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Foraging efficiency in the face of predation risk: a comparative study of desert rodents

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ABSTRACT

Question: What is the adaptive significance of the heteromyid cheek pouch?

Organisms: Two heteromyid rodents (Merriam's kangaroo rat, *Dipodomys merriami*, and desert pocket mouse, *Chaetodipus penicillatus*) from the Mojave Desert, and two gerbils (greater Egyptian gerbil, *Gerbillus pyramidum*, and Allenby's gerbil, *Gerbillus andersoni allenbyi*) from the Negev Desert, Israel.

Site: An outdoor vivarium on the Sede Boqer campus of Ben-Gurion University of the Negev, Israel.

Methods: We measured foraging time in seed trays for heteromyids and gerbils. We also measured the number of trips to food patches, and giving-up densities (GUDs, the amount of seed left behind when an individual left a seed tray).

Predictions: We expected cheek pouches to confer improved heteromyid foraging efficiency by reducing the number of trips between food patches and caching sites. We further expected that, compared with the other species, kangaroo rats would be less inhibited by barn owls, by moonlight, and by risky microhabitats.

Results: The two heteromyid species harvested more food per trip than the two gerbil species. Kangaroo rats had lower GUDs than any other species, particularly in risky microhabitats and at the full moon. Harvest rate curves for greater Egyptian gerbils and kangaroo rats indicated that these two larger bodied species were more vigilant than the two smaller bodied species.

Conclusion: Adaptations such as body size and the external cheek pouch appear to allow kangaroo rats to manage risk and harvest food more effectively than smaller and non-heteromyid rodents.

Keywords: foraging efficiency, gerbil, giving-up density, heteromyid.

INTRODUCTION

Optimal foraging theory shows how animals can forage in ways that maximize their fitness, such as reducing predation or other costs of foraging (Emlen, 1966; MacArthur and Pianka, 1966; Brown,

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1988). Morphological adaptations can enhance a forager's ability to maximize its fitness by allowing it to increase harvest without raising the costs of foraging. For example, a thick pelt can allow a mammal to spend time foraging in cold weather with reduced metabolic costs (Brown, 1988). Similarly, cheek pouches can increase harvest rates without raising predation costs. For example, internal cheek pouches allow cercopithecine monkeys to hold and process fruits while simultaneously retreating to safe microhabitats (Lambert, 2005). External cheek pouches should allow seed caching animals to harvest the capacity of their cheek pouches plus the capacity of their mouths in a single foraging bout. The result may be a reduction in the number of trips between caches and food patches. Reducing overall travel time thus reduces the time exposed to potential predators. We examined external cheek pouches as foraging adaptations by comparing the foraging efficiency of two species with cheek pouches (heteromyids) to two convergent species without cheek pouches (gerbils).

In a single experiment, we compared the foraging efficiency of one large (Merriam's kangaroo rat, *Dipodomys merriami*, 45 g) and one small (desert pocket mouse, *Chaetodipus penicillatus*, 22 g) heteromyid with that of two gerbil species of similar size that do not possess cheek pouches: the greater Egyptian gerbil (*Gerbillus pyramidum*, 40 g) and Allenby's gerbil (*Gerbillus andersoni allenbyi*, 24 g). All four species are granivorous, nocturnal, and store seeds in caches (Price *et al.*, 2000; Ovadia *et al.*, 2001). We define foraging efficiency as the amount of food harvested per foraging trip. To measure food harvest, we measured giving-up density (GUD), i.e. the amount of food left behind in a depletable patch when marginal foraging costs just balance marginal benefits (Brown, 1988). We used video cameras to record the number of trips together with foraging times.

Comparative studies of similar species on different continents provide clues to evolutionary adaptations within those species. In a review of foraging data from both families on different continents, Kotler *et al.* (1994) observed that heteromyids and gerbils respond similarly to the presence of owls, moon illumination, and microhabitats. However, kangaroo rats, likely due to several morphological adaptations – bipedalism, relatively large body size, and inflated auditory bullae (Webster, 1962) – appear to make better use of foraging opportunities in higher risk patches than do pocket mice.

We consider one adaptation, cheek pouches, shared by kangaroo rats and pocket mice. Cheek pouches are fur-lined, external (i.e. not inside the mouth) pockets that open near the mouth. They may amount to a superior foraging technology if they confer the ability to harvest food more efficiently. In a foraging experiment testing all four species' responses to snakes and owls, Kotler *et al.* (2016) observed the most intensive foraging by kangaroo rats. We predicted that kangaroo rats and pocket mice would harvest more food per trip between food trays and caches than would gerbils, due to their ability to store seeds in their cheek pouches. In terms of GUD, we predicted that kangaroo rats would forage most intensively, recording the lowest GUDs. Considering metabolic requirements, the larger greater Egyptian gerbil might be considered to have lower GUDs than the desert pocket mouse and/or Allenby's gerbil. However, previous studies of greater Egyptian gerbils and the smaller Allenby's gerbil have revealed that the former are often observed to have similar or even higher GUDs than Allenby's gerbils (Kotler *et al.*, 1994, 2001, 2004). Regarding predator cues, we predicted that all rodents would be observed to have higher GUDs in 'open' patches, during brighter moon phases, and in the presence of owls.

METHODS

We carried out the study between 13 January and 8 February 2014 on the Sede Boqer campus of Ben-Gurion University of the Negev, in the northern Negev Desert. All trials were conducted in an outdoor vivarium with dimensions of $17 \times 34 \times 4.5$ m. The vivarium is an arena that is fully enclosed with rodent-proof, solid lower walls and mesh upper walls and ceiling, allowing the inside to be exposed to natural environmental conditions. The vivarium is subdivided into four 8.5×17 m sections, using dividers through or under which rodents cannot pass. Every other night, one of two barn owls was given free access to the entire vivarium. Each section contained six pairs of $28 \times 38 \times 8$ cm food patches, with one of each pair exposed to the open and the other sitting under a $76 \times 60 \times 16$ cm wooden frame covered with black cloth and branches to simulate a bush. The rest of the landscape was open loess/sand. Foraging stations were uniform in each section and were not relocated during the course of the experiment. Outside of the vivarium, the landscape was also uniform, open loess with sparse desert herbs. No snake dens were found near the vivarium, nor did we find evidence of other predators nearby. Each section of the vivarium housed one of four rodent species: *D. merriami* (Merriam's kangaroo rat), *C. penicillatus* (desert pocket mouse), *G. pyramidum* (greater Egyptian gerbil), and *G. andersoni allenbyi* (Allenby's gerbil) (6 individuals each). To address conservation concerns, we imported only male heteromyids from the Mojave Desert, thus only male rodents were used in the study. We chose to compare gerbils to heteromyids because the two gerbil species have similar sizes, diets, and ecologies as the two heteromyids, but they lack pouches. Our food patches each contained 3 litres of sand. Each evening, for 16 nights (4 nights in each moon phase: new, 1st quarter, full, and 3rd quarter), we mixed 3 g of millet seed into each food patch. We then sieved each patch the following morning to collect the seeds left behind by the rodents (the giving-up densities or GUDs).

To determine whether the New World rodents that have cheek pouches are able to harvest food from patches at a higher rate than the Old World rodents without cheek pouches, we measured GUDs and observed foraging time and the numbers of provisioning trips to food trays of each species. We did this using infrared video cameras to record (1) mean amount of food taken by each species per foraging trip (measured as initial seed abundance minus GUD divided by the number of new visits to food trays) and (2) the amount of time spent by foragers in each food patch. Measures of foraging time and number of trips were obtained through watching the videos and using Motion Meerkat v.1.9.1 software to reduce video footage to jpeg files in which motion was detected. Because the cameras could not provide accurate data on 'bush' trays, amounts of food per trip and harvest rate curves were calculated only for 'open' food patches. Hence, for measurements of numbers of foraging trips and foraging time, $N = 96$ per species.

Using the initial amount of food in each tray (3 g), final amounts (GUDs), and amount of time spent in each food patch per night, we constructed harvest rate curves as estimates of quitting harvest rates (QHRs) for each species (Kotler and Brown, 1990; Kotler *et al.*, 2010). Harvest rate curves use an integration of Holling's disc equation (Holling, 1959) to graph the relationship between harvests of food and patch resource density. One can use such graphs to compare visually different species' use of their behavioural tools for risk management of time allocation and vigilance (Brown, 1999; Kotler *et al.*, 2010).

We analysed GUD data and harvest per trip using general linear models in SYSTAT v.13 (SPSS Inc., 2009). Our GUD analyses included five models, the first of which included 'species'

in addition to microhabitat, moon phase, and owl presence as independent variables. The model contained 128 data points (4 species × 2 patch types × 16 nights per species). The last four models included microhabitat, moon phase, and owl presence for each species analysed separately. We used daily means of the natural logs of GUDs as the dependent variable in our models for three reasons: to meet the assumption of normality in our model; to eliminate any possibility of non-independence of replicates; and to account for variation between foraging stations within each section of the vivarium.

RESULTS

Ratios of food harvested per foraging trip

Analyses of the amount of food harvested per trip revealed intriguing clues about the value of external cheek pouches. The model included species, owl presence, moon phase, and date as independent variables. Ratios only varied significantly by species ($F_{3,65} = 7.173$, $P < 0.001$). Planned pairwise comparisons confirmed that the two gerbil species did not harvest different amounts of food per trip. Neither did the two heteromyid species differ in their ratios of food per trip. However, both gerbil species harvested significantly less food per trip than did the heteromyid species ($P = 0.003$ for kangaroo rats and greater Egyptian gerbils; $P = 0.007$ for kangaroo rats and Allenby's gerbils; $P < 0.001$ for greater Egyptian gerbils and pocket mice; $P = 0.001$ for Allenby's gerbils and pocket mice) (Fig. 1).

Giving-up densities

When species was included as a variable in the model, all variables significantly affected rodent foraging. Giving-up densities were significantly higher (less foraging) in the riskier open patches than in patches under artificial bushes ($F_{1,104} = 132.645$, $P < 0.001$) (Fig. 2C). Overall, the rodents foraged the least intensively (highest GUDs) at the full moon ($F_{3,104} = 4.904$, $P = 0.003$) and when a barn owl was present in the vivarium ($F_{1,104} = 51.094$,

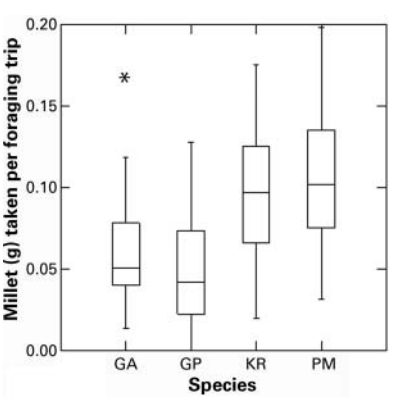

Fig. 1. Box plots of the ratio of food harvested per foraging trip. The heteromyids – kangaroo rats (KR) and pocket mice (PM) – harvested significantly more food per foraging trip than either gerbil species, Allenby's gerbil (GA) or greater Egyptian gerbil (GP).

$P < 0.001$). Overall, GUDs also differed significantly between the different species ($F_{3,104} = 41.068$, $P < 0.001$), with kangaroo rats foraging the most intensively and greater Egyptian gerbils foraging the least intensively. A Tukey *post-hoc* test revealed significant differences between the GUDs of greater Egyptian gerbils and all the other species ($P < 0.001$ for all) and between kangaroo rats and pocket mice ($P = 0.015$), but no difference between the GUDs of the large heteromyid kangaroo rats and the small Allenby's gerbils (Fig. 2A). In addition, we found significant interactions between species and moon phase

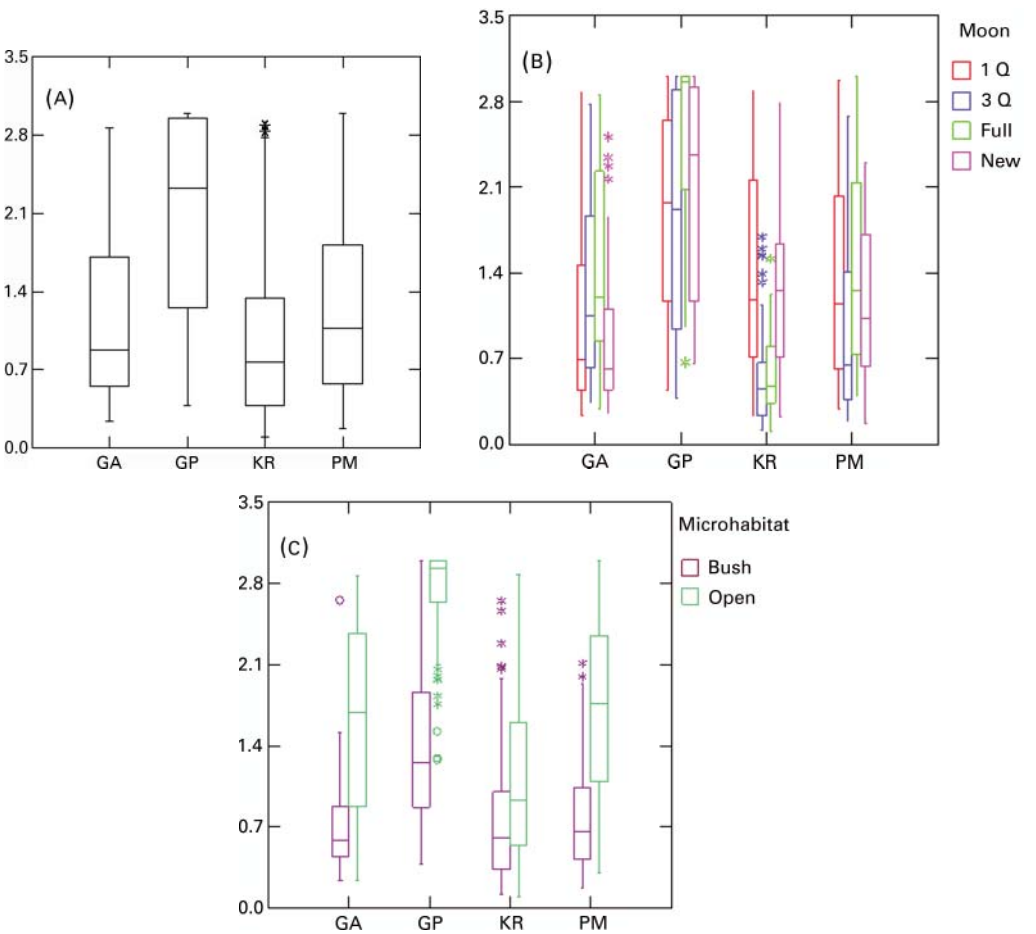

Fig. 2. Box plots of GUDs of the four rodent species: Allenby's gerbil (GA), greater Egyptian gerbil (GP), Merriam's kangaroo rat (KR), and desert pocket mouse (PM). (A) The large-bodied greater Egyptian gerbils harvested the least amount of food overall (highest GUDs), while the large-bodied Merriam's kangaroo rat harvested the most food. (B) The GUDs of Merriam's kangaroo rats were among their lowest during the full moon, while the other three species tended to avoid foraging activity during the full moon. Similarly, most species foraged most intensively at the new moon except for Merriam's kangaroo rats, which reduced their activity at this time. (C) All species foraged more intensively in the covered patches ('bush') than in the open patches. Merriam's kangaroo rats varied the least in their use of the two microhabitats, while the other large-bodied rodents, greater Egyptian gerbils, varied the most in their use of the two microhabitats.

($F_{9,104} = 7.466$, $P < 0.001$) and between species and owl presence ($F_{3,104} = 2.686$, $P = 0.050$). Specifically, kangaroo rats exhibited an almost opposite response to the full moon as the other rodents (Fig. 2B). Greater Egyptian gerbils showed less of a response to owl presence than the other species.

When we analysed responses to predation cues by each species separately, we were able to focus on some specific effects. First, greater Egyptian gerbils were the only species not to have significantly higher GUDs when owls were present. Second, each species responded significantly yet differently to moon phase, with kangaroo rats deviating the most dramatically from the other species. Greater Egyptian gerbils, Allenby's gerbils, and pocket mice showed general trends of foraging the least at the full moon (Fig. 2B). Kangaroo rats appeared to forage the most intensively at the full and 3rd quarter moon phases (Tukey: $P < 0.001$ for differences between 1st and 3rd quarter, 1st quarter and full, 3rd quarter and new, and full and new).

Harvest rates

Greater Egyptian gerbils (GP) used vigilance the most extensively, as revealed by shallow harvest rate curves. The order of vigilance use, was GP > KR > PM > GA, although pocket mice (PM) and Allenby's gerbils (GA), the two small-bodied species, had curves with very similar slopes. The two large-bodied species – kangaroo rats (KR) and greater Egyptian gerbils – obtained GUDs at lower harvest rates than the two small-bodied species. Finally, kangaroo rats were observed to have the lowest GUDs of the four species by allocating the most time to foraging, while greater Egyptian gerbils allocated the least time to foraging (Fig. 3).

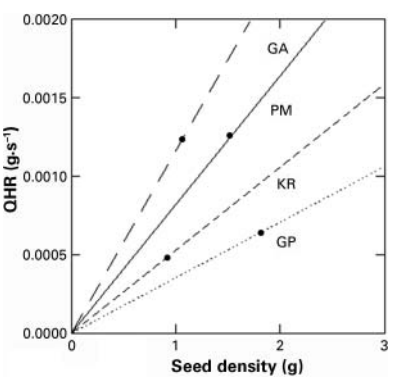

Fig. 3. Summary graph showing harvest rate curves for Merriam's kangaroo rats (KR), desert pocket mice (PM), greater Egyptian gerbils (GP), and Allenby's gerbils (GA) in open patches. Estimates of quitting harvest rates (QHR) appear as functions of seed density in the resource patch. We estimated seed handling time and attack rate using the rodents' total time in trays, initial food abundance, and giving-up density. Curves for more vigilant foragers are shallower as a result of shifting attention from harvesting to predator detection. Patch depletion can be seen by following each curve from initial resource density at the upper right corner down towards the origin at the lower left corner. Points plotted on each curve represent mean GUDs for each species. Points that are closer to the origin reflect greater time allocation (Embar *et al.*, 2011, appendix 1).

DISCUSSION

External cheek pouches may well represent superior foraging technology. The two cheek pouch-bearing heteromyid species in our experiments harvested amounts of millet per foraging trip that were similar to one another and significantly higher than those of either non-pouched gerbil species (Fig. 1). An interesting hypothesis for the evolution of the heteromyid external cheek pouch is that it compensates for a reduced gape (resulting from the enlarged auditory bullae of heteromyids) (Nikolai and Bramble, 1983). Alternatively, fur-lined external cheek pouches may confer an advantage to desert foragers because they prevent salivary water loss to cached seeds (Long, 1976). Of course, it is possible that external cheek pouches have multiple adaptive benefits. Regardless, our data clearly show a striking enhancement in the amount of food that can be carried per trip in the two cheek-pouched heteromyid species. Cheek pouches require fewer trips between foraging and caching sites. Therefore, such an adaptation can improve survival by lowering the overall amount of time exposed to predators.

As predicted and observed previously (Kotler *et al*., 2016), kangaroo rats foraged the most intensively of all species (Fig. 2A). Consistent with previous observations of greater Egyptian gerbils (Kotler *et al*., 1994, 2001, 2004), they were observed to have the highest GUDs of all species, despite their relatively large body size (Fig. 2A). With respect to predator cues, most of the rodents' responses were consistent with our expectations (Kotler *et al*., 1994, 2016). Kangaroo rats recorded some of their lowest GUDs during the full moon. In contrast, the other three species tended to reduce foraging activity during the full moon and forage the most intensively during the new moon (Fig. 2B). All species harvested more millet from the safe (bush) patches than from risky (open) patches, but kangaroo rats discerned the least difference between the two microhabitats (Fig. 2C). Indeed, higher rates of predation on rodents by owls have been observed in open food patches (Kotler *et al*., 1988). Three of the species reduced their foraging activity on nights when a barn owl was present, but greater Egyptian gerbils did not reduce their GUDs significantly in response to owls. It is possible that their GUDs were already so high (Fig. 2A) that there may not have been room for much variation in response to owls, given their basic metabolic requirements.

In terms of harvest rates, both large-bodied species were able to achieve GUDs at lower harvest rates than the two small-bodied species. From the slope of the harvest rate curves, we find that greater Egyptian gerbils were most vigilant, while the small Allenby's gerbil and the desert pocket mouse were least vigilant (Fig. 3). Interestingly, the two large-bodied rodents were more vigilant than the smaller-bodied species, as seen from their harvest rate curves (Fig. 3). This was so despite their vastly different GUDs (Fig. 1), use of microhabitats (Fig. 2C), responses to moonlight (Fig. 2B), and time allocated to foraging (Fig. 3). In fact, Kotler *et al*. (1988) found higher rates of predation by barn owls on larger heteromyid rodents (Bailey's pocket mouse, *Chaetodipus baileyi*, 33 g) than on smaller heteromyids (Arizona pocket mouse, *Perognathus amplus*, 12 g). Rodents such as greater Egyptian gerbils and Merriam's kangaroo rats may be a better size for owls to capture than the two smaller species, requiring the larger rodents to be more vigilant.

Gerbils and heteromyids occur in convergent desert communities on different continents. Different co-evolutionary relationships within these communities may explain observed differences in morphology and behaviour. While both communities have owls and snakes as predators, certain traits in kangaroo rats, such as expanded auditory bullae, short arms, and bipedalism, may have evolved in response to exceptionally talented predators – pit vipers

(Kotler *et al.*, 2016). Moreover, some kangaroo rat species actually confront snakes by foot drumming and kicking sand (Randall, 1993). Heteromyids initially evolved in tropical Central America and already had cheek pouches by the time they invaded deserts (Wahlert and Souza, 1988; Hafner *et al.*, 2007). Possession of external cheek pouches may have made them well suited to dealing with pit vipers in open, arid environments. Indeed, it can be argued that several of the anti-predator traits of kangaroo rats were forged in deserts because of rattlesnakes. In tests involving both snakes and owls, Merriam's kangaroo rats behaved in ways that suggest an evolutionary response to snakes, such as avoidance of foraging during new moon phases, when rattlesnakes are likely to be at their most lethal (Kotler *et al.*, 2016). In the same experiment, Kotler *et al.* (2016) observed that both kangaroo rats and desert pocket mice selected open microhabitats (risky because of owls) over bush microhabitats (risky because of snakes). Our experiments included owls but not snakes, and all of our rodents preferred the bush microhabitats. However, the kangaroo rats displayed the mildest selection for the bush microhabitat (Fig. 2C). Moreover, the kangaroo rats foraged significantly more during the full moon, when owls and kangaroo rats can see best and pit vipers (had they been present) would not have had the advantage. These pieces of evidence, together with that gathered by Kotler *et al.* (2016), suggest that selection pressures on kangaroo rats, and possibly all heteromyids, from rattlesnakes which can 'see' in the dark may outweigh selection pressures from aerial predators that use their eyes and ears to hunt from above.

Our results contrast with those of Upham and Hafner (2013), who found that kangaroo rats, apparently including Merriam's kangaroo rats, in a Great Basin community avoided bright nights more than other sympatric rodent taxa. Our kangaroo rats were captured in the Mojave Desert, a different landscape to the Great Basin. It is possible that the Mojave environment is more strongly dominated by rattlesnakes. In fact, in the open, sandy sampling area used by Upham and Hafner (2013) there were no rattlesnakes. However, several mammalian predator species and long-eared owls (*Asio otus*) were present at their site, raising an interesting question about plasticity in the interaction of landscape and behaviour. Perhaps when a heteromyid is born into an environment rich with rattlesnakes, its behaviour reflects a response to heat-sensing predators. But, when a heteromyid lives in or hails from an area without rattlesnakes, its behaviour instead reflects a response to visual predators.

For seed-caching rodents, more food harvested per foraging bout means fewer foraging trips required and less exposure to predators. Our experiments revealed a link between the evolution of the external heteromyid cheek pouch and an improved capacity to harvest seeds. It is likely that this link is driven by the need to avoid predators (Kotler *et al.*, 2016). Kangaroo rats, in particular, managed risk and harvested food more effectively than smaller and non-heteromyid rodents. We suggest that the relative insensitivity to predator cues by kangaroo rats is possible because of the external cheek pouch and additional morphological adaptations, including bipedalism, shortened forelimbs, sand kicking behaviour (Randall, 1993), relatively large body size, and inflated auditory bullae. Clearly, Merriam's kangaroo rats (and other kangaroo rat species not tested here) provide examples of organisms highly adapted to life in the desert, where relatively sparse foraging opportunities must be profitable and survivable. Our data suggest that heteromyids excel under such conditions.

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