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APPREHENSION AND TIME ALLOCATION IN GERBILS: THE EFFECTS OF PREDATORY RISK AND ENERGETIC STATE

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Abstract. Apprehension is a behavioral response of a forager to risk of predation involving the allocation of the forager's attention away from foraging-related tasks and toward predator detection. It, along with time allocation, can be used by a forager to manage risk. Apprehension should increase, and time allocation should decrease with a forager's energetic state (marginal value of energy). We tested these predictions on Allenby's gerbils (*Gerbillus andersoni allenbyi*) by manipulating the energetic state of the gerbils through augmentations of millet seeds. We also manipulated two risk factors, the microhabitat of the foraging patch (bush or open) and the presence of barn owls (*Tyto alba*). We measured apprehension of gerbils using the selectivity of gerbils for trays that differed in the distribution of seeds that they contained and time allocation using the amount of seeds left behind in trays, the giving-up density (GUD). Gerbils harvested 4.6 times more seeds when supplemental seeds were available, 17.4% fewer seeds when owls were present, 25.8% fewer seeds from the open than the bush microhabitat, and 19.3% fewer seeds from trays when seed augmentations were also present. With regard to time allocation, gerbils had higher GUDs (allocated less time) when risk was higher: in the open microhabitat and in the presence of owls. Also, the response of gerbils to owls was affected both by the seed augmentation and by microhabitat. With regard to apprehension, the gerbils were more apprehensive when extra seeds were added. Their level of apprehension changed little in the bush microhabitat but increased greatly in the open microhabitat when energetic state was manipulated. Thus, gerbils use both time allocation and apprehension in response to predators. Changes in the energetic state of a forager led to the predicted increase in apprehension accordance with Clark's asset protection principle.

Key words: apprehension; energetic state; foraging theory; gerbils; giving-up densities; Negev Desert; optimal patch use; risk of predation; time allocation; tradeoffs of food and safety.

INTRODUCTION

The interactions between predators and prey comprise an important topic in foraging ecology (e.g., Lima and Dill 1990, Hugie and Dill 1994, Lima 1998, Brown et al. 1999, 2001, Kotler et al. 2002, Brown and Kotler 2004). Prey might behave as to manage risk of predation by trading off food and safety. To do so, they can use both time allocation and apprehension (Lima 1996). In regards to time allocation, prey individuals choose when, where, and for how long to be active, based on the number and distribution of predators and food. In regards to apprehension, prey can allocate their attention more either toward gathering information on foraging-related matters or predatory risk.

We define apprehension as the heightened levels of attention that foragers direct toward predator detection. Apprehension should increase the ability of foragers to more easily detect predators. Consequently, as foragers become more and more apprehensive, they should become less catchable by their predators. Apprehension and activities such as foraging can occur at the same time. However, the more that attention is directed toward predators, the less can be directed toward foraging tasks. Thus, the elevated ability to detect predators brought about by apprehension comes at the expense of harvest rates and information on food availability (Brown et al. 1999, 2001, Dall et al. 2001, Kotler et al. 2002).

Apprehension should be tailored by the individual to suit its specific needs and circumstances. For in-

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stance, Clark's (1994) asset protection principle indicates that a well-fed animal has more to lose from predation than an animal with a lower energetic state (i.e., marginal value of energy). Hence the optimal level of apprehension should increase with the energetic state of the animal (McNamara and Houston 1986, 1992). This prediction likewise applies to the use of time allocation, with the response of the forager to risk of predation being comprised of a mix of the two.

Gerbils in the sand dunes of the Negev Desert of Israel are known to use time allocation and apprehension to balance the benefits of foraging with the risk of predation (Kotler et al. 2002). Furthermore, their energetic state has been shown to alter their time allocation in response to risk of predation (Kotler 1997). It is thus of interest whether gerbils also use apprehension in accordance to their energetic state and changing risk of predation.

Here, we tested for the effect of energetic state on a forger's level of apprehension in Allenby's gerbil (*Gerbillus andersoni allenbyi*; 24 g), whose vigilance behaviors are difficult to measure directly. We measured apprehension indirectly via relative patch-use performance of gerbils in food patches that vary in the complexity of food distribution. We then used this measure of apprehension to test for state-dependent apprehension. We used gerbils and owls in an outdoor aviary to test that (1) apprehension should increase as the forager shifts from harvesting safe vs. risky food patches (bush and open microhabitats), (2) apprehension should increase with an increase in the number of predators (presence and absence of owls), (3) apprehension should increase with the energetic state of the forager (control vs. augmented food levels), and (4) animals with a high energetic should respond more strongly to spatial and temporal increases in risk than animals with a low state (Brown 1999).

Measuring Apprehension

We have previously used the patch use behavior of the gerbils to gauge apprehension (Kotler et al. 2002). We are interested in apprehension insofar as it affects foraging, and so we operationally define apprehension as redirection of attention from foraging to predator detection in a manner that lowers both predatory risk and feeding rate (Brown et al. 2001, Dall et al. 2001). While harvesting food, the behaviors of a forager may include detecting the boundaries of resource patches and estimating resource densities (vague boundaries; Schmidt and Brown 1996, Fierer and Kotler 2000). As a result, a more apprehensive forager that has redirected much of its attention toward predator detection should make greater and more frequent mistakes in foraging-related activities such as estimating patch size. Both over- and underestimation of patch size reduce harvest rates and patch value (Schmidt and Brown 1996). The more demanding the foraging task in terms of patch assessment, search, and harvest, the more patch use and patch value should decline with apprehension.

One can reveal changes in apprehension by offering alternative foraging situations that differ in complexity. We used seed trays (a 60 × 45 × 3-cm aluminum tray filled with 2 g of millet seeds mixed into 5 L of sand) to produce three patch types: full, bottom, and side. In the ''full tray,'' we mixed millet seeds randomly into the full 5 L of sand and spread the sand evenly across the tray. This is our standard of comparison, where all patch boundaries are clearly marked by the edges of the tray. In the remaining two tray types, the same 3 g of millet per tray were used, but they were concentrated into micropatches with twice the usual density of seeds. In the ''bottom tray,'' the 2 g of seeds were mixed into half of the sand and spread over the bottom of the tray, with the other half of the sand containing no seeds spread over the top. This creates a greater challenge for the forager since it must forage for deeply buried seeds. In the ''side tray,'' the seeds were mixed into half of the sand and spread to full depth over one-half of the tray, with the remainder of the sand spread over the other half. This creates greater opportunity should the forager be able to accurately locate all patch boundaries accurately. The bottom and side trays are more demanding than the full trays in two respects: first, it is harder to search for seeds lower in the substrate, and second, there is an advantage to accurately assessing the boundary line between the upper (side) half without food and the lower (other side) half with all of the food (Schmidt and Brown 1996).

As a forager's apprehension increases, the information available to it on patch boundaries should decrease. This should have little effect on the value of the full tray as little attention is needed to identify its clearly marked boundaries. In contrast, some of the boundaries of the side and bottom trays are set by changes in seed densities and may require much of the forager's attention to accurately identify. Consequently, greater apprehension should adversely affect patch value of both side and bottom patches. As a result, the value of the full patch type for a more apprehensive forager should increase relative to either of the other two. Thus, we used selectivity for the full tray as our gauge of apprehension. In support of this metric, Schmidt and Brown (1996) found that fox squirrels (*Sciurus niger*) became more selective for a full tray as compared to a side tray when patches were shifted from near trees (safe) to away from trees (risky).

We calculated the selectivity for the full tray in comparison to the bottom or side tray using Manly's index for depletable resources (Chesson 1983, Schmidt and Brown 1996):

$$[\ln(\text{proportion of seeds remaining in full tray})] \div [\ln(\text{proportion of seeds remaining in bottom or side tray}) + \ln(\text{proportion of seeds remaining in full tray})].$$

The selectivity for the full tray compared to the bottom tray should always be >0.5; the selectivity for the full tray compared to the side tray should always be <0.5. In both cases, selectivity for the full tray should increase with higher levels of apprehension. Thus, increases in selectivity for the full tray should reveal increases in apprehension by gerbils.

For quantifying time allocation, we used the giving-up density, or GUD, the amount of seeds remaining in the tray after a night of foraging (Kotler and Brown 1990).

Methods

We performed our experiment in a large, outdoor aviary (18 × 23 × 5 m) located at the Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boker Campus, Israel (e.g., Kotler et al. 1991). The aviary was divided into two equal-sized areas with a 1 m tall rodent-proof fence and contained piles of cut brush placed on 15 cm high trellises to simulate a desert with 30% shrub cover. For more details, see Kotler et al. (1991).

We provided seed resources for gerbils at eight stations on each side of the aviary. At each station, we placed three seed trays arrayed around a trellis/shrub. At each station, we placed one full tray, one bottom tray, and one side tray along the sides of the triangular-shaped trellis. The trellis was topped with a pile of cut brush (''shrub''). The long axis of each tray was placed parallel with a side of the trellis. We used two possible arrangements of trays. In one, trays were pushed under the trellis until the corners of the trays met. In this configuration (bush), approximately half of each tray was covered by the shrub. In the other (open), we pulled trays out such that the edge of each tray was directly underneath the outer edge of the trellis and the entire tray was uncovered. All together, we placed 48 seed trays in the aviary. Following a night of foraging by gerbils, we scored trays for foraging activity, removed remaining seeds from foraged trays (to be taken to the laboratory to be cleaned and weighed to obtain the GUD), and recharged trays with 2 g of millet.

In the experiment, we manipulated risk of predation and energetic state of the gerbils. We placed 12 individuals of Allenby's gerbils on each side of the aviary. We conducted four rounds of four nights each: round 1, 10–13 June 1999; round 2, 21–24 June 1999; round 3, 20–23 July 1999; round 4, 16–19 August 1999. We replaced each gerbil captured by predators with a new individual and all individuals after each round. We manipulated risk of predation in two ways. First, we altered the presence of predators using four barn owls (*Tyto alba*) two at a time in the aviary. We placed owls in the aviary every other night such that in each four-night round, owls were present on two nights. Second, we manipulated risk by placing seed trays at a station in different microhabitats: either the bush position (safe) or the open position (risky). Barn owls are more lethal when striking at gerbils in the open than in the bush microhabitat (Kotler et al. 1991). On any given night, the trays at half of the stations on each side of the aviary were in the bush position and half were in the open position. We switched the microhabitat of each station each night. Finally, we manipulated the energetic states of the gerbils by augmenting the gerbils on one side of the aviary at a time with supplemental millet seeds. In each round, we augmented the energetic states of gerbils for all four nights on one side of the aviary only. We carried out the augmentation by adding 10 g of free seeds at each station each night, i.e., seeds placed in Petri dishes without the impediment of sand (Kotler 1997). Each round, we altered the side of the aviary on which the augmentation took place. We equate the energetic state of the gerbils in this experiment with the amount of seeds they remove from seed trays and Petri dishes.

We used analysis of variance to analyze the data, using GUDs (log-transformed) or selectivities based on stations where both the full tray and the side or bottom tray had been foraged that night. Factors included in the model were side of aviary, round, tray type, microhabitat (a risk factor), seed augmentation (energetic state), and the presence of owls (a risk factor). We also included the two-way interactions with microhabitat, energetic state, and owls.

Results

Over the course of the experiment, foraging gerbils removed a total of 333.7 g of seeds in the absence of seed augmentation and 1549.38 g of seeds when supplemental seeds were present (including supplemental seeds), i.e., 4.6 times more seeds when supplemental seeds were available. This reflects the increase in their energy well-being as a result of the augmentation, regardless of whether these seeds were eaten or cached. The seed tray data collected in this experiment yielded both measurements of GUDs, i.e., measurements of time allocation, and measurements of selectivities, i.e., apprehension.

We start by looking at the GUD results. In response to the risk factors, GUDs were significantly higher in the open microhabitat (MS = 2.254, $F_{1, 243} = 11.559$, $P = 0.001$) and the presence of owls (MS = 4.987, $F_{1, 243} = 25.613$, $P < 0.001$; Fig. 1). That is, gerbils harvested 25.8% less seeds from the open microhabitat than the bush and harvested 17.4% less seeds in the presence of owls than in their absence. There was also a significant interaction between owls and microhabitat, signifying a stronger response in the bush microhabitat (MS = 0.957, $F_{1, 243} = 4.913$, $P = 0.028$; Fig. 1). For comparison, the seed augmentation led gerbils to harvest 19.3% less seeds from seed trays (although gerbils harvested more seeds overall including the augmentation itself). The seed augmentation had its effect on gerbil foraging through its interaction with owls (MS = 2.283, $F_{1, 243} = 11.725$, $P = 0.001$; Fig. 2), with

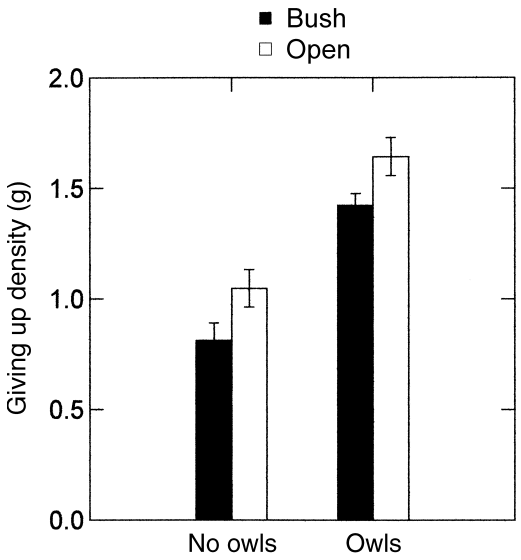


FIG. 1. Mean giving-up densities (back-transformed, with standard errors from the log-transformed data) as a function of the presence or absence of owls and of microhabitat (bush or open). Giving-up densities (GUDs) provide a measure of foraging activity, with lower GUDs signifying greater levels of activity. Gerbils are more active in the bush microhabitat and in the absence of owls.

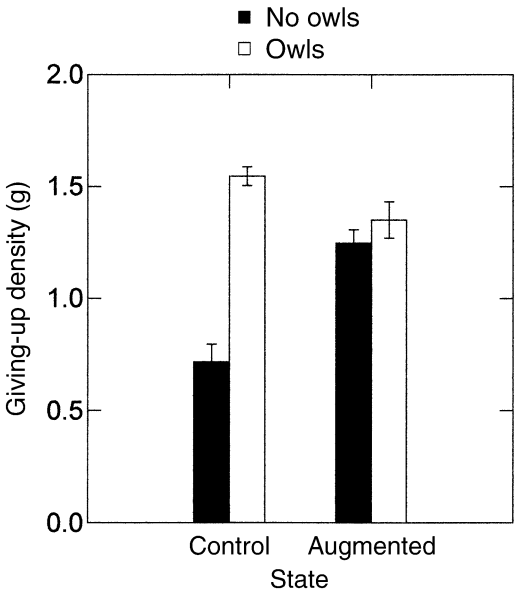


FIG. 2. Mean giving-up densities (back-transformed, with standard errors from the log-transformed data) as a function of energetic state of the forager (whether or not foragers had access to seed augmentations) and the presence or absence of owls. The seed augmentation reduced forager activity in seed trays and reduced the response to the presence of owls.

gerbils showing a stronger response to owls in the absence of supplemental seeds. The augmentation by itself caused GUDs to increase to high values, and left little room for gerbils to show a response to owls when the predators were present. These changes in GUDs are indicative of changes in time allocation in response to factors associated with risk (microhabitat, predators) and energetic state.

Next, we consider the selectivities of the gerbils for the different types of seed trays. Gerbils whose energetic state had been augmented were more apprehensive, as indicated by significantly higher selectivities for the full seed tray (MS = 0.099, $F_{1,94} = 3.035$, $P = 0.042$, one-tailed test; Fig. 3). Furthermore, the response of the gerbils to the supplemental seeds depended on microhabitat (MS = 0.192, $F_{1,94} = 5.891$, $P = 0.017$; Fig. 3). Gerbils foraging in the safer bush microhabitat displayed the same level of selectivity (apprehension) regardless of whether they had received the seed augmentation. In contrast, they displayed greater selectivity (apprehension) in the riskier open microhabitat when receiving supplemental food. That is, animals foraging in safety appear to use a constant level of apprehension, but the gerbils in heightened energetic state responded to the increased risk of the open microhabitat with higher apprehension. Curiously, gerbils without augmentation were more apprehensive in the safe microhabitat. The presence of owls did not affect apprehension in these experiments (mean selectivity when owls were present was 0.479 ± 0.044 (mean ± 1 SE), and when owls were absent was 0.421

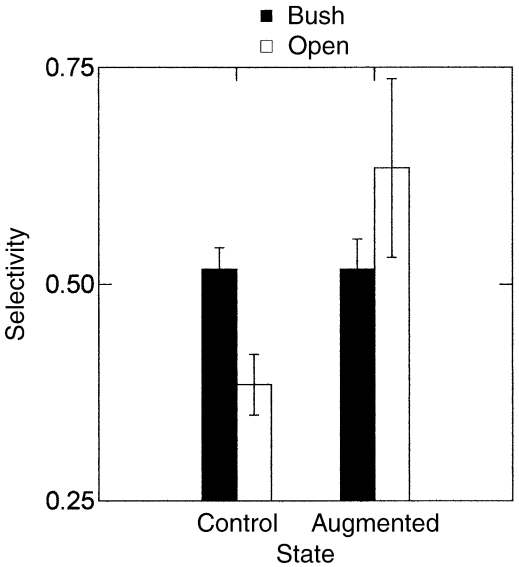


FIG. 3. Mean selectivity for the full tray (apprehension) (±1 SE) as a function of microhabitat and energetic state of the gerbils (whether or not foragers had access to seed augmentations). Selectivity was calculated using Manly's index for depletable resources (Chesson 1983, Schmidt and Brown 1996). Gerbils increased their apprehension when energetic state was augmented with supplemental seeds. Furthermore, apprehension of the gerbils in the bush microhabitat was constant regardless of energetic state, while gerbils with enhanced energetic state responded with increased apprehension in the open microhabitat.

$\pm$ 0.074; owls, MS = 0.002, $F_{1,94} = 0.069$, $P = 0.933$; owls $\times$ state, MS = 0.001, $F_{1,94} = 0.026$, $P = 0.872$; owls $\times$ microhabitat, MS = 0.0001, $F_{1,94} = 0.002$, $P = 0.966$). Interestingly, tray type per se did not affect selectivity, even though the means were in the predicted direction (selectivity for the full tray compared to the side tray was 0.381 $\pm$ 0.032; selectivity for the full tray compared to the bottom tray was 0.589 $\pm$ 0.039; tray type, MS = 0.001, $F_{1,94} = 0.007$, $P = 0.933$; tray type $\times$ seed augmentation, MS = 0.012, $F_{1,94} = 0.335$, $P = 0.553$; tray type $\times$ owls, MS = 0.004, $F_{1,94} = 0.130$, $P = 0.720$; tray type $\times$ microhabitat, MS = 0.031, $F_{1,94} = 0.939$, $P = 0.335$).

Discussion

Our experiment demonstrated that time allocation and apprehension are used by the gerbils in response to the risk of predation. But they appear to be used differently. Gerbils responded to microhabitat by altering both time allocation and apprehension (in accordance with predictions 3 and 4). The prediction that apprehension would increase in the risky microhabitat relative to the safe microhabitat in response to augmenting the gerbils' energetic state was strongly supported. Thus, energetic state does affect apprehension. However, gerbils responded directly to actual presence of predators with only changes in time allocation (contrary to predictions 1 and 2). There was no general trend toward higher apprehension in the risky than safe microhabitat. In fact, with no augmentation, apprehension in the open was lower than that in the bush. Perhaps unsupplemented animals may have actually ''tuned-out'' risk while in the open so as to speed the rate of resource harvest and hence minimize time exposure in the risky microhabitat (Brown 1999). And, there was no effect of owls on apprehension. The differential application of time allocation and apprehension in response to different risk factors (actual predators, microhabitat) suggest that apprehension may be more valuable in determining whether predators are actually present, but once it has been determined that predators are present and close at hand, time allocation is more suitable in buying safety. The difference in how time allocation and apprehension are used appears again in the effect of energetic state via the seed augmentation. Gerbils in heightened energetic state had such high GUDs and such little foraging activity that the addition of owls made little difference. At the same time, they displayed more apprehension, but only in the open microhabitat. Both risk factors are affected by energetic state, but through different behavioral responses. Overall, the use of apprehension is dependent on the needs and circumstances of the forager.

Our experiments help to illuminate the foraging game played out between gerbils and their predators (Brown et al. 2002, Kotler et al. 2002). The gerbils forage on patches of seeds that are renewed daily by wind action on the sandy substrate (G. Ben-Natan et al., *in press*). The daily pulse and depletion of seeds, the ability of the gerbils to respond both to seed availability and to the presence of their predators, and the ability of the predators to respond to the antipredator behavior of the gerbils creates a situation where the values of the behaviors adopted by the gerbils depends on the behavior of the predators and vice versa. In such a situation, payoffs to particular behaviors are frequency dependent and can be modeled using game theory (Brown et al. 2002, Kotler et al. 2002). Game theory predicts that gerbils will be most active and apprehensive early in the night when seeds are most abundant, and predators will be most active then, too. Thereafter, there will be a lock-step of resource depletion, declining gerbil activity, declining gerbil apprehension, and declining predator activity throughout the night. Indeed gerbils are most active and apprehensive early in the night. They are also more apprehensive in the open microhabitat and in moonlit hours and bias their activity to times and places where they are relatively less apprehensive. The gerbils appear to use a combination of time allocation and apprehension that keeps risk-per-seed-harvested constant over the course of the night (Kotler et al. 2002). Our aviary experiments here focus on the gerbils and do not allow the predators to make foraging decisions. Nonetheless, they suggest how gerbils use two classes of behaviors to manage risk of predation.

To date, apprehension in terms of relative task performance has been examined only in gerbils (Dall et al. 2001, Kotler et al. 2002). Experimental works with other species have mostly focused on direct measures of apprehension such as vigilance and scanning behaviors. Bachman (1993) examined the effect of state on the time spent in vigilance versus foraging in Belding's ground squirrels (*Spermophilus beldingi*) by feeding squirrels with either an energy rich or an energy poor diet. Enriched squirrels increased their body mass, decreased their time spent in foraging, and increased the time spent in vigilance and intensity of vigilance; deprived squirrels did the opposite.

Evidence that energetic state affects vigilance also exists for birds. Lima (1995) examined vigilance in juncos (*Junco hyemalis*) as a function of the state of an individual and the rate at which its neighbors performed vigilance versus foraging. He manipulated state by depriving birds of food for 8 h. He then compared pecking rates in deprived vs. nondeprived birds. The slower was the peck rate, the higher was the rate of vigilance. Deprived birds displayed little detectable vigilance. In contrast, nondeprived birds displayed considerable vigilance, with solitary birds taking nearly twice as long as deprived birds to take 10 pecks. Pravosudov and Grubb (1998) examined vigilance in captive tufted titmice (*Baeolophus bicolor*) as a function of body mass of the bird and time of day. They found that scan rate (vigilance) was positively related to body mass independent of time of day (vigilance also in-

creased throughout the day). In both these examples, vigilance rates appear to be a function of energetic state.

Behavioral responses available to gerbils in response to predators include time allocation and apprehension. Clark's (1994) asset protection principle indicates that a well-fed animal has more to lose from predation than an animal with a lower energetic state and should thus be more cautious (e.g., McNamara and Houston 1986, 1992). Here, we have supplemented gerbils in a large aviary with extra food and subjected them to owls and food patches in microhabitats that differ in exposure while quantifying their time allocation and apprehensiveness using behavioral indicators of patch use. The results confirm that energetic state affects the level of apprehensiveness of gerbils in the context of a complex strategy of risk management

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