Stawski & Geiser 2010a, b; Turbill *et al.* 2011). While hibernators respond to an anticipated climatic cooling during winter, daily heterotherms become torpid as a rapid short-term response to unpredictable environmental stresses of low resource levels and/or climatic extremes (Lovegrove *et al.* 1991; Geiser & Ruf 1995), to increased predation risk (e.g. Stawski & Geiser 2010a; Turbill *et al.* 2011), to competition (Levy *et al.* 2011b) and to enhance fat storage for future energy demands (Stawski & Geiser 2010a). Thus, while seasonal hibernation is an evolutionary adaptation to predictable harsh environmental conditions, daily torpor has evolved to respond adaptively to environmental challenges at the ecological scale, allowing individuals to balance their energy budgets in response to foraging success and environmental stress over the short term. It is the latter adaptation that allows individuals to balance their energy budgets in response to their foraging success at the short-term scale; this is the focus of our research.

The individual's balance between energy intake and energy expenditure determines its fitness. However, although various studies have speculated about the relationship between individual-level foraging success and use of daily torpor (e.g. Landry-Cuerrier *et al.* 2008), no field studies to date have tested it. We studied individual-level foraging in desert-dwelling golden spiny mice (*Acomys russatus*) asking how foraging success, measured by sequence of arrival to artificial foraging patches and time spent foraging, manifested in energy intake and, consequently, in use of torpor as an energy-balancing strategy.

The theory of adaptive thermoregulation suggests that endotherms should depress metabolism and T_b only when costs of homeothermy outweigh the benefits (e.g. Humphries *et al.* 2003; Angilletta *et al.* 2010). When costs are high, depressing metabolism and T_b may enhance survivorship and fitness. Under cold environmental conditions, for example, an individual may reduce its T_b and save energy that would have been invested in thermoregulation. However, the physiological performance of this individual will also decrease (Humphries *et al.* 2003; Angilletta *et al.* 2010; Roth *et al.* 2010).

The adaptive value of optimal thermoregulation in endotherms was studied extensively using food availability and/or climate conditions as key factors (e.g. Landry-Cuerrier *et al.* 2008; Stawski & Geiser 2010b). Research reveals that while some daily heterotherms enter torpor spontaneously in response to fixed cues, such as day length, others, such as eastern chipmunks and spiny mice, become torpid in response to adverse environmental conditions, such as limited food and/or colder environmental conditions; conversely, individuals refrain from becoming torpid if conditions allow it (Levy *et al.* 2011a; Humphries *et al.* 2003). Thus, foraging success that impacts individual food availability should impact torpor in such species.

We studied the relationship between foraging success and torpor in individual golden spiny mice, under semi-natural conditions. Golden spiny mice respond to absence of their nocturnal congener, the common spiny mouse (*Acomys cahirinus*), by shifting some of their activity into the night (Shkolnik 1971; Gutman & Dayan 2005). Previous

studies suggested that common spiny mice have competitively displaced golden spiny mice into diurnality, and that food partitioning by arthropod prey activity times is a mechanism of coexistence (Kronfeld-Schor & Dayan 1999; Kronfeld-Schor *et al.* 2001; Kronfeld-Schor & Dayan 2003, 2008; Levy *et al.* 2007; Vonshak *et al.* 2009). Thus, spiny mice in this system appear to be food limited.

Golden spiny mice defend their body mass by using torpor during food shortage periods and gain fat mass when food is plentiful (Kronfeld-Schor *et al.* 2000; Ehrhardt *et al.* 2005; Gutman *et al.* 2006, 2007, 2008). They do not hoard food, have no cheek pouches and consume mainly animal matter, which is difficult to store; therefore, food foraged is food consumed. Golden spiny mice use torpor, probably as a strategy to save energy and water; use of torpor decreases when food is supplemented (Levy *et al.* 2011a). Moreover, golden spiny mice spend more time torpid in presence of *A. cahirinus* (Levy *et al.* 2011b). Nevertheless, part of the high variation in the intensity and duration of torpor in this species remain unexplained; we hypothesised that it reflects individual-level differences in foraging success.

We used artificial foraging patches; the first individual to arrive at a patch will find the highest food density and is expected to get the highest returns per time spent foraging; subsequent foragers will get diminishing returns. We hypothesised that different individuals will exhibit different abilities of energy acquisition, manifested in their sequence of arrival at foraging patches and the amount of energy removed and consequently, in differential use of torpor. All else being equal, individuals that consume more energy and spend less time torpid would have higher fitness. Alternatively, there may be no relationship between foraging sequence and time spent torpid, or, such a relationship may occur, but the sequence of arrival at the foraging patch will be haphazard, hence no long-term differences in energy intake and in torpor will be detected, and no long-term fitness implications are expected.

Our working hypothesis was that there is an inverse relationship between foraging success and use of torpor in this system. Specifically, we asked the following questions: (1) Does sequence of arrival at the foraging patch determines foraging success, where the first forager gains more food from the patch and the other sequentially diminishing returns? (2) Each day, will total amount of food foraged correlate with sequence of arrival at the first foraging patch? (3) Each day, will use of torpor correlate to sequence of arrival to the foraging patch? (4) Is there a regular individual-level sequence of arrival to foraging patches? (5) If such a sequence occurs, will it correlate to use of torpor over time?

MATERIALS AND METHODS

Experimental protocol

Experiments were conducted in the winter of 2007–2008 (November and January). Each month, body mass was taken before the experiment, and T_b, ambient temperature (T_a) and foraging activity were measured for four consecutive days (see below) under new moon conditions.

Experimental enclosures

We conducted our experiments at Ein Gedi nature reserve, in the Judean Desert, near the Dead Sea (31° 28′ N, 35° 23′ E, 300 m below sea level), in three 1000 m^2 field enclosures containing golden and common spiny mice. We trapped and removed all individuals and populated each enclosure with four individuals of each species, maintaining a sex ratio of 1 : 1, at least a month prior to the experiment. Mice were captured in the area, using Sherman live traps, and individually implanted with PIT tags (Passive Integrated Transponder; Destron-Fearing, South St. Paul, MN) for identification. The enclosures were constructed of 10-mm wire mesh buried 30-cm into the ground and standing 70-cm high, allowing mouse predators (foxes, snakes, owls and raptors) and prey (mostly arthropods) to enter and exit freely.

Monitoring T_b and T_a

T_b was measured using single-stage implantable transmitters (*ca.* 2 g; Sirtrack Ltd, Havelock North, New Zealand). Each implanted radiotransmitter uses a unique frequency, enabling individual identification. The transmitter uses a comparison circuit against which the reference pulse period is determined by temperature. We used two RX-900 scanner-receivers (Televilt Ltd, Lindesberg, Sweden) connected to two dipole antennas for data logging, and connected to a solar panel charged battery (450A; Schnapp Ltd, Netanya, Israel) (SQ80; Shell Ltd, Camarillo, CA, USA); they worked constantly during the experimental period. Data for each transmitter were logged once every ~20 min. Before implantation, transmitters were calibrated in a water bath using a precision mercury thermometer. We converted the pulse period to a temperature using the calibration curves produced with five different temperatures. Transmitters were implanted in 12 individuals (n = 4 in each enclosure). Of these, we successfully monitored 11 during November and six during January.

T_a was measured at the 'under boulder' (UB) microhabitat (on a rock terrace with overhead shelter) to the nearest 0.5° C every 30 min using a data logger thermometer (iButton ds1921 thermochron; Dallas Semiconductor, San Jose, CA, USA) placed in one enclosure, representing the microhabitat used most frequently by spiny mice.

Animal surgery

Mice were trapped, anaesthetised with isoflorane in medical grade oxygen using anaesthetic machine (Ohmeda) and implanted with transmitters in the abdominal cavity. The abdominal wall and the skin were sutured with absorbable surgical suture, with cutting needle (5–0 Dexon), and the incision was treated with topical antibiotic (silver sulfadiazine 1%; Silverol Cream). Prophylactic antibiotics (Baytril 5% 24 mg kg^{-1}) and artificial tear ointment (to prevent desiccation) were administered pre-operatively. Mice were returned to their enclosures 48 h after capture. After a week's recovery period, T_b's were monitored continuously.

Monitoring food consumption of spiny mice

We used auto-monitored foraging patches, comprising a plastic tray (25-cm diameter), in which 2 L of local soil were mixed with 3 g of broken sunflower seeds (individual golden spiny mouse energy requirement per day is met with 2 g of sunflower seeds). Food patches were protected from foraging birds by heavy wire frames and fine filament fish netting. Mice reached the trays easily by biting through one strand in the net. We placed a round antenna (20-cm

diameter) and a transceiver (2001F-ISO; Biomark Ltd, Boise, ID) beneath the tray, logging the tag ID and time (in s) of each mouse that entered the patch. Solar panels provided power supply. Three patches were placed in each enclosure, one in each microhabitat: 'UB', 'between boulders' (BB) (on the terrace surrounded by large stones, but no overhead cover) and an 'open' (O) microhabitat (detailed description of microhabitats in Gutman & Dayan (2005)). These microhabitats constitute a gradient in the degree of shelter from predation, with UB the safest from avian predators and O the least protected.

Foraging patches were replenished at dawn, and at dusk; we sieved the soil to retrieve all remaining seed particles and weighed them as a measure of giving-up density (GUD). We approximated the amount of seeds consumed by each individual during each visit, and hence their overall daily seed consumption, using the GUD values and the individual-level data obtained by the auto-monitored foraging patches (see below).

Data and statistical analysis

During each experimental month, a 4-day monitored foraging session took place, yielding in total *c.* 70 000 foraging logs and *c.* 170 000 T_b records. We developed a computer program that computes T_b according to the transmitter-specific calibration curve and enters the foraging, T_b and T_a records into a database (MySQL, version 5.1). 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 as biologically unreasonable (for R code see Levy *et al.* 2011a). We did not include data from the 'open' habitat in the statistical analysis because only three individuals were recorded foraging there, making the sample size too low for statistical inference.

Foraging data

We approximated the amount of seeds consumed from the foraging patches by constructing a harvest rate curve to the foraging activity. We used a generalised Poisson log-normal model to calculate the attack rate (a) and handling time (h), by fitting the data to a modified version of Holling's (1959) disc equation (e.g. Kotler & Brown 1990):

$$t = (1/a)\ln(N_0/N_f) + h(N_0 - N_f)$$

where t is foraging time, a is attack rate (s^{-1}), h is handling time ($s \times g^{-1}$), N_0=3 g of sunflower seeds is the initial amount of food in the patch, and N_f is the remaining amount of seeds in the patch after foraging (GUD). We tested the fit of the model using model efficiency criteria (EF) (Waller *et al.* 2003). For simplicity, we assumed that the function parameters did not vary between microhabitats; we found no improvement in the fit of the model when we allowed the function parameters to vary between microhabitats ($\Delta EF = 0.019$ in favour of the parsimonious model). Our model estimated an attack rate of 5.6×10^{-4} (s^{-1}) and handling time of 12.67 ($s \times g^{-1}$). Using the harvest curve, we were able to model the amount of seeds consumed from a tray as a function of exploitation time (Fig. 1), and hence, to calculate the daily amount of seeds each individual consumed from a specific foraging tray. The modified Holling's (1959) disc equation parameters and the amount of food consumed as a function of exploitation time were estimated using Bayesian inference (see below).

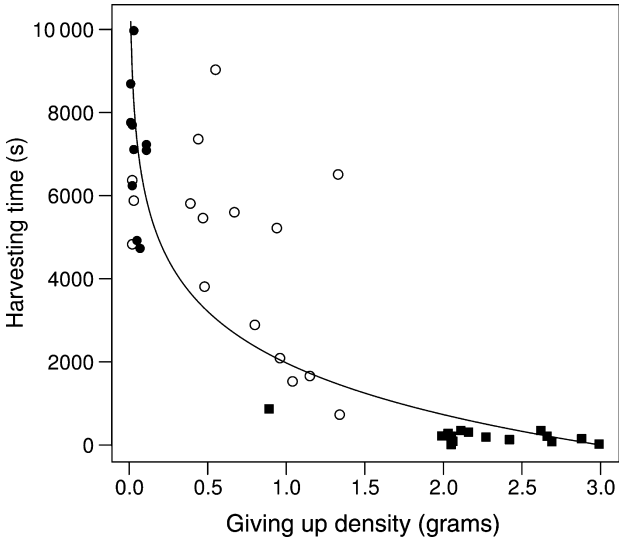

Figure 1 The golden spiny mice harvest curve (line) as predicted by the measured giving-up density (GUD, i.e. the amount of seeds remained in a foraging patch) and the measured harvesting time (i.e. the amount of time mice exploited the patch) at the UB (●), BB (○) and open (■) microhabitats.

As we populated each enclosure with four mice, order of entry to each foraging patch was between nos. 1 and 4, that is, each day, individual no. 1 was the first to enter the patch, no. 2 was the second, no. 3 was the third and no. 4 was the last. Every day, we determined the order of entry in the UB and BB microhabitats for each enclosure. For each individual, we also determined a daily sum order of entries that was the sum of the individual's order of entry into the UB and into the BB microhabitats. The daily sum of orders was between nos. 2 and 8, where no. 2 means that the individual was the first to enter the foraging patch at both UB and BB microhabitats, and no. 8 means that the individual was the last to enter both foraging patches. For each individual, we calculated the mean order of entry of each microhabitat and the mean sum of orders across days.

We asked whether two individuals can forage concurrently within a patch. Spiny mice display aggression when kept in high densities in our zoo colony. We measured the length of each time when two individuals were recorded in the same patch.

T_b data

We calculated individual mean T_b at each 20-minute interval during the entire 4-day experimental session. We quantified use of torpor, defining the torpor T_b threshold as in Willis (2007). For each day, we calculated individual total time torpid, and the time of arousal from torpor. Bout duration was determined as time between the beginning of the torpor bout (first data point when T_b was below torpor threshold), until the animal's T_b returned to normothermy range (first data point when T_b increased above the torpor threshold).

Statistical analysis

We tested (1) the relationship between daily order of entry and daily amount of food consumed by individuals; (2) the relationship between body mass and daily order of entry; (3) the relationship between daily order of entry and between daily time spent torpid; (4) the relationship between the time of arousal from torpor and daily order of entry; (5) the relationship between the time of arousal from

torpor and daily time spent torpid; (6) the relationship between mean order of entries of each individual to mean order of entries of the other three individuals from the same enclosure and (7) the relationship between mean order of entries and between mean daily seeds consumed of each individual and mean daily time spent torpid.

We used linear mixed effects ANCOVA for all tests with individuals or enclosures as the random factor. We used Bayesian inference because of the observational nature of the study (Anderson *et al.* 2000) and ran the statistical models using a Markov Chain Monte Carlo (MCMC) simulation implemented in the JAGS computer program (Plummer 2008). We used non-informative priors for all model parameters. The R CODA software package (Plummer *et al.* 2009) was used to calculate parameters' estimation (with standard deviations, 95% confidence intervals [95% CI] and *P*-values) and to test their convergence.

For all tests, all statistical models were built separately for each microhabitat, and the effect of the tested covariate was statistically compared between the two microhabitats. This approach is similar to the addition of a covariate × microhabitat interaction term, but it also enabled us to determine the variance explained by each covariate (determined by R^2) separately for each microhabitat. We also used deviance information criterion (DIC; Spiegelhalter *et al.* 2002) to compare the predictive values of the three orders of entry (UB, BB or the sum of both) as factors affecting the daily time spent torpid (i.e. in tests 3, 7); the DIC is the Bayesian counterpart of AIC. In test 3, we added the daily minimum T_a as a covariate and a 'power of the covariance' variance structure with minimum T_a as the variance covariate to deal with heterogeneity in the data (see Zuur *et al.* 2009). In test 7, we added an exponential variance structure with the mean order of entry as a variance covariate to deal with heterogeneity in the data (see Zuur *et al.* 2009). We used DIC to decide whether each of the variance structures in tests 3 and 7 contributed to the models adequacy (tests not shown). We report estimates ± SD, 95% CI, *P*-values and R^2.

RESULTS

Daily order of entry and the amount of food consumed

Order of foraging in the patches had a significant negative effect on the calculated amount of food consumed. The amount of food consumed was lower by 0.35 ± 0.10 g (95% CI – [−0.54, −0.15], $P < 0.01$, $R^2 = 0.65$) in the UB microhabitat and by 0.17 ± 0.06 g (95% CI – [−0.29, −0.06], $P < 0.01$, $R^2 = 0.46$) in the BB microhabitat with each increase in one order of entry (Fig. 2A and B). There was no significant difference in the effect between the two microhabitats (ΔUB-BB = −0.18 ± 0.11, $P = 0.13$, 95% CI – [−0.4, 0.1]). This negative correlation was also observed when analysed for both microhabitats: the amount of food consumed was lower by 0.26 ± 0.07 g (95% CI – [−0.40, −0.11], $P < 0.001$, $R^2 = 0.66$) with each increase (i.e. delay) in one order of entry (Fig. 2C).

Body mass and daily order of entry

Mean body mass of golden spiny mice was 63 ± 9 g (± SD). Body mass did not significantly affect order of entry to the foraging patches, when analysed for each microhabitat separately (mass effect: UB: 0.04 ± 0.02, 95% CI – [−0.002, 0.076], $P = 0.07$, $R^2 = 0.15$; BB: 0.03 ± 0.02, 95% CI – [−0.015, 0.072], $P = 0.2$, $R^2 = 0.12$) or when analysed for both together (mass effect: 0.06 ± 0.04, 95% CI – [−0.01, 0.13], $P = 0.1$, $R^2 = 0.16$).

Daily order of entry and torpor

Spiny mouse individuals varied in use of torpor during the study period (Fig. 3). Daily order of entry was significantly correlated with time spent torpid. Each day, time spent torpid increased by 120 ± 21 min (95% CI – [79, 161], $P < 0.001$, $R^2 = 0.44$) and by 104 ± 24 min (95% CI – [56, 150], $P < 0.001$, $R^2 = 0.44$) with each increase in order of entry in the UB microhabitat and in the BB microhabitat, respectively (Fig. 2D, E), with no significant difference between the two microhabitats (ΔUB-BB = 16 ± 32, 95% CI – [−46, 82], $P = 0.61$). However, the order of entry in the UB microhabitat was a better predictor ($DIC_{UB} = 738.2$, $DIC_{BB} = 742.2$). When testing the effect of order of entry at both microhabitats, daily torpor duration increased significantly by 67 ± 11 min (95% CI – [44, 89], $P < 0.001$, $R^2 = 0.47$) with each increase in one order of entry (Fig. 2F). The order of entry at both microhabitats was the best predictor for the daily time spent torpid ($DIC_{BOTH} = 735.1$).

Daily order of entry and time of arousal from torpor

Daily order of patch entry was significantly correlated with time of arousal. Each day, the order of entry increased by 0.16 ± 0.07 (95% CI – [0.04, 0.29], $P < 0.05$, $R^2 = 0.78$) at the UB microhabitat and by 0.26 ± 0.09 (95% CI – [0.09, 0.45], $P < 0.01$, $R^2 = 0.61$) at the BB microhabitat with each increase of 1 h in the time of arousal, with no significant difference between microhabitats (ΔUB-BB = −0.10, 95% CI – [−0.32, 0.12], $P = 0.38$). When testing the effect of arousal time at both microhabitats, order of entry was significantly increased by 0.38 ± 0.13 (95% CI – [0.13, 0.63], $P < 0.01$, $R^2 = 0.78$) with each increase of 1 h in time of arousal.

Daily time spent torpid and time of arousal from torpor

Daily time spent torpid was significantly correlated with time of arousal. Each day, individuals spent 108 ± 20 min more time torpid (95% CI – [70, 147], $P < 0.001$, $R^2 = 0.48$) with each increase of 1 h in the time of arousal.

Mean order of entry of individuals from the same enclosure

Individuals from the same enclosure entered the foraging patches in a constant order 61% of the days (linear relationship between their mean order of entry, $R^2 = 0.61$) (Fig. 4). Mean order of entry to a foraging patch of two consecutive foragers was constant 66% of the days (0.66 ± 0.08, 95% CI – [0.50, 0.82], $P < 0.001$) with no significant habitat effect (UB effect: −0.21 ± 0.32, 95% CI – [−0.81, 0.38], $P = 0.47$; UB × mean order of entry: 0.07 ± 0.12, 95% CI – [−0.15, 0.29], $P = 0.5$).

Mean order of entry and the mean amount of seeds consumed by each individual

Mean order of entry had a significant negative relationship with mean calculated amount of seeds consumed. This relationship was significant in the UB microhabitat (Fig. 5A), where the mean amount of seeds that each individual consumed each day was

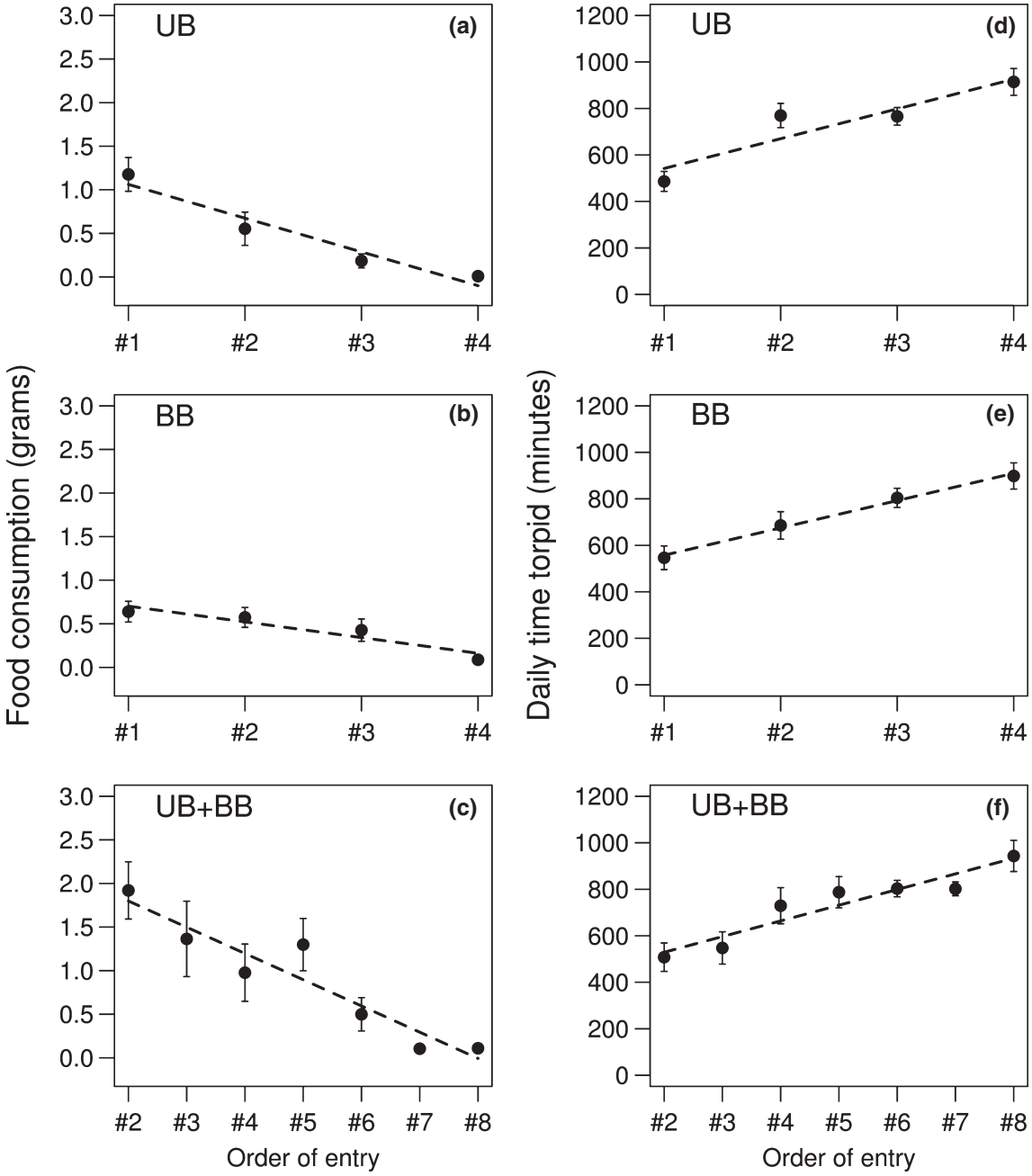

Figure 2 The relationship between the daily order of entry to a foraging patch and the mean daily approximated amount of seeds consumed (g ± SE, A, B, C), and the mean daily time spent torpid (min ± SE, D, E, F). For each microhabitat, the order of entry represents the order in which the individuals entered the foraging patch. For panels C and F, the order of entry is the sum order of entry from both microhabitats. For panel C, the calculated seeds consumption each day is the sum of calculated seeds consumption from both microhabitats. Dashed lines represent significant regression curves (A, R^2 = 0.65; B, R^2 = 0.46; C, R^2 = 0.66; D, R^2 = 0.44; E, R^2 = 0.44; F, R^2 = 0.47; G, R^2 = 0.65; H, R^2 = 0.64; I, R^2 = 0.65).

decreased by 0.4 ± 0.2 g (95% CI – [−0.8, −0.01], $P < 0.05$, R^2=0.40) for each increase in the mean order of entry. However, the relationship was not significant at the BB microhabitat (Fig. 5B), where mean amount of seeds that each individual consumed each day decreased by 0.2 ± 0.2 g (95% CI – [−0.5, 0.1], $P = 0.19$, R^2=0.24) for each increase in the mean order of entry. The relationship was also significant when summing the amount of seeds consumed at both microhabitats (Fig. 5C), where mean amount of seeds that each individual consumed each day was decreased by 0.4 ± 0.1 g (95% CI – [−0.7, −0.1], $P < 0.05$, $R^2 = 0.39$) for each increase in the mean order of entry.

Mean order of entry and daily time spent torpid

Mean order of entry had a significant positive relationship with time spent torpid. Mean time spent torpid increased by 137 ± 41 min (95% CI – [57, 221], $P < 0.01$, $R^2 = 0.63$) for each increase in the mean order of entry at the UB microhabitat (Fig. 5D), by

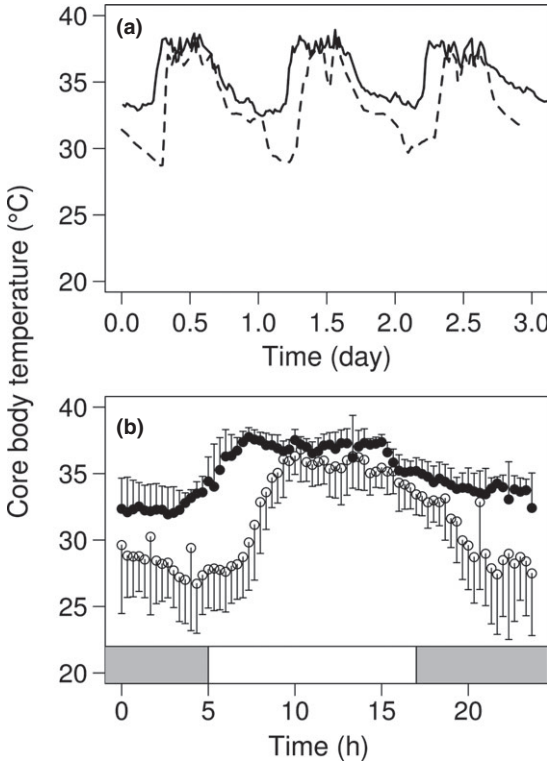

Figure 3 T_b rhythms (A) of two golden spiny mice in one enclosure (solid line – an early arrival individual, dashed line – a late arrival individual) and mean daily core body temperature rhythms (B) (± SD, $n = 11$) of individuals that either was the first to enter the foraging trays at both microhabitats (●) or was the last to enter the foraging trays at both microhabitats (○). Grey area represents dark hours.

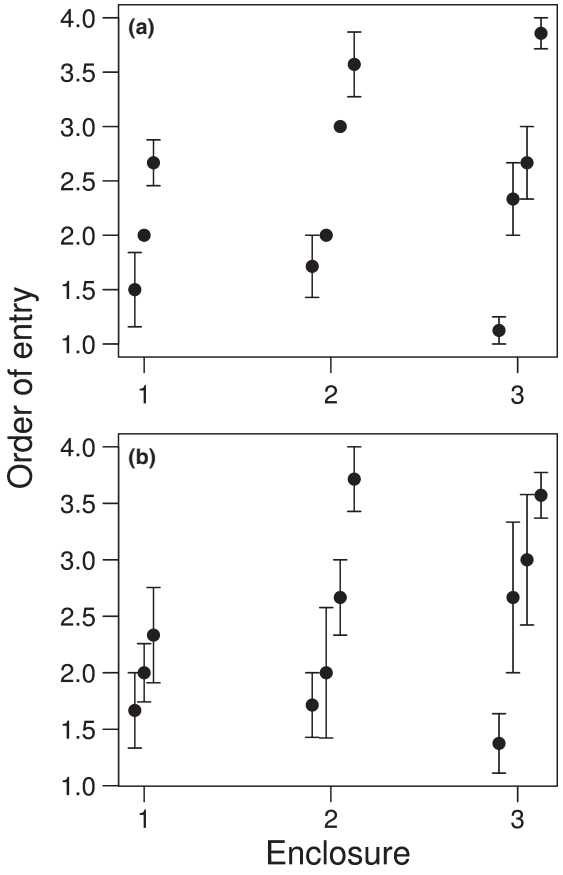

Figure 4 Individuals' mean (± SE, $n = 11$) order of entry in each enclosure at the UB (A) and BB (B) microhabitats. Each point represents a different individual, which has a mean order of entry for each microhabitat.

132 ± 53 min (95% CI – [25, 237], $P < 0.05$, $R^2 = 0.48$) at the BB microhabitat (Fig. 5E), and by 71 ± 23 min (95% CI – [24, 117], $P < 0.01$, $R^2 = 0.48$) when summing the order at both microhabitats for each individual (Fig. 5F). There was no significant difference in the effect of the order of entry between the two microhabitats (UB-BB: 5 ± 67, 95% CI – [−124, 138], $P = 0.95$). However, the mean order of entry at the UB microhabitat was the best predictor for the mean time spent torpid ($DIC_{UB} = 136.5$, $DIC_{BB} = 139.8$, $DIC_{BOTH} = 137.6$).

We recorded 225 encounters of individuals foraging within the same patch; 93% of these events lasted under 2 s (Fig. 6).

DISCUSSION

We found strong relationships between sequence of arrival at a foraging patch, amount of food foraged and time spent torpid. Individuals that arrived early gained more energy both from this patch and from other patches foraged, and spent less time torpid. Sequence of arrival at a patch was not random; some individuals tended to arrive early, while others tended to arrive late. Thus, different individuals tended to receive consistently greater or lower energy returns, and over time, certain individuals spent much time torpid, whereas other spent relatively little time in torpor. These relationships were stronger for patches in the UB microhabitat, and somewhat weaker for the BB microhabitat, suggesting that in the latter anti-predatory risk behaviours also impacted both foraging and torpor. In our system, energetic gain is translated into fitness and torpor has a fitness cost; we show here, for the first time, how individual abilities of energy acquisition vary consistently, giving a fitness edge to some individuals within the population.

Previous research (Levy *et al.* 2011a) revealed that spiny mice reduced use of torpor in response to supplementing them with food *ad libitum*. In winter, they refrained from becoming torpid almost entirely, and in summer, torpor was reduced significantly (Levy *et al.* 2011a). This indicates that lack of food drives torpor (rather than the reverse) and that becoming torpid carries a cost for golden spiny mice.

The obvious benefit of torpor is reduction in energy expenditure and therefore food requirements, implying that an animal will spend less time foraging and will be less exposed to predation or interference competition. Nevertheless, when possible, many animals refrain from using torpor (e.g. Landry-Cuerrier *et al.* 2008; Levy *et al.* 2011a), suggesting that use of torpor also entails substantial costs. These costs are often subtle (and in some cases debatable); many physiological functions are negatively affected by the low body temperature and metabolic depression during torpor, although some of these effects are still controversial. These include, for example, reduced immuno-competence (Prendergast *et al.* 2002), oxidative stress and DNA damage (Giroud *et al.* 2009). Torpor also impacts individual performance. For example, hibernating animals do not sleep, and torpor was found to alter the composition and quality of sleep, so torpor may result in sleep deficit (e.g. Deboer

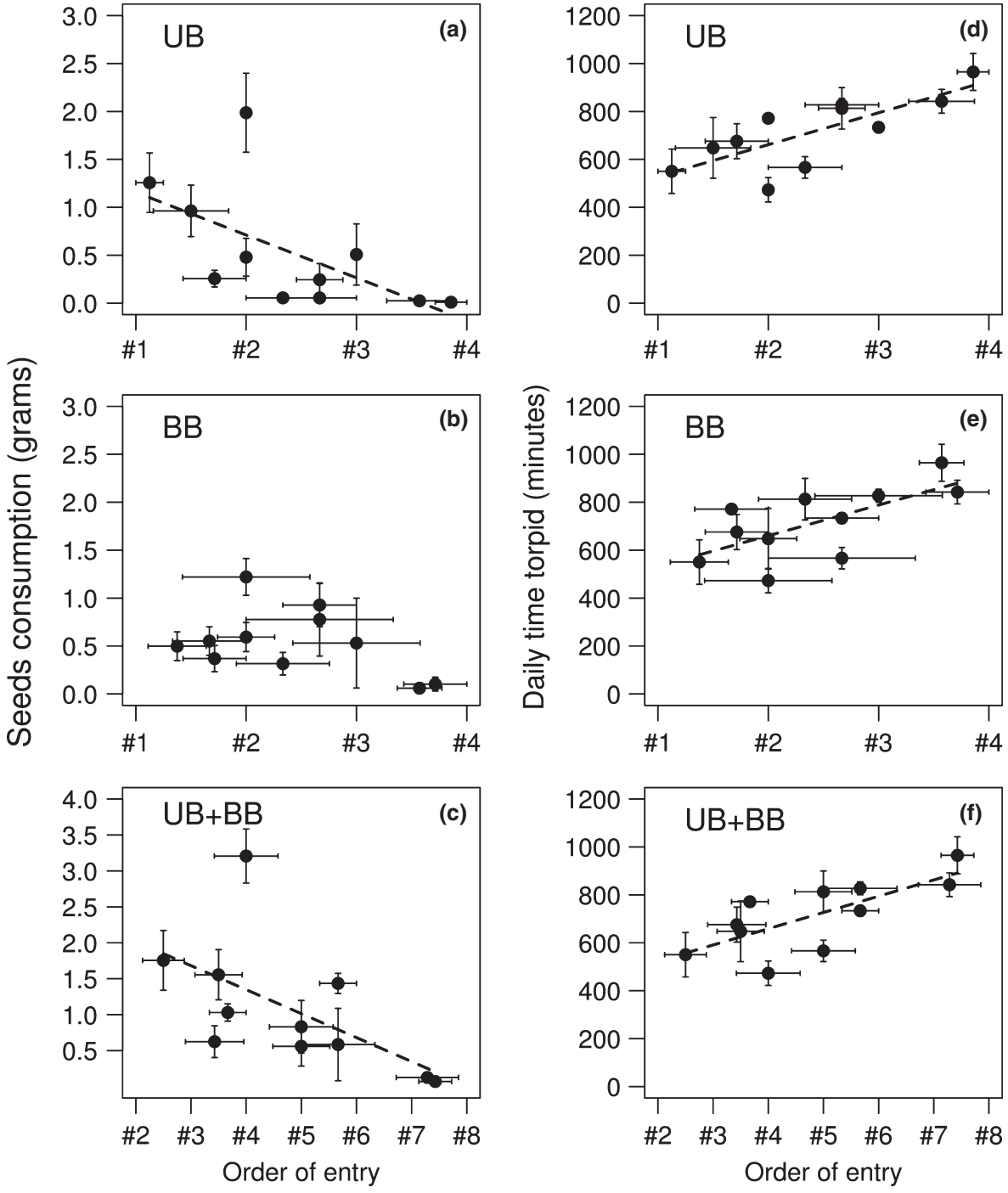

Figure 5 The relationship between the mean order of entry (± SE) to the foraging patches and the mean daily approximated amount of seeds consumed (g ± SE, A, B, C), and the mean daily time spent torpid (min ± SE, D, E, F), by each individual (n = 11). Each point represents a different individual, that has a mean order of entry to each microhabitat, and to both microhabitats together (the sum of the mean order of entry to each microhabitat); and has a mean daily seeds consumption from each microhabitat, and from both microhabitats (the sum of seeds consumption from each microhabitat). Dashed lines represent significant regression curves (A, R^2=0.41; C, R^2 = 0.40; D, R^2 = 0.63; E, R^2 = 0.48; F, R^2 = 0.58).

2005; reviewed by Roth *et al.* 2010). Moreover, torpor impairs object recognition (Palchykova *et al.* 2006; Palchykova & Tobler 2006) and memory (Roth *et al.* 2010). These, in turn, are important for diverse ecologically relevant tasks, such as consolidation of spatial information (location of food, shelter and other resources), processing social information (e.g. recognising individual conspecifics) and communication (Roth *et al.* 2010).

As fitness involves both survival and reproduction, it is impacted directly by energy acquisition (Stephens *et al.* 2007). Our study shows that some individuals are repeatedly more capable at acquiring resources than others. Over the long run, these individuals are expected to do better in terms of their fitness. Variation in energy gaining abilities within a population is perhaps not surprising, but to the best of our knowledge, this is a unique example of

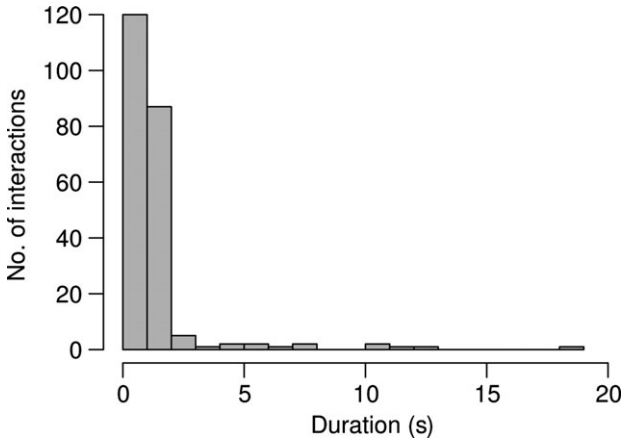

Figure 6 The distribution of the duration (s) of two individuals foraging in the same patch at the same time.

intrapopulation differences in foraging abilities recorded in small mammals.

Our study, however, reveals a complex relationship between foraging and torpor: mice that used more torpor aroused later in the day (Fig. 3), arrived at foraging patches later in the sequence, and therefore tended to do poorly in terms of energy acquisition and coped by becoming torpid for much longer time stretches than other mice. Mammals may be assisted by elevated ambient temperatures and sun radiation in their arousal from torpor (Pavey & Geiser 2008), so this may confer some benefit on later arousing individuals.

In our experimental setup, individuals were well acquainted with the foraging patches, so individual differences in ability to locate profitable foraging patches cannot account for the perceived patterns. It is possible that more dominant individuals foraged earlier to the aggressive exclusion of others; only rarely did two individuals forage at the same time (Fig. 6). It is possible that these aggressive individuals had higher levels of testosterone, which was found to inhibit the use of torpor in Siberian hamsters, *Phodopus sungorus sungurus* (Ruby *et al.* 1993). Another possibility is that the circadian clock of the earlier foragers has shorter free-running period (tau), and therefore, they tend to be active earlier in the day (e.g. Helm & Visser 2010).

Be that as it may, spiny mice appear to use heterothermy to allow them to ride out times of low energy availability. In the short term, this strategy allows them to cope with energy limitation caused by low resource availability and/or their relatively poor ability to exploit available resources. However, in the long run, costs of this energy-balancing strategy may be highly significant. The fact that the same individuals resort to this strategy suggests that they pay a significant price in fitness. In simple terms, the fact that some individuals spend over 15 h a day torpid limits their foraging activity times dramatically. It appears that fitness-enhancing activities of these individuals are limited to a very narrow window of activity, when individual performance may be impaired (see above).

Predation risk has a significant role in golden spiny mouse physiology and behaviour (e.g. Shargal *et al.* 1999; Jones *et al.* 2001; Mandelik *et al.* 2003). Using a stochastic modelling approach, Pravosudov & Lucas (2000) showed that birds should avoid nocturnal torpor, when foraging success is high because torpid birds are more susceptible to predation. Moreover, Laurila & Hohtola (2005) showed that introducing a predator decreases nocturnal hypothermia of fasting pigeons (*Columba livia*). Thus, if less successful foragers consume less food and spend more time torpid, they may expose themselves to higher predation risk during the night. Conversely, if torpor reduces foraging activity then it could reduce aboveground predation risk.

While our results point to deterministic interindividual differences in fitness-enhancing energetic balance, this pattern may hold only in periods of severe resource limitation. Possibly, between such periods spiny mice experience phases where resources are relatively plentiful and foraging opportunities diverse. Under such conditions, individuals that do repeatedly poorly in our study may do well and make up to some extent for periods of low resource availability. The rate at which periods of resource limitation occurs may determine the degree of selection exerted by foraging abilities.

Here, for the first time, we explored how individual-level foraging success impacts use of torpor. Thermoregulation is more accurate among successful foragers; this conforms to current understanding that accurate thermoregulation is beneficial and should be avoided only when costs outweigh its benefits. Our results suggest that successful foragers tend to be successful also over the longer run and consequently spend less time torpid. This finding may indicate that less successful foraging bears a fitness cost not only in limited energy for maintenance and reproduction but possibly also impaired performance and fewer opportunities to forage and perform other fitness-enhancing activities.

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AUTHORSHIP

The research was conceived and designed by D.T and K.S.N. D.T, K. N., and R.S. developed and installed the experimental design at the research site. R.S. and L.O. collected the data. L.O., D.T. and K.N. discussed the data analyses, and L.O. performed them and wrote the first draft of the manuscript. All authors contributed substantially to revisions. We declare that we do not have conflict of interests.

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