

LETTER

Complex state-dependent games between owls and gerbils

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Abstract

Predator–prey interactions are often behaviourally sophisticated games in which the predator and prey are players. Past studies teach us that hungrier prey take higher risks when foraging and that hungrier predators increase their foraging activity and are willing to take higher risks of injury. Yet no study has looked at the simultaneous responses of predator and prey to their own and each other's hunger levels in a controlled environment. We looked for evidence of a state-dependent game between predators and their prey by simultaneously manipulating the hunger state of barn owls, and Allenby's gerbils as prey. The owls significantly increased their activity when hungry. However, they did not appear to respond to changes in the hunger state of the gerbils. The gerbils reacted strongly to the owls' state, as well as to their own state when the risk was perceived as high. Our study shows that predator–prey interactions give rise to a complex state-dependent game.

Keywords

Allenby's gerbils, apprehension and vigilance, barn owls, foraging, game theory, giving-up density, harvest rate curves, predator–prey interactions, predator state, risk management.

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INTRODUCTION

Predator–prey interactions are often viewed as a behaviourally sophisticated game in which the predator and the prey are players (e.g. Brown *et al.* 1999; Hammond *et al.* 2007) that show simultaneous reciprocal adaptive responses (Sih 1998). Games exist when the value of a particular set of actions undertaken by a player depends not only on its own choices, but also on those of others (Riechert & Hammerstein 1983). Thus, any change in the behaviour of one of the players in the game should result in changes to the behaviour of the other players (Sih 1998). Despite this linkage, the predator–prey game has mostly been studied from the prey's perspective, ignoring any variation to the predator behaviour by treating the predator as an abstract source of risk to which the prey respond rather than an active participant in a larger behavioural dynamic (Lima 2002).

Many studies have shown that the hunger state of a forager strongly affects its foraging behaviour (e.g. McNamara & Houston 1986; Lima 1988; Whitham & Mathis

2000). As a forager grows hungrier, its marginal value of energy increases (i.e. food is more valuable to the forager, and thus it is ready to take higher risks for it). As a result, hungry foragers spend more time looking for food (Kotler 1997), and are willing to spend more time in riskier habitats (Kotler 1997; Berger-Tal *et al.* 2009).

A typical predator–prey interaction consists of two kinds of foragers: A prey individual, which in most cases forages on sedentary non-responsive resources such as plants or seeds, and a predator, which hunts the prey. As both predator and prey are foragers, they should respond strongly to their own state, but as they interact with each other, they should also respond to changes in each other's behaviour. Thus, predator–prey interactions give rise to a complex state-dependent game.

Past studies teach us that hungrier prey take higher risks when foraging by increasing the amount of time spent foraging (Kotler 1997), decreasing their apprehension or vigilance (Lima 1995; Kotler *et al.* 2004), and choosing riskier habitats (e.g. Pettersson & Bronmark 1993; Kotler 1997). We also know that hungrier predators increase their

foraging activity (Berger-Tal & Kotler 2010), and are willing to take higher risks of injury (Berger-Tal *et al.* 2009). Yet all of the above studies have looked at only one half of the equation, as predators and prey can respond to each other and to the environment simultaneously (e.g. Winnie *et al.* 2006, Liley & Creel 2008). However, to date, the concurrent responses of predator and prey to their own and each other's hunger levels have never been tested in a controlled environment.

We investigated whether a state-dependent game exists between predators and their prey by simultaneously manipulating the hunger state of barn owls, *Tyto alba*, and their prey, *Gerbillus andersoni allenbyi*, in a large outdoor vivarium. We hypothesized that both the owls and the gerbils will react to their own state, as well as to each other's, representing the state-dependent game between them. More specifically, we predicted that the owls' activity would increase with hunger. We also expected that the gerbils would be most active and efficient when hungry and while the owls are well fed and least active when they're well fed and the owls are hungry. Finally, we predicted that the owls would respond to the gerbils' state and be less active when the gerbils are well fed. By looking into the responses of both predator and prey to their own state, as well as to the state of each other simultaneously, we can begin to unravel the complex state-dependent game between predators and their prey.

MATERIALS AND METHODS

We performed our experiment between August and October 2008 in a large outdoor vivarium (34 × 17 × 4.5 m) located at the Blaustein Institutes for Desert Research, Ben Gurion University of the Negev, Midreshet Ben-Gurion, Israel. The vivarium was divided into two equal-sized areas by a 1 m tall rodent-proof fence. Each half contained 36 trellises (each measuring 1 × 1 m, 15 cm high) spaced evenly in a 6 × 6 setup. Upon each trellis we placed a pile of brush to mimic shrubs in the natural system. Shrubs are known to provide safety to gerbils from their predators by offering concealment and physical protection.

Two nights prior to the start of the experiment, we released 11 gerbils into each half of the vivarium. We marked the gerbils individually with passive induction transponder (PIT) tags. We provided experimental resource patches for the gerbils using plastic trays (37 × 28 × 7 cm) filled with 3 L of sifted sand into which we mixed 3 g of millet seeds. Gerbils foraging from the trays experience diminishing returns: the rate at which they harvest seeds declines with time spent exploiting the tray due to resource depletion (Kotler & Brown 1990; Kotler & Blaustein 1995). We placed 18 seed trays on each side of the vivarium, one

next to every other trellis. These served as feeding stations for the gerbils. We put half of the trays under trellises to represent the bush microhabitat and the other half in the open at a distance of 0.5 m from the 'bushes'. These microhabitats differ greatly in the level of risk that is associated with them, with the open microhabitat representing a far riskier environment in the face of aerial predators such as barn owls (Kotler *et al.* 1991). We changed the microhabitat location of each tray every night, alternating between the bush and open positions. Twenty of the trays (10 on each side), distributed evenly across the vivarium, were equipped with a PIT tag reader and logger (model SQUID; Vantro Systems, Burnsville MN, USA) to record the foraging sessions of the gerbils. The PIT tag reader and logger recorded electronically every visit by a gerbil to the tray, the identity of the visitor, the time of the visit, and the duration of the visit.

Our experiment called for manipulating the hunger state of the gerbils and owls and quantifying the gerbils' foraging behaviour. To do so, we needed to quantify the behaviour of starved and augmented gerbils under standard conditions. This meant that we could not manipulate gerbil hunger state at the same time that we collected gerbil foraging data. Consequently, we decided to collect data every other night, allowing us to manipulate gerbil state in the intervening nights (see below). In total, we had four combinations of treatments: Hungry owl + hungry gerbils, hungry owl + fed gerbils, fed owl + hungry gerbils, and fed owl + fed gerbils. Since the foraging activity of gerbils is strongly affected by moon phase (Kotler *et al.* 1993, 2002) our experimental treatments were centred on two moon phases: new and full moon. In each phase, the sequence of treatments was randomly selected. We repeated this design in two different months.

We quantified the foraging behaviour of owls by direct observations. On an experiment night, we released one barn owl into the vivarium for the entire night. The owl had free access to both sides of the vivarium. An observer was positioned approximately 30 m outside the vivarium, and viewed the owls using Nikon Monarch 10 × 42 binoculars. We observed the owls for 3 h each night – 1 h early in the night (between 21:30 and 22:30), one hour in the middle of the night (between 01:00 and 02:00), and 1 h towards the end of the night (between 04:30 and 05:30). During an observation session, we counted the number of dives an owl performed. A dive was recorded when an owl dropped to the ground and then returned to sit on one of the 16 perches (situated at a height of 3 m above the ground) around the vivarium.

We quantified the foraging behaviour of the gerbils as follows. In the morning following an experimental night, we recorded which trays had been foraged the previous night, sifted the seeds from the sand of each of the trays and

collected the remaining seeds into individually marked plastic bags. We then cleaned debris from the seeds and weighed the remainder to obtain the giving-up density (GUD) for each tray. As GUD is directly related to the harvest rate of the forager at the time it quit the patch (Brown 1988; Kotler & Brown 1990), it measures the forager's marginal benefit from the patch at the time that it left it (Brown 1988; Kotler & Blaustein 1995). An optimal forager should exploit a patch so long as its harvest rate of resources from the patch exceeds its energetic, predation, and missed opportunity costs for foraging in that patch (Charnov 1976; Brown 1988, 1992). Thus, GUDs measure the marginal costs of patch use.

For the trays that were equipped with PIT tags readers we calculated the cumulative amount of time that gerbils spent in each resource patch each night. We combined this information with the GUD data from each corresponding patch to construct harvest rate curves (i.e. the relationship between the seeds remaining in a tray and the expected instantaneous harvest rate of the gerbil exploiting the patch, Kotler & Brown 1990). Comparing between different harvest rate curves constructed for resource patches under particular treatments can reveal changes in the foraging strategies of the foragers (Ovadia *et al.* 2001), including the forager's use of vigilance and apprehension for managing risk of predation (Brown 1999).

We manipulated the hunger state of the gerbils by altering the amount of food given to the gerbils on the night preceding an experiment night. Hungry gerbils were gerbils that did not receive any food on the night before, while fed gerbils were gerbils that had access to 18 seeds trays. Each of these trays had 3 g of millet seeds mixed into the sand and an additional 3 g of seeds sprinkled on top of the sand. These additional seeds required minimum effort to forage, and thus ensured that the gerbils collected extra food and were in a higher state, either by eating more or caching more. The gerbils were not exposed to the owls on these 'starvation' and 'augmentation' nights.

We also manipulated the hunger state of the owls as follows. For the fed owl treatment, the owl was given two dead chicken chicks 12 h prior to the beginning of the experiment and another chick at the beginning of the experiment. For the hungry owl treatment, the owl was given one dead chicken chick 36 h prior to the beginning of the experiment. On the morning following the experiment, the owl received two chicks. On non-experimental days, we gave the owl one chick per day. Each chicken chick weighed *c.* 30 g. We alternated between two owls for the different experimental nights, and their order was reversed in the following month.

An owl captured a gerbil on three separate occasions during the experiment, (twice on nights when the owl was hungry, and once when the owl was fed). In all of these

cases, another gerbil was introduced to the vivarium the following morning in order to maintain gerbil density.

Data analysis

We used a multi-factor ANOVA to analyse the GUD data. We used the GUD from individual feeding trays as the sampling units and tested for the effects of the owl hunger state, gerbil hunger state, moon phase, microhabitat, and the side of the vivarium. We repeated the analysis using nightly GUD means as the sampling unit. The results were unchanged, and therefore we only report the results for the tray analysis.

In order to compute the harvest rate curves for the gerbils we used the integration of the Holling disc equation (Holling 1959) that describes the functional response of predators to decreasing prey density (in this case, the gerbils response to seed density). The interval of the integration corresponds to patch residency time and was developed specifically to fit the gerbil system by Kotler & Brown (1990) and used successfully many times since (e.g. Ziv *et al.* 1995; Ovadia *et al.* 2001). We assumed that gerbils harvesting seeds from our feeding trays require the activities of searching for seeds and handling seeds. The proportionality constant that determines the encounter rate of a gerbil with seeds is defined as the attack rate (*a*). It is influenced by the ability of gerbils to search for seeds and is given in units of trays searched per second. The time required for a gerbil to extract a seed from the substrate, husk it and place it in its mouth before resuming search is its handling time (*b*), given in units of seconds/gram of seeds (Kotler & Brown 1990; Kotler *et al.* 2010). When integrating the Holling's disc equation (Holling 1959) and solving it for *t* (the time spent foraging within a patch), the following equation emerges:

$$t = (1/a)[\ln(N_o/N_f)] + b(N_o - N_f)$$

where *a* is the attack rate, *b* is the handling time, *N_o* is the initial abundance of seeds in the patch and *N_f* is the final abundance of seeds in the patch (GUD). The first term on the right hand side of the equation is the time spent searching for seeds, and the second term is the time spent handling the seeds that are encountered (for more details on the development of this equation and the construction of harvest rate curves, see Kotler & Brown 1990 and Kotler *et al.* 2010). We constructed harvest rate curves and calculated the attack rates and handling times of the gerbils by regressing the values of (*N_o* - *N_f*) and $\ln(N_o/N_f)$ against patch residency time (cumulative duration) in a multiple regression analysis. The attack rate is the reciprocal of the coefficient of $\ln(N_o/N_f)$; the handling time is the coefficient of (*N_o* - *N_f*).

The statistical analyses were done using STATISTICA 8.0 software (StatSoft, Inc., Tulsa, OK, USA) for the GUDs and

owl activity analyses, and SPSS 15.0 software (SPSS Inc., Chicago, IL, USA) for the harvest rates analyses.

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RESULTS

Owl activity

The hunger state of the owls significantly affected their activity. Owls dived more when hungry (4.25 ± 0.50 dives per hour, numbers here and throughout the text represent means ± 1 SE) than when well fed (1.54 ± 0.37 dives per hour) (ANOVA, $MS = 88.02$, $F_{1,44} = 18.597$, $P < 0.001$). However, the hunger state of the gerbils did not affect the activity of the owls (hungry gerbils: 2.79 ± 0.52 ; fed gerbils: 3.0 ± 0.52 ; $MS = 0.52$, $F_{1,44} = 0.11$, $P = 0.742$) (Fig. 1). The time of night, the identity of the owl, and the moon phase did not affect the owls' activity (ANOVA, $P > 0.4$ for all).

Giving-up densities

Gerbils on either side of the vivarium showed similar GUDs on seeds collected from the feeding trays (west: 1.35 ± 0.05 g; east: 1.43 ± 0.05 g; ANOVA, $MS = 0.9$, $F_{1,559} = 2.84$, $P = 0.093$). In addition, all of the effects that are detailed below showed identical trends in both sides. Thus, we performed all of the following analyses on data pooled from both sides.

We tested for the effects of the hunger state of the owl, the hunger state of the gerbils, the moon phase and the

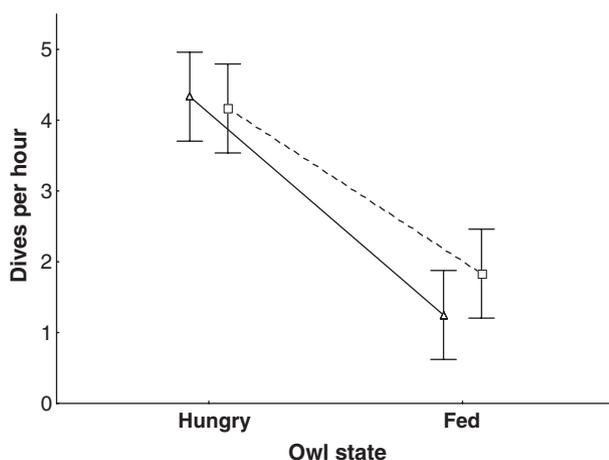


Figure 1 The effects of the owl and gerbils state on the owls' activity (number of dive per hour). Solid lines represent hungry gerbils, dashed lines represent fed gerbils. Error bars represent 1 SE.

Table 1 Multi-factor ANOVA table describing the main effects and two-ways interactions between effects on the giving up densities. Significant effects and interactions are in bold

Effect	MS	d.f.	<i>F</i>	<i>P</i> -value
Intercept	1109.38	1	3630.75	< 0.001
Owl state	27.61	1	90.36	< 0.001
Gerbils state	2.31	1	7.56	0.006
Moon phase	23.81	1	77.91	< 0.001
Microhabitat	203.89	1	667.30	< 0.001
Owl state × gerbils state	4.14	1	13.54	< 0.001
Owl state × moon phase	0.002	1	0.007	0.931
Owl state × microhabitat	1.86	1	6.09	0.014
Gerbils state × moon phase	13.65	1	44.66	< 0.001
Gerbils state × microhabitat	0.42	1	1.38	0.241
Moon phase × microhabitat	0.50	1	1.63	0.203
Error	0.31	561		

microhabitat on the GUDs. The results are summarized in Table 1. Both the state of the owls and the state of the gerbils affected giving-up densities. A hungry owl present in the vivarium caused gerbils to increase their GUDs (i.e. harvest less seeds, hungry owl: 1.61 ± 0.05 g; fed owl: 1.17 ± 0.05 g), as did the gerbils themselves being well fed (fed gerbils: 1.45 ± 0.05 ; hungry gerbils: 1.33 ± 0.05 g). Owl state and gerbil state interacted to affect GUDs. Gerbils responded strongly to their own state when facing a hungry owl, but showed no response to internal state when a well fed owl was present (Fig. 2a).

Moon phase also had a strong effect on the GUDs. Gerbils increased their GUDs under a full moon (full moon: 1.59 ± 0.05 g; new moon: 1.19 ± 0.05 g). Furthermore, moon phase and gerbil state interacted, with the state showing a strong effect under the full moon, but showing no effect under the new moon (Fig. 2b).

Lastly, the microhabitat strongly effected GUDs. Gerbils had higher GUDs in the open microhabitat compared to the bush (open: 1.98 ± 0.04 g; bush: 0.79 ± 0.04 g). Also, microhabitat interacted with the state of the owl to affect GUDs, with the differences between bush and open increasing in the presence of a more active and dangerous hungry owl (Fig. 3).

Harvest rates

Table 2 summarizes the estimated attack rates and handling times for the different harvest rate curves constructed for each of the different state treatments, moon phases, and microhabitats.

We used an analysis of covariance to test whether the treatments had significant effect on the gerbils' attack rate and handling time. The interactions between the owl state and both the gerbils' attack rate and handling time were

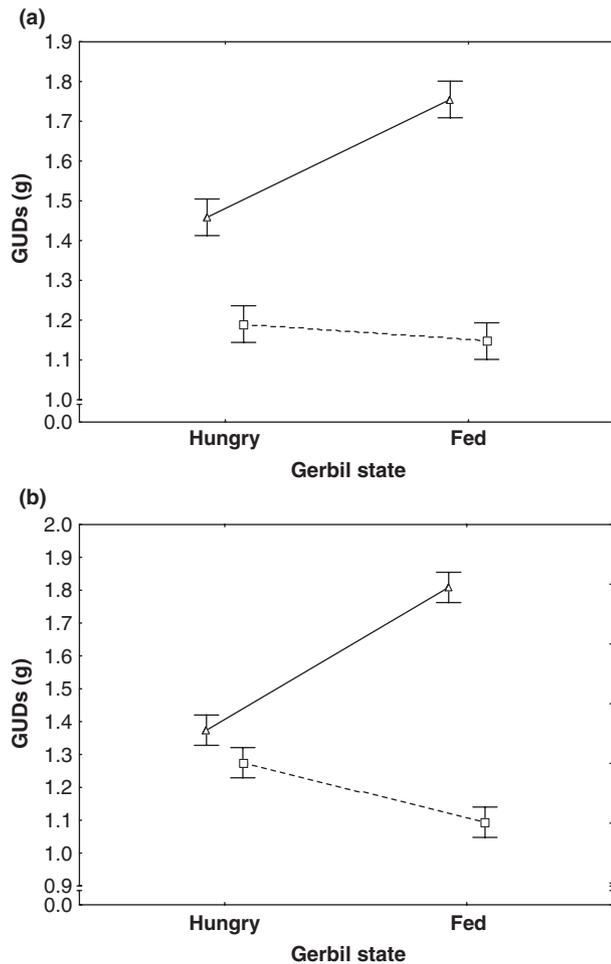


Figure 2 The interactions between the effects of owl state and gerbil state (graph a – solid lines represent hungry owls, dashed lines represent fed owls), and moon phase and gerbil state (graph b – solid lines represent full moon, dashed lines represent new moon) on the GUDs. In both cases the solid line represent the riskier situation. Error bars represent 1 SE.

significant (ANCOVA, owl state \times attack rate: MS = 3.30×10^6 , $F_{1,236} = 4.38$, $P = 0.037$, owl state \times handling time: MS = 3.43×10^6 , $F_{1,236} = 4.56$, $P = 0.034$). Thus, the state of the owls affected the gerbils harvest rate curves by reducing their attack rates and handling times. The moon phase had a marginally significant effect on the gerbils attack rate, reducing it in full moon (moon phase \times attack rate: MS = 2.83×10^6 , $F_{1,236} = 3.76$, $P = 0.054$). Finally, the gerbils reduced their handling times in the open microhabitat (microhabitat \times handling time: MS = 2.94×10^6 , $F_{1,236} = 3.91$, $P = 0.049$).

The harvest rate curves allow us to derive estimates of the quitting harvest rates for the different treatments. To do so, we plugged the appropriate estimate of a and b back into Holling's disc equation to estimate the appropriate quitting

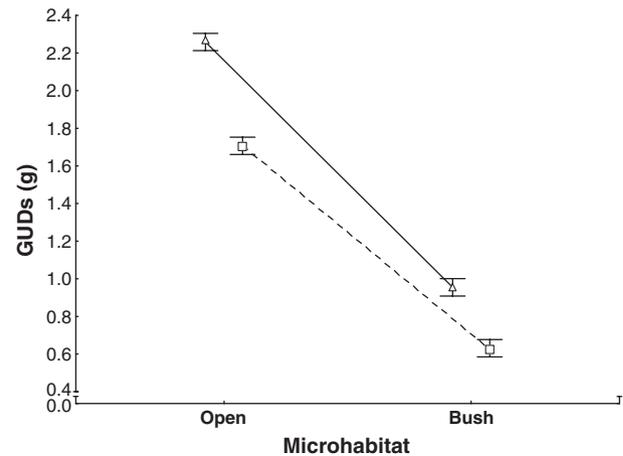


Figure 3 The effects of the microhabitat location of the feeding tray on the GUDs. Solid lines represent hungry owls, dashed lines represent fed owls. Error bars represent 1 SE.

harvest rate for each seed tray: $QHR = (a \times GUD)/(1 + a \times b \times GUD)$. We can also plug in the mean GUD for a given set of conditions using the appropriate values of a and b to obtain the characteristic QHR for those sets of conditions.

When the owl was hungry, the quitting harvest rate was $8.47 \times 10^{-4} \text{ g s}^{-1}$. When the owl was well fed, the quitting harvest rate dropped to $6.82 \times 10^{-4} \text{ g s}^{-1}$. In both moon phases, the quitting harvest rate was 7.82×10^{-4} (Fig. 4).

DISCUSSION

Our results clearly show that the interactions between barn owls and their gerbil prey represent a complex state-dependent game. We simultaneously manipulated the hunger state of both owls and gerbils in a controlled environment. The owls and the gerbils both reacted strongly to changes in their own state, and changed their behaviour accordingly. The gerbils also reacted to changes in the state of the owls.

As predicted, the owls were significantly more active when hungry (Fig. 1). This change in owl behaviour increased the risk to gerbils associated with leaving the safety of the burrow to forage; thus, when the owls were hungry, the gerbils foraged less. In general, the gerbils harvested more food when they were hungry. However, the impact of the gerbils' state on their foraging decisions was greatly influenced by the degree of peril associated with the act of foraging. When the gerbils perceived their environment to be risky (i.e. when a hungry owl was active in the vivarium, or when the moon was full), they harvested significantly less food provided they were well fed (Fig. 2). Gerbils in good condition have more to lose from predation

Table 2 Attack rates and handling times for the foraging gerbils in each of the different treatments. These results were obtained using a multiple linear regressions analysis to the equation of the form $t = (1/a)[\ln(N_o/N_i)] + b(N_o - N_i)$ where a is the attack rate (trays/s) and b is handling time ($s\ g^{-1}$)

Treatment	Regression R^2	P -value	Attack rate (per seconds)	P -value	Handling time ($s\ g^{-1}$)	P -value
All trays	0.873	< 0.001	1.034×10^{-3}	< 0.001	574.598	< 0.001
Hungry owls	0.874	< 0.001	0.930×10^{-3}	< 0.001	509.276	0.002
Fed owls	0.873	< 0.001	1.148×10^{-3}	0.002	638.048	0.002
Full moon	0.848	< 0.001	0.728×10^{-3}	< 0.001	423.389	0.06
New moon	0.910	< 0.001	1.106×10^{-3}	< 0.001	537.010	< 0.001
Fed gerbils	0.885	< 0.001	0.922×10^{-3}	< 0.001	512.194	0.005
Hungry gerbils	0.864	< 0.001	1.086×10^{-3}	< 0.001	594.358	0.002
Open microhabitat	0.878	< 0.001	1.493×10^{-3}	0.063	556.452	0.005
Bush microhabitat	0.882	< 0.001	2.191×10^{-3}	0.115	1023.909	< 0.001

Significant results are in bold. The treatments in italic fonts are the treatments in which the risk for the foraging gerbils was perceived as higher.

and less to gain from food, and therefore it is expected that well-fed gerbils will be less inclined to forage when at greater risk. Past studies confirm that gerbils perceive both hungry predators and full moon nights to be highly risky (Kotler *et al.* 2002; Berger-Tal & Kotler 2010). However, when a satiated owl was present in the vivarium or on moonless nights, the hunger state of the gerbils did not have any significant effect on the amount of food they harvested (Fig. 2). Thus, the state of the gerbils influenced their foraging behaviour only when the risks of foraging are perceived as high.

This lack of response on the part of the gerbils could be interpreted as indicating that fed owls are not perceived as risky by the foraging gerbils. However, Berger-Tal & Kotler (2010) showed that on a continuum of perceived danger, the presence of a fed owl is intermediate to no owl present and to the presence of a hungry owl. Thus, we should expect the gerbils to behaviourally respond to a fed owl, although not as strongly as to a hungry owl. This lack of response could occur if by the end of the night, the gerbils have eaten enough to obscure the prey hunger treatments (i.e. when the owl was well fed, the gerbils could feed more safely, and by the end of the trial they might have no longer been hungry regardless of their earlier hunger level). An alternative explanation is that the apparent lack of a response is a result of the foraging game between the gerbils and the owl. The lack of a gerbil response to their own state can come about if gerbils are responding to owls that are responding to gerbils, (i.e. the gerbils ‘know’ that the fed owls target them when they are hungry and equalize their foraging activity between states accordingly). Thus, it is the fed owls that are most sensitive to the behaviour of the gerbils.

In a state-dependent foraging game, players may be responding to each other’s behaviours or may actually be responding to each other’s states. We showed here that gerbils respond to the state of the owl. But perhaps their

response was primarily due to the change in owl attack rate, brought on by the owl’s state and therefore gerbil behaviour is only indirectly dependent on owl state. Alternatively, gerbils may respond directly to predator state or respond to state above and beyond any obvious effect mediated by changes in the predator’s overt behaviours. The latter might reflect prey ability to detect predator hunger per se, which could induce prey to ‘anticipate’ immediate or future predator behaviour above and beyond obvious behaviours that predators have already exhibited. To examine this, we repeated the GUDs analysis, adding the owl attack rate (average for the night) as a covariate. The owl attack rate produced no effect on the GUDs ($P = 0.41$). Thus, we can view the gerbils as responding directly to the hunger state of the owl rather than to the attack rate.

The harvest rates analysis revealed that in an environment perceived as riskier by the gerbils (in the presence of a hungry owl, full moon, open microhabitat, or when the gerbils were well fed), both their encounter rate with seeds (attack rate) and the time that was required of them to handle a seed (handling time) were lower than those of safer environments. Although only significant in some cases (owl state, microhabitat), this trend is internally consistent and was repeated in all of the comparisons for both the attack rates and the handling times (Table 2). This suggests that the gerbils searched less efficiently in the face of danger, but once they found a seed were quicker to take it out of the patch, probably foregoing husking in order to minimize their time in the resource patch (so called ‘Grab and Go’ foraging, J. St. Juliana, personal communications). It is important to note that well-fed gerbils perceived their environment as more dangerous. This is in accordance with Clark’s asset protection principle that indicates that a well-fed animal has more to lose from predation, and therefore sees what is effectively a scarier world (even for the same amount of risk) (Clark 1994; Kotler *et al.* 2004).

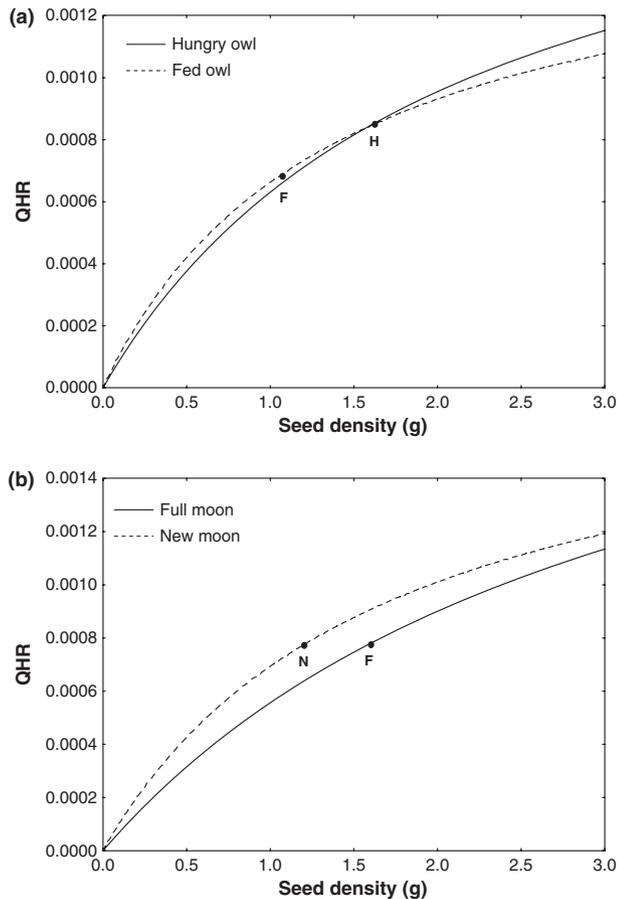


Figure 4 Quitting harvest rate (QHR) curves for the foraging gerbils. QHR are given as a function of seed density in the resource patches. Curves are arrived at using estimated attack rates and handling times from the data by fitting the time spent foraging and the amount foraged to the Holling disc equation. The points on the plots represent: (a) Average giving up densities (GUDs) when a hungry owl was present (H), and when a fed owl was present (F), and (b) Average GUDs on full moon nights (F), and on new moon nights (N). Shallower plots correspond to higher level of apprehension. GUDs lying closer to the origin correspond to greater time allocation.

Although the gerbils responded to all forms of risks in a uniform way, the strategies through which they changed their foraging behaviour may have differed depending on the type of risk they were facing. In order to manage their risk of predation, gerbils employ two main behavioural tools: time allocation (where, when and for how long to forage; e.g. Kotler & Blaustein 1995; Kotler *et al.* 2002), and apprehension (reduction in attention to other activities as a result of reallocating attention to detect and respond to predators, Brown 1999; Dall *et al.* 2001). Quitting harvest rate curves can be used to shed light on the strategies foragers employ to manage risk of predation (Brown 1999;

Kotler *et al.* 2010). In regards to apprehension, when plotting harvest rate as a function of resource density in a patch, shallower plots correspond to higher level of apprehension because they indicate slower harvest for the same density of seeds. In regards to time allocation, animals that only use time allocation would display the same level of apprehension and be on the same quitting harvest curve regardless of the risk. In this case, smaller GUD values correspond to a greater time allocation to foraging. In our experiment the gerbils managed the risks ensuing from the change in owl state in a different manner than the risk resulting from the different moon phases. They managed the risks from the owls by changing their time allocation alone (Fig. 4a), and the risks of the full moon by using apprehension alone (Fig. 4b). As apprehension in gerbils relies on visual cues, it may be that on moonless nights apprehension is less needed. On brighter moonlit nights, apprehension becomes more effective, and thus, the gerbils shift to a more apprehensive foraging strategy. This is well supported by the findings of Kotler *et al.* (2010) that followed the foraging strategies of *G. allenbyi* throughout a full lunar cycle. But why would the gerbils not increase their apprehension in response to a hungrier and more dangerous predator? Very high levels of risk may render apprehension ineffective. Altwegg (2003) for example, found that in the presence of hungry predators, the anti-predatory behaviour of tadpoles become ineffective. If indeed hungry owls pose such a risk that they render the apprehension of gerbils ineffective, then the optimal response of the gerbils would be not to increase apprehension levels, but rather to quit harvesting in order to spend less time in the exposed resource patch (Brown 1999).

Interestingly, the owls did not react to changes in the hunger state of their prey. This is despite the fact that the gerbils were less active when satiated, and assuming that the gerbils only left their burrows to feed, this reduction in foraging activity most likely caused a reduction in the average density of active gerbils in the vivarium. However, it may be that in a closed vivarium, equipped with perches that allow the owls full view of the whole enclosed area, activity is not the most suitable measurement of the owls response to changes in the gerbils density or state. Reduction in the density of the prey in a closed defined area does not necessarily give rise to an increase in the energetic expenditures of the owls, unlike in open habitats where a reduction in prey activity or density would require the owl to fly over larger areas to encounter as many prey. Examining the time allocation of an owl between two habitats, one occupied by hungry prey and the other by satiated one, might provide a better indication to whether the owls respond to changes in the state of their prey, and indeed new data (S. Mukherjee, K. Embar & B.P. Kotler, unpublished data) reveal that changes to the state of the gerbils greatly affect the time allocation of captive barn owls. Thus,

predators can respond to changes in the state of their prey, only under our experimental conditions, they chose not to.

Much of the attention to predator–prey games in the literature concerns the joint ideal free distribution (IFD) of both predator and prey (e.g. Hugie & Dill 1994; Morris 2003). According to the IFD, given the assumptions that animals are ideal consumers (having perfect knowledge of their environment), and free to move between patches without cost, they should be distributed such that no consumer could increase its intake rate by switching patches (Fretwell & Lucas 1969). When applying the IFD to the predator–prey game, the quality of a patch for a predator is determined by the amount of prey it can encounter in the patch, while the presence of predators in a patch reduces the patch quality for foraging prey individuals (e.g. Hammond *et al.* 2007; Krivan *et al.* 2008). However, it is now clear that the behaviour of both predator and prey can have an even greater effect on the predator–prey game than just their distribution (Brown *et al.* 2001). Alonzo (2002) presented a model that demonstrates the importance of the hunger state and behaviour to the habitat selection of both predator and prey. As we have shown in this study, although IFD can in many cases be used successfully to predict the distribution of animals (Flaxman & deRoos 2007), it is imperative to have knowledge of the behaviour of both the predator and the prey, as well as the motivation behind it, in order to understand the dynamics of predator–prey interactions.

An emerging theme in modern community ecology is that behavioural responses should be incorporated into population and community ecology because they can mediate indirect interactions (Abrams 1995) and considerably increase the complexity of interactions between species (e.g. Fryxell & Lundberg 1998; Moir & Weissburg 2009). In some situations, state-dependent decisions by individuals can have important implications for community dynamics (e.g. through condition-dependent risk sensitive foraging of prey species, Luttbegg *et al.* 2003; Heithaus *et al.* 2007). It is yet to be shown whether state-dependent foraging by Allenby's gerbils affects their community dynamics, either by altering the co-existence with other rodent species competing for the same resources (Brown *et al.* 1994), or by mediating changes to the hunting behaviour and prey preference of their predators. However, it is clear now that understanding what drives the behaviour of both predators and their prey is of utmost importance, since only through this understanding we will be able to comprehend the full predator–prey game and its consequences for community dynamics.

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