

Foraging behavior of golden hamsters (*Mesocricetus auratus*) in the wild

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Abstract Foraging theory posits that animals should maximize energy gains while minimizing risks, the largest of which is usually predation. For small burrowing mammals the best measure of risk avoidance may be the time spent in the burrow, although this measure is rarely examined. During the spring of 2005 and 2006 we recorded the foraging behavior of female golden hamsters in their natural habitat in southern Turkey. Data were collected with a data logger and by direct observations. Female golden hamsters averaged 64 min per day above ground in a series of foraging trips with a mean duration of 5.5 min. Two nursing females increased their time out of the burrow

by a factor of 6–8 times over the course of 16 days by increasing both the number of trips and the length of each trip. These results show that hamsters spend little time out of the burrow, thus minimizing risk, but they also show that time spent out of the burrow is related to the energy needs of the hamsters; lactating females with high energy needs exposed themselves to much greater risk than did non-lactating females.

Keywords Foraging · Hoarding · Time budget analysis · Predator avoidance · Energy allocation · Lactation

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Introduction

Foraging theory posits that foraging decisions balance the energy benefit of the food obtained against the costs of foraging, predation, and forgoing other activities such as mating (Emlen 1966; MacArthur and Pianka 1966; Lima and Dill 1990). Many studies have focused on aspects of the environment that can affect an animal's foraging decisions, with a recent focus on variables that affect the perceived risk of predation (see a meta-analysis by Verdolin 2006).

One of the most common methods that has been used for measuring perceived threat is to determine the giving up density (GUD), which is the amount of experimentally provided food that is left at a site. The logic behind this method is that the effort necessary to gather the remaining food is not worth the perceived risk; in general, as the perceived risk increases, the number of seeds left behind should also increase (Brown 1988).

A more detailed analysis of decision making can be made by time-budget analysis in which the amount of time that an animal spends foraging, in vigilance, and in other

behavior is recorded during periods of time in which there are different levels of perceived threat of predation (Kramer and Nowell 1980; Sharpe and Van Horne 1998; Arenz and Leger 2000). In most of these studies the percentage of time spent in several different behaviors is compared. For semi-fossorial rodents, the best strategy for predator avoidance is to remain in the burrow, but very little research has included the time spent below ground as part of time-budget analysis. We suggest that the amount of time inside of the burrow is an important variable that must be systematically investigated. Having a food hoard can provide animals with even more freedom from foraging, as they can rely on stores during times of intense predation, harsh environmental conditions, or other threats (Lea and Tarpay 1986; Whishaw 1993).

Golden hamsters, *Mesocricetus auratus* (Waterhouse 1839), belong to the family Cricetidae, one of 17 mammalian taxa that includes individuals known to have cheek pouches. “Cheek pouches” is actually a misnomer for *Mesocricetus* because in nature hamsters fill the incredibly flexible membranes of these pouches such that they extend beneath the skin down the side of the body to the hip (personal observation), earning them the Syrian name “father of the saddlebags” (Lea and Tarpay 1986). *Mesocricetus auratus* is one of the most assiduous of hoarding animals (Lanier et al. 1974; Lea and Tarpay 1986), thus potentially allowing them greater flexibility in the timing of their foraging. Golden hamsters are multi-load, central place foragers; their huge pouches allow them to collect food from multiple sites before depositing it in the burrow for later consumption. In the laboratory hamsters collect food that they find in their environment and deposit it in a hoard, rather than directly consuming it (Jones et al. 1990), suggesting an innate tendency to minimize time spent in risky environments. In the field, known or probable risks include predation from raptors, storks, owls, foxes, snakes, cats, and dogs, and exposure to severe weather conditions that can create metabolic demands not present in the laboratory.

Despite numerous studies on the behavior of golden hamsters in laboratory environments, including several studies of hoarding behavior (Lea and Tarpay 1986; Etienne et al. 1991; Guerra and Ades 2002; Buckley and Schneider 2003; Keen-Rhinehart et al. 2010), this species has never been studied in the field until our studies in the spring of 2005, 2006, and 2007. Laboratory studies are a poor substitute for field studies when questions concerning energy/threat tradeoffs are the central issue, and the foraging behavior of rodents in the laboratory can be dramatically different from that in the field (Ovadia et al. 2001).

As part of the first behavioral study of hamsters in the wild, we examined hamster foraging behavior and evaluated it as an example of predator avoidance through

minimization of time spent above ground. Research was conducted during the breeding season, enabling comparison of activity patterns and foraging activity of females in several reproductive states, during which hamsters have different energy needs.

Study area

Observations were carried out during April and May of 2005 and March–May of 2006 near Elbeyli, Turkey (36°40′27N, 37°27′57E, 512 m above sea level). This is an area of agricultural fields and rocky grazing areas surrounded by semi-arid steppe. Daily temperatures ranged from an average of 3–14°C in March to 12–26°C in May. Elbeyli experiences a cold, rainy season from November through March. Predominant crops in the fields of interest were lentils (*Lens culinaris*), wheat (*Triticum* sp.), and barley (*Hordeum vulgare*), all of which were planted in October and harvested in late May. Other crops, for example corn, peppers, and melons were occasionally planted at other times of year, during which the field conditions were augmented by irrigation.

Materials and methods

Hamsters were trapped by means of Sherman traps and homemade live traps placed around entrances to burrows late in the day, baited with a masticated mixture of peanuts and bread (2005) or with a mixture of bread, peanuts, peanut butter, chocolate, and sunflower oil (2006). Traps were checked shortly after dawn. Trapped animals were sexed, weighed, implanted with a passive integrated transponder (PIT tag) under the skin for individual identification, and released at the capture site. Once trapped, animals were not intentionally trapped again, except in a few cases in which the transponder was lost and it was necessary to insert another.

Golden hamster burrows usually have only one entrance (Gattermann et al. 2001). We placed a field animal identification system (FAIS), designed and built by Martin-Luther University of Halle-Wittenberg, Germany, in the burrow entrance of focal animals to record the identity of each tagged individual and the time of day it left or entered the burrow. The system consists of a plastic ring which contains a PIT tag antenna and two infra-red light beams approximately 1 cm apart, one above the other; the order in which these beams were broken enabled us to determine if the animal was entering or exiting the burrow. In this way, we knew whether the animal was in or out of its burrow for every second of each 24-h period that we monitored. Records of transponder passage and light-beam interruption were

recorded with a time signature on a battery-powered data logger. In this study data from 20 females were analyzed.

In addition to this automatically recorded activity, five researchers observed animals' burrows twice daily between the hours of, approximately, 0600–0800 and 1600–1930, corresponding to the primary periods of activity, as indicated by the data automatically collected by the FAIS (Gattermann et al. 2008). Morning observation periods were extended for individual animals when that animal was still active at 0800 hours, in order to include its complete foraging bout for that morning. Some animals were regularly active as late as 0930. The data collected from the automatic FAIS and by direct observation show over 90% concordance with one another for instances when data were simultaneously collected in both ways (Larimer 2007). Observed behavior was recorded in real time to the nearest second, using hand held voice recorders or paper and pencil. Observers stood 5–10 m from the entrance to the burrow, depending on ability to see through vegetation and the animal's perceived comfort with an observer.

Observed behaviors were divided into two categories: vigilance and foraging. Vigilance included periods of time during which the animal's head protruded from the burrow opening to survey the surroundings but her body remained in the burrow ("head vigilance") and periods of time during which she was completely out of the burrow but sitting within 50 cm of the burrow entrance ("near vigilance"). This latter category contained occasional grooming, but most time was spent in watchful immobility. Foraging included moving to food sources, investigating those sources, detaching parts of the plants, stuffing those parts into the cheek pouches, and returning to the burrow. Animals frequently moved from plant to plant within a single trip, but the density of vegetation and/or the distance traveled from the burrow often prevented more detailed description of what happened on any given foraging trip. An individual occasionally "disappeared" for an hour or more. We believe some of these long disappearances were real, and not because of human error, because the FAIS also recorded occasional long absences from the burrow. However, at least some were because of human error, because the FAIS registered an entrance in those cases, and the longer trips were rare and unlikely to be for foraging. Therefore, any trip longer than 30 min was systematically removed from the analyses.

In the 2005 field season (April 21–May 30), we accumulated 161 h of direct observation of burrow entrances in the field; of that time 39 h and 24 min contained adult female hamster activity. This activity consisted of 458 instances of animals sticking their heads out of the burrow; 87% of these instances resulted in the animal exiting the burrow entrance and leaving the area immediately surrounding the burrow (50 cm) to forage. Seven females

were observed regularly (more than 30 trips), and we observed pups at two of these burrows. During the 2006 field season (March 15–May 19) we accumulated an additional 316 h of observation, resulting in 57 h and 55 min of recorded adult female activity (a 2-year total of 97 h, 19 min). Six burrows, two of which had pups that weaned, were watched regularly (more than 30 trips), yielding 712 instances of heads protruding out of the burrow, of which 85% resulted in foraging trips. An additional nine animals were observed at least once in 2005 or 2006. There were no significant differences in the data between the two years (data not shown), so the data were collapsed across years for all analyses.

Data were analyzed using SPSS 11 for Macintosh computers (SPSS, Chicago, IL, USA). The amount of data collected for each focal animal varied from 40 to 150 foraging trips. To avoid problems of dependent samples, we averaged the data from each animal such that each animal contributed only one data point to the final analysis. Because of the different number of trips recorded per animal, each animal's data point represents a different number of trips averaged together. Animals were included in the analysis only if they had at least 30 trips. Effect sizes were calculated using the formula $r^2 = (t^2)/(t^2 + df)$ for t tests that were significant (Gravetter and Wallnau 2004). All procedures were in accordance with the Guide for the Care and Use of Laboratory Animals and the review board of the university primarily responsible for that aspect of the project (Martin Luther University for the PIT tags; Cornell University for the direct observations).

Results

Based on direct observation of the 12 individuals most frequently watched, adult females were above ground for a mean of 52 min 3 s per day (± 2 min 57 s), during a mean number of 10.1 (± 0.6) separate trips. Data from the FAIS, registering activity during our observations and also for the rest of the day and night, were available for 9 of the 12 females and indicated that for this more complete record the 9 females were out of the burrow an average of 64 min (± 3 min 54 s), indicating that we did indeed record most of an animal's daily activity during our direct observations. The average length of each trip, based on data collected through our direct observations, was 5 min 34 s (± 8 s), with 14% of this time (43 (± 2) s) spent in pre-foraging vigilance behavior. Vigilance was characterized by the animal either having only her head above ground, or by her sitting within half a meter of the burrow, not actively gathering food, and often motionless (Table 1).

The duration of foraging and vigilance did not seem to be meaningfully related to one another. A one-sample t test

Table 1 Mean (\pm SEM) seconds spent per trip on each of the three above-ground behaviors recorded

Animal ^a	Head vigilance (s)	Near vigilance (s)	Foraging (s)
#2 ($N = 52$)	31 (± 5)	38 (± 7)	400 (± 62)
#5 (23)	38 (± 6)	14 (± 4)	267 (± 64)
#17 (47)	6 (± 2)	41 (± 7)	157 (± 9)
#42 (56)	29 (± 4)	54 (± 10)	267 (± 21)
#64 (64)	13 (± 2)	19 (± 4)	449 (± 53)
#233 (124)	28 (± 4)	40 (± 5)	301 (± 13)
#245 (107)	13 (± 2)	37 (± 7)	283 (± 13)
#308 (142)	22 (± 2)	35 (± 5)	202 (± 13)
#801 (65)	40 (± 5)	17 (± 4)	283 (± 24)
#802 (44)	13 (± 2)	33 (± 15)	547 (± 36)
#K06 (33)	22 (± 4)	21 (± 4)	368 (± 24)
#K14 (54)	20 (± 3)	40 (± 9)	219 (± 12)
#P20 (124)	15 (± 1)	20 (± 3)	257 (± 23)

^a Number of trips resulting in foraging shown in parentheses; number of trips for the two types of vigilance may be slightly higher

revealed that the slope of the regression line for all animals combined (mean slope = 37.35 ± 9.35) was significantly different from 0 ($t(11) = 4.170$, $p = 0.002$) suggesting that longer foraging bouts were correlated with longer periods of vigilance before that bout. However, when the duration of foraging and vigilance for each individual animal was examined by using a regression line fit to a scatterplot, no common trend across the animals was observed. Three animals showed a positive correlation, one showed a negative correlation, and the remaining eight animals showed no apparent correlation. Therefore, we conclude that the overall trend shown by the one-sample t test was most likely not representative of a meaningful pattern for most of the animals, but rather was driven by the data of a few.

Effect of observer's presence

On some days it was not possible to go to our field site. In addition we were not present to observe animals at times other than peak periods of activity. Thus we observed between 18 and 52% of each animal's total above-ground activity during the period that each animal was considered a subject. For 7 animals there were at least 30 trips with an observer present and 30 trips with no observer present, enabling us to determine if our presence altered the behavior of these females. The presence of an observer did not systematically affect the time out of the burrow (paired t test, no one present 4 min, 21 s (± 17 s), someone present 5 min, 13 s (± 38 s), $t(6) = 1.266$, $p = 0.253$) or the time spent in vigilance with just the head sticking out of the hole (paired t test, no one present 16 s (± 6 s), someone present 20 s (± 7 s), $t(6) = 1.422$, $p = 0.199$).

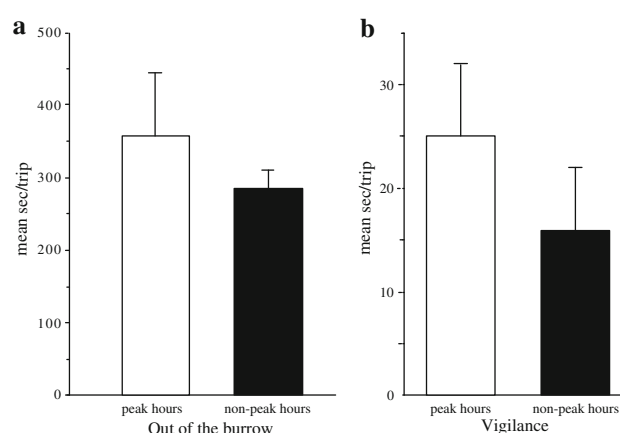


Fig. 1 Comparison of duration of golden hamster (*Mesocricetus auratus*) activity per trip depending on the time of day the activity occurred. Peak hours are 0600–0800 and 1600–1930. Non-peak hours are 0801–1559, 1931–0559. **a** Average time out of the burrow per trip (head up until body down). **b** Average vigilance per trip (head up until body out)

Effect of the time of day

Most of our direct behavioral observations were confined to the two peak periods of activity determined by examining the data automatically collected by the FAIS (0600–0800 hours, 1600–1930 hours as defined in Gattermann et al. 2008); both peak periods occurred during daylight. To confirm that the behavior recorded by the observers during these peak periods was representative of behavior during time periods when observers were not present, we compared data from the transponders during peak and non-peak periods of activity for six animals. The mean duration of time spent out of the burrow did not differ between peak and non-peak periods (Fig. 1a, paired t test, peak period 5 min, 58 s (± 1 min, 26 s), non-peak period 4 min, 46 s (± 24 s), $t(5) = 1.048$, $p = 0.343$). The duration of head-up vigilance, however, was significantly longer for animals when they were foraging during peak hours compared with when they were foraging during non-peak hours (Fig. 1b, paired t test, peak period 25 s (± 7 s), non-peak period 16 s (± 6 s), $t(5) = 6.337$, $p < 0.001$, $r^2 = 0.889$). For four of these six animals, both peak and non-peak activity occurred during the daylight only, indicating that illumination was not responsible for the animals' reduced vigilance.

Effect of maternal state

Time spent foraging was dramatically increased by the presence of pups that were about to be weaned. The overall mean duration of foraging by females was 64 min (± 3 min, 54 s) per day. This average included mothers in various reproductive states. For two mothers we obtained detailed foraging data during lactation. Before the final

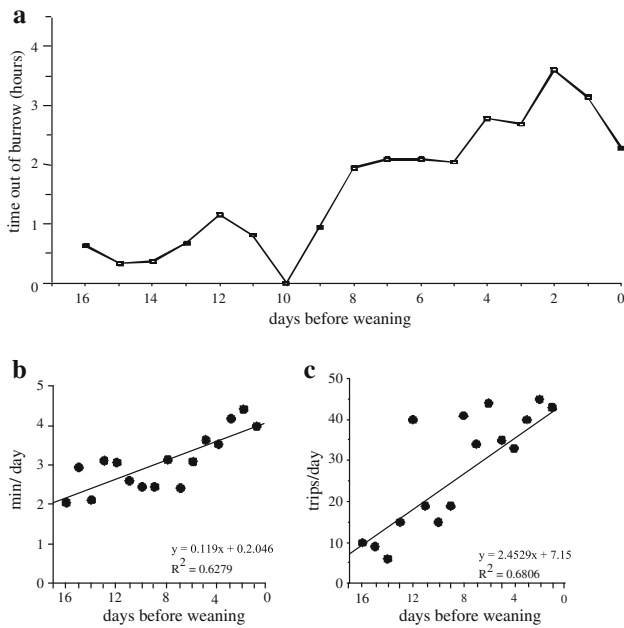


Fig. 2 The change in the foraging behavior of golden hamster (*Mesocricetus auratus*) mother #308 across 16 days of lactation as the pups aged. **a** The total time out of the burrow for mother #308 each day. Day 0 is the day before she deserted the burrow. On day 10, there was a heavy rain. **b** The mean length of trip per day. **c** The number of trips per day

2 weeks of nursing, these two mothers foraged for approximately 30 min per day (Figs. 2a, 3a), a length of time similar to that for many other female hamsters of unknown reproductive state that we observed. During the final 2 weeks before weaning, however, the duration of foraging increased steadily; immediately before weaning mother #308 was out of the burrow for approximately 3 h per day (Fig. 2a), and mother #P20 was out for approximately 4 h per day (Fig. 3a). This increase in time out of the burrow was because of increases in both the duration of each foraging trip (Figs. 2b, 3b) and the number of trips per day (Figs. 2c, 3c). Vigilance activity also declined significantly for mother #308 as her pups matured (regression slope = 1.73, $r^2 = 0.390$), but whether this was because of habituation to our presence or to a need to collect food as quickly as possible is unclear.

Discussion

A semi-fossorial animal’s best line of defense against predators is to remain in its burrow, yet we were unable to find many studies that systematically recorded the time spent in the burrow throughout the day and night, probably because of the difficulty of collecting continuous data (see Corp et al. 1997; Sharpe and Rosell 2003; Koprowski and Corse 2005; Rehmeier 2005 for some exceptions).

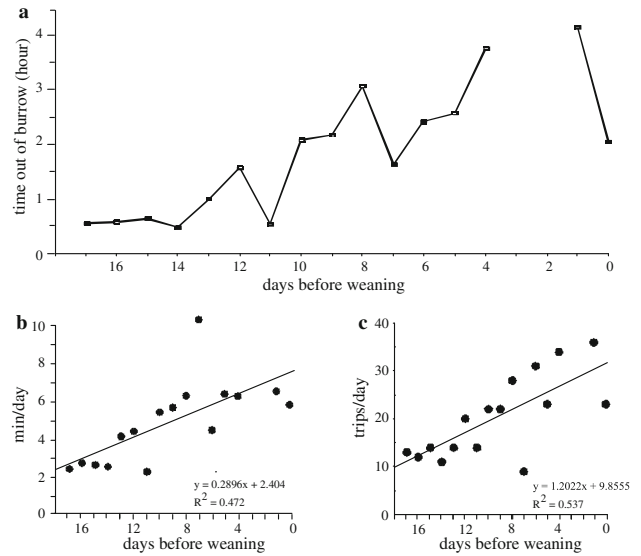


Fig. 3 The change in the foraging behavior of golden hamster (*Mesocricetus auratus*) mother #P20 across 16 days of lactation as the pups aged. **a** The total time out of the burrow for mother #P20 each day. Day 0 is the day before she deserted the burrow. Data were not available for days 1 and 2 because of equipment malfunction. **b** The mean length of trip per day. **c** The number of trips per day

Virtually all previous studies on foraging behavior have focused on decisions made once animals are out of their burrows (e.g. time spent vigilant, locations chosen for foraging). Nonetheless, we suggest that total time out of the burrow is a valuable measure because it more accurately reflects energy expenditure and predation avoidance than does the percentage of time spent in each activity out of the burrow.

Overall, female golden hamsters spent very little time out of their burrows compared with what is known for other species (Table 2), averaging approximately 64 min per 24-h day. As far as we know, the only published reference to other rodents that forage for only a few hours per day is a casual comment without supporting data on unspecified members of the heteromyid family (Kenagy 1973). Three to four hours of activity per day in rodents has been described as “surprisingly short” (Kenagy et al. 2002).

Across a variety of taxonomic groups, body size and duration of activity per day seem to be correlated, with larger animals being active for longer periods of time. Larger animals do not take longer to gather food appropriate to their increased body mass (Reichman and Roberts 1994), but they are less susceptible to predation and exhibit foraging behavior that demonstrates less fear (Smith 1995; Thorson et al. 1998; Kotler et al. 2002). The particularly low duration of activity per day shown by golden hamsters cannot be ascribed to size alone, however, because they are larger than many other rodents that forage 3–4 h per day

Table 2 Amount of time spent out of the burrow by various species

Scientific name	Common name	Representative citation
1–2 h		
<i>Mesocricetus auratus</i> (females)	Golden hamsters (females)	This study
Heteromyids	(Species not specified)	Kenagy (1973)
3–4 h		
<i>Spermophilus citellus</i>	European ground squirrels	Everts et al. (2004)
<i>Spermophilus tridecemlineatus</i>	Thirteen-lined ground squirrels	Vispo and Bakken (1993)
<i>Apodemus sylvaticus</i>	Wood mice	Corp et al. (1997)
<i>Octodon degus</i>	Degus	Kenagy et al. (2002)
Most of day or night		
<i>Talpa europaea</i>	European moles	Macdonald et al. (1997)
<i>Parotomys brantsii</i>	Brant's whistling rats	Jackson (2001)
<i>Castor fiber</i>	Eurasian beavers	Sharpe and Rosell (2003)
<i>Sciurus nayaritensis chiricahuae</i>	Mexican fox squirrels	Koprowski and Corse (2005)

(Table 2). The ability to carry a large quantity of food in the pouches instead of eating it on the surface saves considerable time (e.g. greater Egyptian sand gerbil, *Gerbillus pyramidum* and Allenby's gerbil, *G. allenbyi* (Ovadia et al. 2001)), and thus pouches are likely to contribute to the hamster's ability to minimize time spent out of the burrow.

Predation pressure on the Elbeyli population of hamsters has not been quantified. However, occasional foxes, dogs, storks, raptors, owls, and snakes were observed near fields in which the hamster burrows were located. The radio transmitter from one marked animal was found in a pile of fox feces. Of the bones examined in owl pellets, 6% belonged to hamsters. Therefore, predation is known to occur on our population of animals. One sign of abnormally heavy levels of predation is altered patterns of timing of activity (e.g. rats, *Rattus norvegicus* (Fenn and MacDonald 1995) and coyotes, *Canis latrans* (Kitchen et al. 2000)). The timing of hamsters' activity periods in our field site—predominantly during daylight hours—is dramatically different than activity cycles observed in the laboratory and in outdoor enclosures (Gattermann et al. 2008), possibly indicating high pressure from predators at night.

Support for the idea that the burrow is an individual's safest option is that distance from the burrow has been shown to be one of the variables most affecting rodent foraging (Loughry 1993; Thorson et al. 1998; Blumstein et al. 2004). Most animals have small home ranges when possible (Hubbs and Boonstra 1998) and are less likely to fully utilize food sources further from their burrow (Thorson et al. 1998). For pikas, *Ochotona collaris*, distance from the burrow does not affect foraging behavior, but distance from good cover does, suggesting that, for pikas, predation risk alone, and not energy costs, determines the timing and duration of foraging (Morrison et al. 2004). Similarly, foraging by eastern chipmunks, *Tamias striatus*, is primarily affected by the amount of protective

cover but only when they are far from the burrow (Bowers and Ellis 1993; Bowers 1995). Protective cover also affects how degus use their burrow systems (Hayes et al. 2007). The distance traveled by the monogamous rat *Hypogeomys antimena* has been linked to different mortality of the sexes. In this species the male travels much farther than the female (Sommer 2000).

In laboratory studies golden hamsters have a tendency to visit sites farther from the nest less often than sites closer to the nest (Guerra and Ades 2002). When given an option between otherwise similar home burrows, they choose the one closer to the source of bedding and food (Otoni and Ades 1991). Unfortunately, thick vegetation prevented us from accurately gauging the total distance traveled on most foraging trips.

The hamsters we observed in the field had plentiful food and the temperatures were moderate. They were not storing food for hibernation because most mothers abandoned their burrow for a new one when their pups had been weaned (personal observation). Similarly, common hamsters (*Cricetus cricetus*) have been documented to have separate breeding and wintering burrows (Weinhold and Kayser 2006). In addition, the density of food was high in the agricultural fields in which we worked, especially when pups were being weaned in May and early June, a period when the lentils, wheat, and barley were maturing. Therefore, our findings may represent the minimum amount of time that hamsters spend out of the burrow. During other seasons food density is probably lower; at these times foraging duration may be more comparable with that of other small rodents. It may be, however, that the large stores of seeds hoarded by hamsters enable them to limit foraging time during all seasons, not just in the plentiful spring. One way that we examined how hamsters alter their foraging under duress was to examine foraging by mothers as their energy needs changed. Although we did

not have enough mothers to draw strong conclusions, we did document dramatic changes in foraging time during lactation in two females.

Metabolic changes, including reproductive hormones, are strongly linked to changes in food hoarding, though exact details vary by species (Keen-Rhinehart et al. 2010). In contrast with many animals golden hamsters in the laboratory do not increase food intake during pregnancy (Zucker et al. 1972; Fleming 1978; Wade et al. 1986; Quek and Trayhurn 1990; Bhatia and Wade 1991; but see Bhatia et al. 1995), relying instead on internal stores of energy (Quek and Trayhurn 1990; Garton et al. 1994). Using these internal stores of energy results in mothers who, at the end of their pregnancy, have a 72% decrease in the amount of white adipose tissue (Wade et al. 1986). Brown adipose tissue activity also decreases, reducing the energy requirements of pregnant females (Wade et al. 1986). Laboratory hamsters do increase hoarding behavior dramatically during pregnancy, however, with pregnant females increasing foraging by as much as 770% (Miceli and Malsbury 1982). This increased hoarding may allow females freedom from increased foraging once pups are born.

Hamsters in the laboratory do increase food intake during lactation, even doubling their intake in some cases (Fleming 1978; Fleming and Miceli 1983; Bhatia et al. 1995). These hamsters have exhausted most of their stored energy during pregnancy (Wade et al. 1986), and thus must rely on increased external energy sources. Mothers have the additional burden of building back up their adipose tissue they lost during pregnancy (Wade et al. 1986). In addition, lactation is a much more energy-intensive process than gestation (Hsu et al. 1999). The extent of the increase in food intake depends on litter size (Fleming 1978), temperature (Bhatia et al. 1995), and type of food (Fleming and Miceli 1983). The mother's increase in food intake, coupled with her pups' consumption of stored food as they wean, may require an increased foraging effort near the end of lactation as the food hoard dwindles.

To our knowledge, no studies have examined foraging time (as opposed to hoarding of readily available food) in the golden hamster across reproductive cycles. However, in laboratory experiments in which hamsters must press a lever for food, those that receive a protein-free diet exert more work than hamsters fed a complete diet (DiBattista 1999), suggesting that hamsters are able to increase their effort to satisfy nutritional demands. The foraging effort of deer mice (*Peromyscus maniculatus*) across lactation has been studied both in the laboratory and in the wild. In the laboratory, deer mice increased feeding throughout lactation both in situations where food was available ad libitum (Millar 1979) and in situations where foraging effort was necessary (Perrigo 1987), suggesting that increases in

feeding related to reproduction do in fact result in increases in foraging effort. A field study of deer mice across various stages of reproduction did not find a significant increase in the total duration of foraging across lactation, but it did show differences in some related variables and trends in others, suggesting the laboratory and field experiments may parallel one another in this regard (Rehmeier 2005).

Based on studies showing increased hoarding during pregnancy and increased intake during lactation, one would expect the foraging effort of hamsters to be much higher during pregnancy than during the pre-breeding season, and to further increase throughout lactation. We have little data that we can confidently assign to pregnant females, but for our lactating mothers with known weaning dates a significant increase in foraging duration was observed throughout lactation, as expected (Figs 2, 3).

Although review of the literature supports the interpretation that increased foraging is because of increased energy needs, thermoregulation, also, may be important. Hamsters are poikilothermic when they are first born and lack brown adipose tissue for the first few weeks (Rink 1969). Therefore, huddling with other hamster pups does not provide much warmth (Sokoloff and Blumberg 2002), and the pups are reliant on their mother's heat, thus limiting how often she can leave the nest to forage. In contrast, when hamster pups are older, they may increase their mother's temperature too much, encouraging her to leave the huddle and perhaps the burrow, as has been shown in rats (*Rattus norvegicus*) (reviewed by Woodside and Jans 1988) and dwarf hamsters (*Phodopus campbelli* and *P. sungorus*) (Scribner and Wynne-Edwards 1994). Temperature loggers 70 cm below ground at our field site registered temperatures between 12.0 and 14.5°C over the course of the field season, but temperatures inside a nest in an active burrow are unknown.

This study is the first on the foraging behavior of hamsters in their natural habitat, and it suggests that hamsters minimize the amount of time spent above-ground. Nonetheless, the variables that affect the duration of time spent out of the burrow must still be further delineated. We suggest that laboratory studies that require hamsters to show increased effort to gather food (foraging rather than hoarding) may help to determine the circumstances in which this species is willing to spend more time out of its burrow. Such an artificial foraging system was used by Bronson and Perrigo (reviewed by Perrigo 1990) for study of deer mice in the laboratory, and initial field studies on the same species show promising correlations (Rehmeier 2005).

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References

- Arenz CL, Leger DW (2000) Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Anim Behav* 59(3):35–541
- Bhatia AJ, Wade GN (1991) Effects of pregnancy and ovarian steroids on fatty acid synthesis and uptake in Syrian hamsters. *Am J Physiol Regul Integr Comp Physiol* 260(1):R153–R158
- Bhatia AJ, Schneider JE, Wade GN (1995) Thermoregulatory and maternal nest building in Syrian hamsters: interaction of ovarian steroids and energy demand. *Physiol Behav* 58(1):141–146
- Blumstein DT, Runyan A, Seymour M, Nicodemus A, Ozgul A, Ransler F, Im S, Stark T, Zugmeyer C, Daniel JC (2004) Locomotor ability and wariness in yellow-bellied marmots. *Ethology* 110(8):615–634
- Bowers MA (1995) Use of space and habitats by the eastern chipmunk, *Tamias striatus*. *J Mammal* 76(1):12–21
- Bowers MA, Ellis A (1993) Load size variation in the Eastern chipmunk, *Tamias striatus*: the importance of distance from burrow and canopy cover. *Ethology* 94:72–82
- Brown JS (1988) Patch use as an indicator of habitat preference, predation risk, and competition. *Behav Ecol Sociobiol* 22(1):37–47
- Buckley CA, Schneider JE (2003) Food hoarding, but not food intake is increased by food deprivation and decreased by leptin treatment in Syrian hamsters. *Am J Physiol Regul Integr Comp Physiol* 285(5):R1021–R1029
- Corp N, Gorman ML, Speakman JR (1997) Ranging behaviour and time budgets of male wood mice *Apodemus sylvaticus* in different habitats and seasons. *Oecologia* 109(2):242–250
- DiBattista D (1999) Operant responding for dietary protein in the golden hamster (*Mesocricetus auratus*). *Physiol Behav* 67(1):95–98
- Emlen JM (1966) The role of time and energy in food preference. *Am Nat* 100(916):611–617
- Etienne AS, Hurni C, Maurer R, Seguinot V (1991) Twofold path integration during hoarding in the golden hamster? *Ethol Ecol Evol* 3(1):1–11
- Everts LG, Strijkstra AM, Hut RA, Hoffmann IE, Millesi E (2004) Seasonal variation in daily activity patterns of free-ranging European ground squirrels (*Spermophilus citellus*). *Chronobiol Int* 21:57–71
- Fenn MGP, MacDonald DW (1995) Use of middens by red foxes: risk reverses rhythms of rats. *J Mammal* 76(1):130–136
- Fleming AS (1978) Food intake and body weight regulation during the reproductive cycle of the golden hamster (*Mesocricetus auratus*). *Behav Biol* 24:291–306
- Fleming AS, Miceli M (1983) Effects of diet on feeding and body weight regulation during pregnancy and lactation in the golden hamster (*Mesocricetus auratus*). *Behav Neurosci* 97(2):246–254
- Garton DW, Hsu MJ, Harder JD (1994) Environmental temperature and metabolic rates during gestation and lactation in golden hamsters (*Mesocricetus auratus*). *Physiol Zool* 67:497–514
- Gattermann R, Fritzsche P, Neumann K, Al-Hussein I, Kayser A, Abiad M, Yakti R (2001) Notes on the current distribution and the ecology of wild golden hamsters (*Mesocricetus auratus*). *J Zool* 254(3):359–365
- Gattermann R, Johnston RE, Yigit RN, Fritzsche P, Larimer S, Özkurt S, Neumann K, Song Z, Colak E, Johnston J, McPhee ME (2008) Golden hamsters are nocturnal in captivity but diurnal in nature. *Biol Lett* 4:253–255
- Gravetter FJ, Wallnau LB (2004) Statistics for the behavioral sciences, 6th edn. Thomson Wadsworth, Belmont
- Guerra RF, Ades C (2002) An analysis of travel costs on transport of load and nest building in golden hamster. *Behav Process* 57(1):7–28
- Hayes LD, Chesh AS, Ebensperger LA (2007) Ecological predictors of range areas and use of burrow systems in the diurnal rodent *Octodon degus*. *Ethology* 113:155–165
- Hsu MJ, Garton DW, Harder JD (1999) Energetics of offspring production: a comparison of a marsupial (*Monodelphis domestica*) and a eutherian (*Mesocricetus auratus*). *J Comp Physiol B Biochem Syst Environ Physiol* 169(1):67–76
- Hubbs AH, Boonstra R (1998) Effects of food and predators on the home-range sizes of Arctic ground squirrels (*Spermophilus parryii*). *Can J Zool* 76(3):592–596
- Jackson TP (2001) Factors influencing food collection behaviour of Brants' whistling rat (*Parotomys brantsii*): a central place forager. *J Zool Lond* 255:15–23
- Jones CH, McGhee R, Wilkie DM (1990) Hamsters (*Mesocricetus auratus*) use spatial memory in foraging for food to hoard. *Behav Process* 21:179–187
- Keen-Rhinehart E, Dailey MJ, Bartness T (2010) Physiological mechanisms for food-hoarding motivation in animals. *Philos Trans R Soc B* 365:961–975
- Kenagy GJ (1973) Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology* 54(6):1201–1219
- Kenagy GJ, Vasquez RA, Nespolo RF, Bozinovic F (2002) A time-energy analysis of daytime surface activity in degus, *Octodon degus*. *Rev Chil Hist Nat* 75(1):149–156
- Kitchen AM, Gese EM, Schauster ER (2000) Changes in coyote activity patterns due to reduced exposure to human persecution. *Can J Zool* 78(5):853–857
- Koprowski JL, Corse MC (2005) Time budgets, activity periods, and behavior of Mexican fox squirrels. *J Mammal* 86(5):947–952
- Kotler BP, Brown JS, Dall SRX, Gresser S, Ganey D, Bouskila A (2002) Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evol Ecol Res* 4(4):495–518
- Kramer DL, Nowell W (1980) Central place foraging in the Eastern chipmunk, *Tamias striatus*. *Anim Behav* 28(3):772–778
- Lanier DL, Estep DQ, Dewsbury DA (1974) Food hoarding in murid rodents. *Behav Biol* 11:177–187
- Larimer SC (2007) Golden hamsters, *Mesocricetus auratus*, as a model species for studying circadian rhythms and olfactory memory: studies in lab and in nature. Ph.D. dissertation, Department of Psychology, Cornell University, Ithaca, NY
- Lea SEG, Tarpay RM (1986) Hamsters' demand for food to eat and hoard as a function of deprivation and cost. *Anim Behav* 34(6):1759–1768
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68(4):619–640
- Loughry WJ (1993) Determinants of time allocation by adult and yearling black-tailed prairie dogs. *Behaviour* 124(1–2):23–43
- MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* 100(916):603–609
- Macdonald DW, Atkinson RPD, Blanchard G (1997) Spatial and temporal patterns in the activity of European moles. *Oecologia* 109:88–97
- Miceli MO, Malsbury CW (1982) Sagittal knife cuts in the near and far lateral preoptic area-hypothalamus disrupt maternal behaviour in female hamsters. *Physiol Behav* 28(5):857–867

- Millar JS (1979) Energetics of lactation in *Peromyscus maniculatus*. *Can J Zool* 57:1015–1019
- Morrison S, Barton L, Caputa P, Hik DS (2004) Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. *Can J Zool* 82(4):533–540
- Otoni EB, Ades C (1991) Resource location and structural properties of the nestbox as determinants of nest-site selection in the golden hamster. *Anim Learn Behav* 19(3):234–240
- Ovadia O, Ziv Y, Abramsky Z, Pinshow B, Kotler BP (2001) Harvest rates and foraging strategies in Negev Desert gerbils. *Behav Ecol* 12(2):219–226
- Perrigo G (1987) Breeding and feeding strategies in deer mice and house mice when females are challenged to work for their food. *Anim Behav* 35:1298–1316
- Perrigo G (1990) Food, sex, time, and effort in a small mammal: energy allocation strategies for survival and reproduction. *Behaviour* 114(1/4):191–205
- Quek VS, Trayhurn P (1990) Calorimetric study of the energetics of pregnancy in golden hamsters. *Am J Physiol Regul Integr Comp Physiol* 259(4):R807–R812
- Rehmeier RL (2005) Factors influencing nightly activity of deer mice (*Peromyscus maniculatus*) in tallgrass prairie. Ph.D. dissertation, Division of Biology, Kansas State University, Manhattan, KS
- Reichman OJ, Roberts E (1994) Computer simulation analysis of foraging by heteromyid rodents in relation to seed distributions: implications for coexistence. *Aust J Zool* 42(4):467–477
- Rink RD (1969) Oxygen consumption, body temperature, and brown adipose tissue in the postnatal golden hamster (*Mesocricetus auratus*). *J Exp Zool* 170(1):117–123
- Scribner SJ, Wynne-Edwards KE (1994) Disruption of body temperature and behavior rhythms during reproduction in dwarf hamsters (*Phodopus*). *Physiol Behav* 55(2):361–369
- Sharpe F, Rosell F (2003) Time budgets and sex differences in the Eurasian beaver. *Anim Behav* 66(6):1059–1067
- Sharpe PB, Van Horne B (1998) Influence of habitat on behavior of Townsend's ground squirrels (*Spermophilus townsendii*). *J Mammal* 79(3):906–918
- Smith RJ (1995) Harvest rates and escape speeds in two coexisting species of montane ground squirrels. *J Mammal* 76(1):189–195
- Sokoloff G, Blumberg MS (2002) Contributions of endothermy to huddling behavior in infant Norway rats (*Rattus norvegicus*) and Syrian golden hamsters (*Mesocricetus auratus*). *J Comp Psychol* 116(3):240–246
- Sommer S (2000) Sex-specific predation on a monogamous rat, *Hypogeomys antimena* (Muridae: Nesomyinae). *Anim Behav* 59(6):1087–1094
- Thorson JM, Morgan RA, Brown JS, Norman JE (1998) Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. *Behav Ecol* 9(2):151–157
- Verdolin JL (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behav Ecol Sociobiol* 60(4):457–464
- Vispo CR, Bakken GS (1993) The influence of thermal conditions on the surface activity of thirteen-lined ground squirrels. *Ecology* 74:377–389
- Wade GN, Jennings G, Trayhurn P (1986) Energy balance and brown adipose tissue thermogenesis during pregnancy in Syrian hamsters. *Am J Physiol Regul Integr Comp Physiol* 250(5):R845–R850
- Weinhold U, Kayser A (2006) *Der Feldhamster. Die neue Brehmbücherei* Bd. 625, Westarp Wissenschaften, Hohenwarsleben
- Whishaw IQ (1993) Activation, travel distance, and environmental change influence food carrying in rats with hippocampal, medial thalamic and septal lesions: implications for studies on hoarding and theories of hippocampal function. *Hippocampus* 3(3):373–385
- Woodside B, Jans JE (1988) Neuroendocrine basis of thermally regulated maternal responses to young in the rat. *Psychoneuroendocrinology* 13(1/2):79–98
- Zucker I, Wade GN, Ziegler R (1972) Sexual and hormonal influences on eating, taste preferences, and body weight of hamsters. *Physiol Behav* 8(1):101–111