

What do predators really want? The role of gerbil energetic state in determining prey choice by Barn Owls

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Abstract. In predator–prey foraging games, predators should respond to variations in prey state. The value of energy for the prey changes depending on season. Prey in a low energetic state and/or in a reproductive state should invest more in foraging and tolerate higher predation risk. This should make the prey more catchable, and thereby, more preferable to predators. We ask, can predators respond to prey state? How does season and state affect the foraging game from the predator’s perspective? By letting owls choose between gerbils whose states we experimentally manipulated, we could demonstrate predator sensitivity to prey state and predator selectivity that otherwise may be obscured by the foraging game. During spring, owls invested more time and attacks in the patch with well-fed gerbils. During summer, owls attacked both patches equally, yet allocated more time to the patch with hungry gerbils. Energetic state per se does not seem to be the basis of owl choice. The owls strongly responded to these subtle differences. In summer, gerbils managed their behavior primarily for survival, and the owls equalized capture opportunities by attacking both patches equally.

Key words: *Allenby’s gerbil*, *Gerbillus andersoni allenbyi*; *Barn Owls*, *Tyto alba*; *coexistence*; *community ecology*; *foraging game*; *predator–prey interactions*.

INTRODUCTION

Game theory models suggest that predator–prey interactions are often sophisticated games of stealth and fear, where the prey’s best behavior depends on the predators, and vice versa (Bouskila 2001, Brown et al. 2001). Within these multi-trophic-level games, predators manage the fear they evoke in the prey by using behavioral tools of habitat selection and time allocation to navigate the landscape of fear in order to hunt where and when the prey are least wary and most catchable (Brown et al. 1999). At the same time, the prey manage their exposure to the risk of predation (Penteriani et al. 2013). To do so, they can use habitat selection and time allocation behaviors to navigate the landscape of risk and determine where and when to be active, and vigilance behavior to improve their chances of predator detection (Dall et al. 2001, Kotler et al. 2004). The use of these tools make prey harder to capture, but often at the cost of reducing the prey’s harvest rate of resources.

To successfully manage fear, predators must be able to assess their prey’s fearfulness. If not, it will be difficult for them to modulate their own behavior appropriately (Quinn and Cresswell 2004). How can we empirically assess whether predators can do so? In many cases, the

intensity of the prey’s response to predators is affected by changes in their own energetic state (Berger-Tal and Kotler 2010, Berger-Tal et al. 2010). Clark’s “asset protection principle” states that prey in a better state should take fewer risks, and the optimal behavior of the prey should account for both the environmental factors and its’ current reproductive prospects (Clark 1994). We can take advantage of this as follows. We can manipulate prey energetic state experimentally, thus altering prey risk taking, and see whether predators can choose between prey in a high energetic state vs. prey in a low energetic state. For example, prey in a low energetic state should try to find food also when the predation risk is higher, because they cannot afford to invest as much in wariness and other anti-predator behaviors (Berger-Tal and Kotler 2010, Berger-Tal et al. 2010). Therefore prey in a lower energetic state should be easier to catch, and predators should be able to respond to this. Similarly we can compare the game between reproductive and non-reproductive seasons, to assess the importance of prey reproductive prospects, the value of energy to the prey, and see whether predators can choose the prey that values energy the most. Prey in a reproductive state can convert energy directly to fitness and therefore reproducing prey should harvest more food and accept greater risks, and predators should be able to respond to this.

Do predators actually behave in this manner? When Berger-Tal et al. (2010) manipulated the state of both predators (Barn Owls) and prey (gerbils) by allowing hungry or well-fed owls to hunt either hungry or well-fed

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gerbils, they found that gerbils were able to react both to their own state and the state of the owls. But the owls responded only to their own state, hunting more actively when they were hungrier and less actively when well fed. Their hunting intensity remained unchanged regardless of whether their gerbil prey were in a high or low energetic state. Was this because owls cannot respond to gerbil state? Or was it because the foraging game between responsive predators and responsive prey obscures predator selectivity, since the prey may have behaviorally managed its risk of predation in a manner that presented the predator with equal opportunities?

To examine this, we build on Berger-Tal et al.'s (2010) work by presenting the owl simultaneously with two patches, one with hungry gerbils and the other with well-fed gerbils. This allows the owl to choose freely where to forage. We further manipulate the value of energy to the prey by comparing the responses of owls and gerbils during spring, the reproductive season when energy is more valuable, since it can be more directly translated into fitness (offspring), and during summer, when they are not in reproductive state. We predict the owl should be able to detect and respond to the prey state, and should choose gerbils (1) in a lower energetic state and (2) that value energy more.

METHODS

Vivarium.—We conducted this research in a large, 17 × 34 m outdoor vivarium, fully exposed to the natural environmental conditions. The vivarium is located on the Sede Boker Campus of Ben-Gurion University in the northern Negev Desert of Israel. It is divided into two equal-sized compartments by a 1 m tall rodent-proof metal partition. The partition prevents gerbils from crossing sides while permitting owls to fly freely throughout. Each compartment contains 36 evenly distributed stations each with an artificial bush made of a low-lying, 76 × 60 × 16 cm wooden trellis with a pile of cut brush placed on top.

Model animals.—For foragers we chose Allenby's gerbil, *Gerbillus andersoni allenbyi*, a small (24 g), nocturnal, granivorous rodent native to the Negev Desert. Gerbils were trapped from the field before the experiment, uniquely marked with numbered electronic passive induction transponder (PIT) tags, and released into the vivarium. A constant population of 15 individuals per side was maintained within the vivarium during the experiment. The gerbil population had equal proportions of both genders, to account for as natural a response as possible to the seasonal changes. Before the start of the experiment, we allowed gerbils a five-day acclimatization period to the vivarium setup during which they were fed their daily requirements in order to maintain their state at a constant healthy level. For predators we chose Barn Owls, *Tyto alba*, a natural predator of the gerbils in the Negev Desert. The owls were acclimatized to the vivarium setup before we introduced gerbils into it.

Treatment.—We provided resource patches for gerbils in which they experience diminishing returns (Kotler and Brown 1990) as follows. On each side of the vivarium, under 18 artificial bushes (every other station) we placed a 28 × 38 × 8 cm tray filled with 3 L of sifted sand into which we mixed 3 g of millet seeds to form resource patches for the gerbils. All together, there were 36 seed trays spread throughout the vivarium. Under one-half of these seed trays, we placed an electronic PIT tag reader that logged the identity of each gerbil to visit the tray (Model SQID; Vantro Systems, Burnsville, Minnesota, USA), along with the time and the duration of the visit.

We collected data on alternating nights. On the night before an experimental night, we manipulated the energetic states of the gerbils on the different sides of the vivarium by providing them with different amounts of food. We did this to create two populations of gerbils from which the owls could choose, one with individuals in a high energetic state on one side of the vivarium, and one with individuals in a low energetic state on the other. To do so, we placed 6 g of millet in each tray (3 g mixed into the sand, plus 3 g sprinkled onto the surface) on one side, but entirely withheld seeds from trays on the other side. This allowed gerbils on one side to eat well, and gerbils on the other side to eat poorly or even to starve some. On experimental nights, we mixed 3 g of seeds into every tray on both sides of the vivarium. This allowed gerbils on both sides of the vivarium to start the night with different energetic states, but to experience equal foraging opportunities. It also allowed us to quantify gerbil foraging behavior. We then allowed the gerbils to forage under predation risk from an owl.

Gerbil data collection.—Following each night of experiment, we recorded which trays had been foraged by gerbils, and sifted the remaining seeds from the tray to obtain the giving-up density (GUD). The GUD is a measure of foraging costs and reflects the foraging efficiency of the last gerbil to thoroughly exploit the resource patch (optimal patch use theory [Brown 1988]). Electronic readers under the trays supply data about the identity of each gerbil to visit the patch during the night, the time of the visit, and its duration. They also provide a measure of the cumulative duration of time that gerbils spent in each tray each night. Using initial amount of food in a tray (3 g), GUD, and activity duration, we can construct harvest rate curves for both hungry and well-fed gerbils using Holling's disc equation (Kotler and Brown 1990, Kotler et al. 2010). The curves graph the relationship between foraging success and patch resource density and allow us to visually portray the gerbils' use of their behavioral tools for risk management of time allocation and vigilance (Brown 1999, Kotler et al. 2010). To interpret these curves, one has to know two things. First, harvest rate curves for more vigilant animals are shallower as a consequence of shifting attention from harvesting activities to predator detection and consequently harvesting less food per unit

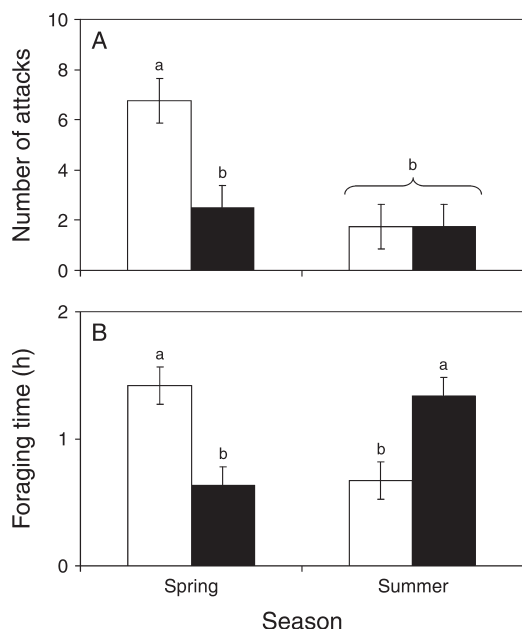


FIG. 1. The effect of gerbil state (open bars, high energetic state; solid bars, low energetic state) and season on (A) the number of owl attacks (mean and SE) and (B) the proportion of time the owl spent in the side of the vivarium where gerbils were experiencing each state (mean and SE). Different lowercase letters associated with bars represent significantly different values ($P < 0.05$, Tukey's HSD post hoc analysis).

effort of time. Second, the location of mean GUD on the harvest rate curve reveals time allocation, with points closer to the origin corresponding to greater time allocation (more patch depletion). Thus we can use these harvest rate curves to deconstruct the gerbils' risk management behavior into time allocation and vigilance (Berger-Tal et al. 2010, Kotler et al. 2010, Raveh et al. 2011).

Owl data collection.—On experimental nights, we allowed a single Barn Owl to spend the night hunting throughout the vivarium. To quantify owl foraging behavior and prey choice, we observed the owl for two periods each night, one hour starting one hour after sunset and one hour around midnight. In pilot studies, we found that the two one-hour samples were representative of the entire night (K. Embar, unpublished data). We recorded the number of attacks the owl made and how much time the owl spent on each side of the vivarium.

Duration.—The experiment ran for two months: April 2009 and June 2009. The experiment ran for a total of eight nights each month, centered on the new moon (16 nights total). These months present gerbils in different reproductive conditions, with gerbils in April being reproductively active and valuing energy highly, and gerbils in June being several months away from the next breeding season and valuing survivorship highly (S. Mukherjee, unpublished data). We chose to run the experiment only during the new moon phases in order to

maximize gerbil activity and minimize owl predation risk. Gerbils are significantly more active when the night is dark (Kotler et al. 2002) and we wanted to ensure the owls get as many cues from the gerbils as possible. On the other hand, when the moon is full, owls pose a higher risk of predation (Kotler et al. 1991), and, from previous experiments in the vivarium (e.g., Embar et al. 2011), we know that gerbils often forgo foraging altogether under owl predation when the moon is full. Therefore, we chose not to run the experiment during full moon phases.

Data analysis.—We analyzed owl attacks and attack duration using analysis of variance (ANOVA). To control for possible nonindependence of owl attacks in neighboring stations, we performed our analysis on daily totals. We analyzed gerbil GUD data from seed trays and cumulative duration data from PIT tag readers using ANOVA. (See complete ANOVA tables in the Appendix for owl attacks, owl attack duration, gerbil GUDs, and gerbil cumulative time).

RESULTS

Owl behavior.—Owls chose high-energy-state gerbils in spring and low-energy-state gerbils in the summer (Fig. 1). In the spring, owls directed significantly more attacks ($MS = 18.06$, $F_{1,16} = 5.82$, $P = 0.03$; Fig. 1A) and spent significantly more time hunting ($MS = 2.7 \times 10^6$, $F_{1,16} = 24.14$, $P = 0.01$; Fig. 1B) on the side of the vivarium with the well-fed gerbils. In summer, owls attacked gerbils in both states equally ($MS = 18.06$, $F_{1,16} = 5.82$, $P = 1.00$; Fig. 1A), but spent significantly more time hunting hungry gerbils ($MS = 2.7 \times 10^6$, $F_{1,16} = 24.14$, $P = 0.03$; Fig. 1B). This behavioral response implies that owls are able to perceive the state-induced difference in gerbil behavior, even though they choose gerbils in different states in the different seasons.

Gerbil behavior.—Gerbil behavior varied significantly with gerbil state only in the summer. In the summer, hungry gerbils left significantly lower GUDs in feeding trays ($MS = 1.77$, $F_{1,324} = 7.95$, $P < 0.01$; Fig. 2A) than did well-fed gerbils. GUDs in the spring did not differ with gerbil state, although well-fed gerbils foraged for nominally more time than hungry gerbils ($MS = 2.4 \times 10^7$, $F_{1,147} = 10.94$, $P = 0.07$; Fig. 2B). In addition, gerbils had significantly lower GUDs ($MS = 38.54$, $F_{1,324} = 173.00$, $P < 0.01$; Fig. 2A) and foraged significantly more time ($MS = 2.4 \times 10^7$, $F_{1,147} = 10.94$, $P < 0.01$; Fig. 2B) in the spring than in the summer. These results imply a seasonal shift in behavior, with gerbils during the spring reproductive season showing especially low GUDs and especially long foraging times, with little apparent behavioral response to changing energetic state. In contrast, gerbils in the summer appear to change to less demanding time and energy budgets that expose them less to predators, and they show clear differences in GUDs in response to changes in energetic state.

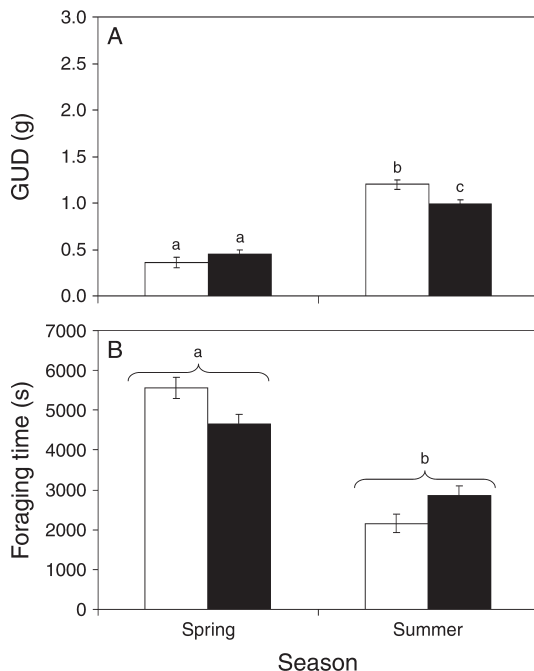


FIG. 2. The effect of the interaction between gerbil state (open bars, high energetic state; solid bars, low energetic state) and season on (A) the giving-up density (GUD; mean and SE) left in an assay tray and (B) the gerbil's foraging time (mean and SE). Different lowercase letters associated with bars represent significantly different values ($P < 0.05$, Tukey's HSD post hoc analysis).

The harvest curves show that gerbils differ in risk management behavior in spring vs. summer and when hungry vs. well fed (Fig. 3). The gerbils' strongest response is to the season, with more vigilance and less time allocation used in spring than in summer. Within each season, we see contrasting reactions to state. In spring, the well-fed gerbils are more vigilant and show greater time allocation; in contrast, in summer, it is the starved gerbils that are the more vigilant and show greater time allocation, as seen by the shallower slope of the curve and the location of the average GUD. This corresponds to owl behavior where, in the spring reproductive season, owls aimed more attacks at well-fed gerbils and, in summer, owls spent more time in the hungry-gerbil patch, i.e., in each season, owls are targeting gerbils that allocate more time to foraging.

DISCUSSION

The results of this experiment support our prediction that owls can respond to the state of their prey. In the spring, the owls directed more attacks and devoted more time to the patches with well-fed gerbils in a high energetic state. In summer, the owls changed their preference to invest more time hunting the low-energetic-state, hungry gerbils. In both cases, the owls differentiated between two sets of prey that differed in state and chose one of them.

How do the owls make their choice? The answer appears to be by following gerbil activity, which in turn is affected by gerbil state. In particular, owls always choose to spend more time with the most active gerbils, i.e., those with the greatest foraging time and foraging tenacity and tendency toward the lowest GUDs. Namely, owls choose the more active gerbils, which appear to present more capture opportunities.

Season influences the owl's choice. Interestingly, in spring, owls attacked well-fed gerbils three times more frequently per unit time than they did hungry gerbils. In contrast, in summer, owls directed an equal number of attacks to gerbils in either state. Owl choice is clearly expressed in the spring, but if there is a choice in the summer, it is obscured by the foraging game in which owls respond to gerbils while at the same time gerbils respond to owls.

The key to understanding the clarity of the owl's choice may lie in the effect of seasons on gerbil behavior. Spring is the reproductive season for gerbils, and they appear to prioritize energy for reproduction over safety, as foraging translates more immediately into fitness (Kotler 1997). And indeed, in spring the gerbils were generally much more active than in summer, foraging twice as long and harvesting nearly twice as many seeds from the trays. This implies that, during the spring, acquiring energy is more important to the gerbils than avoiding predation. And as the high-energetic-state gerbils were marginally more active, the owls picked up on these slight differences and clearly focused their hunting effort on them. During summer, gerbils instead

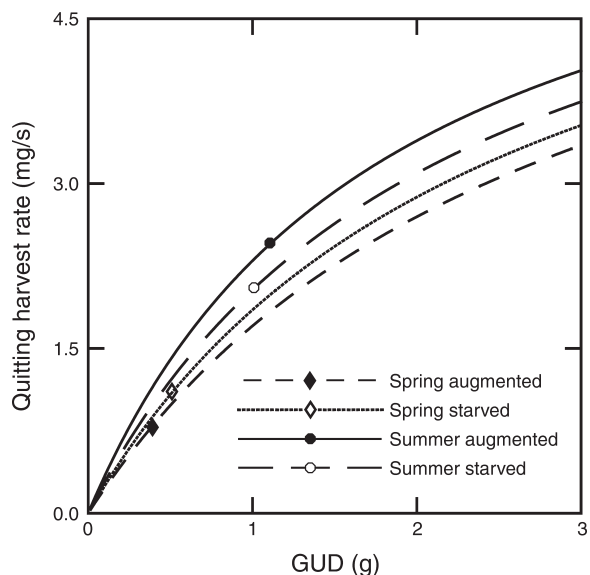


FIG. 3. The effect of the interaction between gerbil state ("augmented" refers to high energetic state; "starved" refers to low energetic state) and season on the harvest curves of foraging gerbils. Symbols represent mean GUD. The steeper the slope, the less the gerbil invest in vigilance. The bigger the GUD, the less time the gerbils spend under these conditions.

appear to prioritize survival until the next reproduction season, still months in the future. In that time period, gerbils in both states harvested less food compared to spring and considerably reduced the time allocated to foraging. This implies that, during the summer, managing predation risk is more important to the gerbils than competing for energy. By thus avoiding risks of predation, which were acceptable during spring (compare Kotler [1997] with Kotler et al. [2004]), the gerbils in the summer presented the owl with two patches equal in their hunting opportunities, as evidenced by the owl's choice to attack them equally.

We show here that owls are able to choose among two patches differing in prey state, which raises the question, why didn't Berger-Tal et al. (2010) see owls responding to gerbil state in their experiment? We think the answer lies within the foraging game context. The foraging game between owls and gerbils reflects how both predator and prey simultaneously use behavioral tools in response and counter response to the behavior of the other species.

In spring, gerbils maximized foraging, thereby increasing their availability to the owls, while the owls increased their attack rate. In response to this added predation pressure, the gerbils increased their wariness (i.e., vigilance), but not enough to compensate for their increased activity, to which the owls clearly responded. During summer, gerbils reduced foraging considerably, managing the risk of predation by restricting time allocation to foraging. The low-energetic-state gerbils foraged more and were more active than the high-energetic-state gerbils, but they appear to have used sufficient vigilance to compensate for the effect of their increased activity. At the same time, the high-energetic-state gerbils could afford to reduce their foraging more than the low-energetic-state gerbils, which allowed them to reduce their investment in vigilance to achieve the same effect. Thus both patches presented the owl with equal hunting opportunities, and the owl's choice became less sharp for us to discern. This may be "the curious incident of the dog in the night time" where in a Sherlock Holmes story, the detective deduced the identity of the culprit and his actions based on what did not happen (namely, a dog not barking [Conan Doyle 1892]). In our case, the owls' appearance of not choosing despite their ability to do so implies that opposing factors affected the gerbil activity to which the owls respond. In this way, both players affect the game in compounding ways, and these reactions and counter-reactions obscure any observable net effect. Berger-Tal et al. (2010) conducted their experiment during the summer, and similar dynamics may have also prevented observable responses of owls to manipulations of gerbil state. In both cases, the lack of a net response reveals the machinations of the foraging game.

What do predators really "want"? The answer seems to be "more opportunities to capture prey." Opportunities can arise due to blatant risk taking, for example,

sharks prefer to hunt the inexperienced, risk-taking, young seals over the more cautious adult seals (Laroche et al. 2008). Opportunities can also arise from environmental constraints. Leopards, for example, prefer to hunt in intermediate levels of cover that allow them the full benefit of ambush without impeding their attack too much (Balme et al. 2007). And, under hypoxic conditions, predatory whelks change their preference to favor the prey clam species that is most forced by the hypoxia to forsake its protection in the sediments in favor of oxygen acquisition (Munari and Mistri 2011). Here we show that owls choose gerbils that are more committed to foraging activity, and they can do so even when the differences are very subtle. That is, owls want more active prey. Cues for prey catchability can be extremely subtle. In predation of seagulls by raptors, predators focus their hunt on the weak, young, and sick and are able to spot signals of sickness that we can identify only in the laboratory (Genovart et al. 2010). And mountain lions (*Puma concolor*) inflict nearly four times the mortality rate on prion-infected deer, even if few of the deer killed were recorded as "noticeably ill" by field observers prior to their deaths (Miller et al. 2008).

Wirsing and Ripple (2011) compared gray wolves and tiger sharks, to show that top predators in both terrestrial and marine ecosystems trigger similar behavioral responses among their respective prey species. This observation suggests that they play similar ecological roles. We add to that here by showing that aerial top predators play the same role, reinforcing the universality of this game interaction.

Letting owls choose between gerbils whose states we experimentally manipulated allowed us to demonstrate predator sensitivity and selectivity, where previously these multi-layered reactions may have obscured the predator's choice. We show that owls can actively choose their prey, and we disentangle the complex game interactions to reveal how predator and prey react and counter-react to each other's choices, within the context of the foraging game, their mutual energetic states, and the effects of season and reproduction.

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SUPPLEMENTAL MATERIAL

Appendix

ANOVA tables showing how season and gerbil state affect owl attacks, owl attack duration, gerbil GUDs, and gerbil cumulative time analyses ([Ecological Archives E095-024-A1](#)).