The foraging response of gerbils to a gradient of owl numbers

Justin R. St. Juliana[1,2], Burt P. Kotler[2], Joel S. Brown[3],
Shomen Mukherjee[4] and Amos Bouskila[5]

[1]*Department of Biology, Indiana State University, Terre Haute, Indiana, USA,*
[2]*Mitrani Department of Desert Ecology, Blaustein Institutes for Desert Research,*
Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel,
[3]*Department of Biological Sciences, University of Illinois at Chicago, Chicago, Illinois, USA,*
[4]*Marine Sciences Program, Department of Biology, Florida International University, North Miami,*
Florida, USA and [5]*Department of Life Sciences, Ben-Gurion University of the Negev, Be'er Sheva, Israel*

ABSTRACT

Background: While many studies have addressed a prey's behavioural responses to predators, very few have tested how the prey's anti-predator behaviour changes as a function of predator number.

Hypotheses: Encounter rate with predators should increase with increasing numbers of predators, thus increasing the predation risk (a cost of foraging) for prey individuals. With increased predation risk, prey animals should quit foraging sooner, and leave more resources behind. Increased predation risk should also cause prey to devote more attention to predator detection and less to foraging. This redirection of attention should result in lower harvest rates, and a higher quitting harvest rate for the prey.

Organisms: Prey: Allenbyi's gerbil, *Gerbillus andersoni allenbyi*, a psammophilic, 25-g desert rodent. Predator: barn owl, *Tyto alba*.

Methods: We allowed gerbils to forage in a large outdoor aviary in Sede Boker, Israel, subject to various risks of predation (i.e. in the presence of 0, 1, 2, or 3 barn owls). We measured gerbil giving-up densities (GUDs), the amount of food left behind by gerbils foraging in artificial resource patches. In each trial, resource patches were set up in different microhabitats with different arrangements of seeds. Comparing GUDs between these resource patches provided a gauge of the gerbils' perceived risk of predation and apprehension (a forager's redirection of attention from foraging to predator detection).

Results: Gerbils had higher GUDs when owls were present. Furthermore, gerbils increased their apprehensiveness when more owls were present in the aviary. The increase in gerbil GUD with each additional owl was less than additive.

Keywords: foraging, foraging theory, gerbil, giving-up density, multiple predators, optimal foraging, owl, prey behaviour, predator, predation.

INTRODUCTION

Research on the non-lethal effects of predation risk has been primarily limited to two treatments. Foraging animals are typically exposed to a high- or to a low-risk treatment that is varied in either time or space (Lima, 1998; Brown and Kotler, 2007). In reality, animals experience continuous variation in risk. The variability in predator numbers represents one of the most common challenges experienced by prey individuals. The more the animal can finely adjust its perception of this risk, the more it can finely tune its response.

Predation risk as a function of the number of predators has the potential to influence a wide range of prey behaviours (Lima and Dill, 1990), including foraging behaviour. In almost all systems in which predation risk and foraging have been studied, a trade-off between harvest rates of energy and risk of mortality has been demonstrated (Lima, 1998). Although it has been suggested that there may be non-additive changes in mortality risk as a function of predator density (Abrams, 1993; Sih *et al.*, 1998), actual tests of prey behavioural responses to graded numbers of predators are limited (see Sih *et al.*, 1998). Results in aquatic systems have shown both additive (Anholt *et al.*, 2000) and non-additive (Peacor and Werner, 2001; Van Buskirk and Arioli, 2002; Relyea, 2004) changes in prey behaviour as a function of changing numbers of predators.

One useful way to measure foraging behaviour is using the giving-up density (GUD) technique (Brown, 1988). The GUD is the amount of food that a forager leaves behind in a resource patch following exploitation. When harvest rate is a function of the density of food in a patch, the GUD provides a surrogate for a quitting harvest rate (QHR) (e.g. Kotler and Brown, 1990). The GUD technique can be used when an animal's harvest rate in a patch declines over time. There is some density of a resource at which an animal will quit foraging in a patch. In Brown's (1988) model, the harvest rate at which an animal quits foraging is described as $H = C + P + MOC$, where C is the energetic cost of foraging; MOC is the missed opportunity cost (i.e. the cost incurred by foregoing other fitness-enhancing activities that it could perform instead of foraging); and P is the additional cost of foraging due to predation risk. When all foraging costs (C, P, and MOC) are equal to the benefits, or harvest rate (H), an animal will leave the patch. As predation risk increases, so should P, the GUD, and the QHR. This increase in GUD is due to the reduction in the value of food if an animal must risk death to attain it.

Regarding predation, an animal can reach its GUD within a resource patch as a function of two factors. One is to allocate less time to foraging such that it quits a patch at a higher resource density. The second is to alter its level of apprehension. Apprehension is an animal's penalty of multi-tasking when directing attention away from foraging to predator detection, although it continues to forage. The redirection of attention is associated with a reduction in the forager's harvest rate due to less actual foraging while at the foraging location (head-up time for instance) and an increased number of errors while foraging (Dall *et al.*, 2001; Abramsky *et al.*, 2002; Kotler *et al.*, 2002, 2004).

Three factors may combine to determine how foragers should adjust their foraging behaviour with changing numbers of predators. The first concerns how actual risk of predation increases with predator numbers. An additive increase in predation risk with the number of predators provides a linear, null expectation and the starting assumption of many predator–prey models (e.g. Lokta, 1925; Volterra, 1926). However, interference among the predators (Skalski and Gilliam, 2001) and/or a fixed number of capture opportunities will cause risk to increase more slowly than the number of predators. On the other hand, facilitation

among predators – the presence of one predator individual enhancing the hunting success of another – will cause risk to increase more rapidly than the null expectation.

A second factor is the prey's ability accurately to assess predation risk as the number of predators varies. For instance, the perceived number of predators may increase more slowly (hyposensitivity), equally, or more rapidly (hypersensitivity) than the actual numbers. These errors in estimation do not imply that the animal is not foraging optimally, but rather that optimal foraging is subject to some set of constraints. For example, prey may simply perceive the presence or absence of predators and not be able to perceive the varying number of predators. Or prey, having sought refuge from one predator, could miss perceiving additional predators.

Yet another possibility is that a prey's behavioural responses could alter risk such that a response to additional predators could be different from additive. Prey have many ways to adjust their behaviour to reduce risk (Lima and Dill, 1990). For example, a foraging animal could adjust the time that it spends foraging (Kie, 1999; Komdeur and Kats, 1999; Blumstein et al., 2003; Molinari-Jobin et al., 2004), its use of safe and risky microhabitats (Sih, 1984; Brown, 1988; Kotler et al., 1994; Crowder et al., 1997; Relyea, 2003; Orrock et al., 2004), or its level of vigilance and apprehension (Lima, 1992; Bednekoff and Lima, 1998; Arenz and Leger, 1999). In response to the presence of owls, desert rodents spend dramatically less time foraging, shift their foraging activity towards safer microhabitat (Kotler et al., 1991; Longland and Price, 1991; Abramsky et al., 1997; Kotler, 1997), and increase their level of apprehension. A non-linear relationship between the cost of a defensive behaviour and the safety it buys could cause non-additive changes in prey behaviour with additional predators. Prey increasing their apprehension level could lead to such non-linearity. With the increase in the number of predators, one would expect an increase in apprehension. Yet when dealing with multiple predators that are similar in their abilities (e.g. all of the same species), a given level of defensive behaviour could buy more than a linear response in safety. For instance, if a prey animal is using a moderate level of apprehension or vigilance against one predator, it may also be able simultaneously to detect a second predator if present. Thus the same level of apprehension or vigilance may buy more safety. Therefore, risk would decline asymptotically with predator number as prey individuals employ more and more of their anti-predator tools. The opposite could be true for multiple predators of different types.

Our considerations led us to make two major predictions that are the focus of this paper. First, we predicted that additional predators would cause a less than additive increase in prey GUDs. Second, we predicted an increase in the prey's use of apprehension with additional predators.

METHODS

We performed our experiment during September and October of 2002, at the Sede Boker Campus of Ben-Gurion University (30°51′N, 34°47′E, 475 m above sea level) in the Negev Desert of southern Israel. Our study organisms were the desert rodent, Allenby's gerbil, *Gerbillus andersoni allenbyi*, and the barn owl, *Tyto alba*. The research was conducted in compliance with the provisions of the Israel Nature and Parks Authority Animal Care Office and within the guidelines of the American Society of Mammalogists (Sikes et al., 2011).

Granivorous desert rodents such as Allenby's gerbils have been used in many studies involving predation risk. Known factors that affect risk of predation in *G. a. allenbyi* include: owl presence and absence (Kotler, 1997); number of encounters with owls (Abramsky et al.,

1997); snake presence or absence (Kotler *et al.*, 1992); illumination (Kotler, 1992); interactions of illumination, snakes, and owls (Kotler *et al.*, 1992); escape substrate (Kotler *et al.*, 2001); prey density; and time after encounter with predators (Kotler, 1992).

We caught wild gerbils, ear-tagged them, and then released 24 of them into a large outdoor aviary measuring $18 \times 23 \times 5$ m. The only cover for the gerbils were cover stations provided for the experiment (see below). A large number of burrows in the aviary were readily used by the gerbils. The gerbil sex ratio was approximately 50:50. We gave the gerbils 2 weeks to acclimatize to the experimental conditions before we began taking experimental data. Because previous studies (Kotler *et al.*, 1991) showed a strong influence of moonlight on the foraging behaviour of these animals, our experiments took the four main moon phases (full, waning, new, and waxing) into account. We were not interested in testing predictions related to moon phase, but needed to control for this factor in our analysis. During each phase we ran the following four treatments: 0, 1, 2, or 3 owls. The treatments were randomized around each of the four moon phases. On the experimental nights with owls, the owls were released into the aviary just before dusk.

Throughout the experiment, we maintained the density of gerbils by replacing those killed by owls the previous night. On any given night, owls managed to kill two or fewer gerbils (0, 1, 2, and 4 total deaths during the experiment for the 0, 1, 2, and 3 owl treatment, respectively). This low mortality rate was desired for logistical and ethical reasons; we achieved it by feeding the owls hatchling chickens during the experiment. While this likely reduced the owls' overall motivation to forage, it should not have influenced the experimental results because the owls' condition was similar across all treatments. The very few replacement gerbils were only briefly less familiar with the experimental set-up and their naivety should not have greatly affected our results. Furthermore, after a session the gerbils had at least 3 days before the next moon phase to become familiar with the experimental set-up. Between the treatments and the next moon phase, we kept the gerbils in conditions similar to those for the experiment, but without collecting data.

To evaluate rodent behaviour, we used the giving-up density (GUD) technique (Brown, 1988). The aviary had 24 stations. Each station contained a simple wooden trellis (15 cm off the ground) with brush piled on top to provide cover, and two assay trays to provide seed resources and to quantify rodent behaviour. We created experimental resource patches by mixing 3 g of millet into 5 litres of sand and placed the mixture into an aluminium tray ($60 \times 40 \times 2.5$ cm). These patches mimicked the natural depletable resource patches in which gerbils forage in the sandy habitats (Kotler and Brown, 1990). On a given night, the trays at half of the stations were placed under trellises, representing the bush microhabitat, and the trays in the remaining stations were placed in the open, immediately adjacent to the trellises, representing open microhabitat. The position of the trays (bush/open) at all the stations was changed every other night. Each station had two different types of trays: a full tray and a bottom tray. For each full tray, we mixed the 3 g of millet evenly into 5 litres of sand. For each bottom tray, we mixed the 3 g of millet into 2.5 litres of sand spread over the bottom of the tray, with the remaining 2.5 litres of sand devoid of seeds spread on top, thus creating a more complex resource patch. The gerbils readily used both types of trays without any training. At the end of the foraging night, we sifted the remaining millet from the sand of each tray. We stored the millet at room temperature for approximately one month, and then weighed all samples on the same day. In each tray, we cleaned the remaining millet of debris, and weighed the amount of millet remaining for that tray to obtain the GUD. The mean GUD in these patches measured changes in overall foraging effort. The amount of seeds

harvested from seed trays placed in the open compared with the bush microhabitat measured shifts in foraging in different microhabitats as a function of predation risk.

For analysis of the GUD data, we log-transformed the GUDs and then for each microhabitat (bush or open) averaged these values for a given night. (This average included both the full and bottom trays.) This reduced our sample from 768 measured GUDs to 32 average values used for analysis. To analyse the data, we ran a general linear model as outlined in Table 1. The #Owls^2 variable was included to test for a non-linear polynomial component.

The selectivity [Manly's index (Chesson, 1983)] of gerbils for full trays relative to food patches with a more complex and disadvantageous distribution of food (all seeds mixed into the bottom layer of sand = bottom tray) provided an indirect measure of apprehension. This is because a tray that is hard to harvest and requires much attention (in this case, the bottom tray) should become relatively harder to harvest when more attention is directed to other activities, say predator detection. Therefore, selectivity for the easy to harvest tray (in this case, the full tray) should increase with increasing activities (apprehension) that make harvest more difficult (Kotler et al., 2002, 2004). For further explanation, see Dall et al. (2001) and Kotler et al. (2002, 2004).

For the selectivity data, we ran a general linear model as outlined in Table 2. For analysis of the selectivity data, we excluded any pair of trays that did not have both trays foraged. We averaged the selectivity values for each microhabitat type on a given night to arrive at 32 values that we used for analysis. We initially included the polynomial term in the model but dropped it because it was not significant.

RESULTS

Gerbils varied their GUDs in response to changes in predator numbers (Table 1, Fig. 1). With an increase in the number of predators, we observed an asymptotic increase in the GUDs (Fig. 1, Table 1). Gerbils displayed higher GUDs in the bush microhabitat compared with the open (Fig. 1, Table 1). The significant interaction between number of owls (#Owls) and microhabitat indicates that the difference in GUDs between microhabitats decreased with an increasing number of owls (Fig. 1, Table 1). There was a significant difference in the GUDs among moon phases (mean GUDs: wane = 2.15 g; new = 2.25 g; wax = 2.27 g; full = 2.43 g) (Table 1). There was also a significant interaction between moon phase and number of owls, with effect of moon phase declining with increasing numbers of owls (Table 1).

Selectivity increased with increasing number of owls (Table 2, Fig. 2). Selectivity was higher in the open trays (open = 0.58; bush = 0.55) (Table 2), but was not affected by moon phase. However, there was a significant interaction between microhabitat and moon phase with a large difference between open and bush trays during full and waning moons, but not new and waxing moons (Table 2).

DISCUSSION

Gerbils altered their foraging behaviour in response to changing number of predators. As risk increased, the marginal value of safety should have also increased, and this was reflected in the gerbils' sacrificing harvest rate for increased safety. Both GUDs and selectivity for the full tray (apprehension) increased with additional predators.

Table 1. Giving-up density GLM statistics: the statistical output for the GLM of GUDs (natural-log-transformed) for the factors listed in the table

Source	d.f.	MS	*F*-ratio	*P*
#Owls	1	0.548	111.36	<0.0001
#Owls^2	1	0.195	39.70	<0.0001
Microhabitat	1	0.514	104.33	<0.0001
Moon phase	3	0.027	5.55	0.0071
#Owls × Microhabitat	1	0.053	10.68	0.0043
#Owls × Moon phase	3	0.027	5.41	0.0079
Microhabitat × Moon phase	3	0.007	1.40	0.2763
Error	18	0.005		

Note: #Owls and #Owls^2 were continuous variables. Categorical variables were microhabitat (tray in or out of cover) and moon phase (new, wax, wane, full).
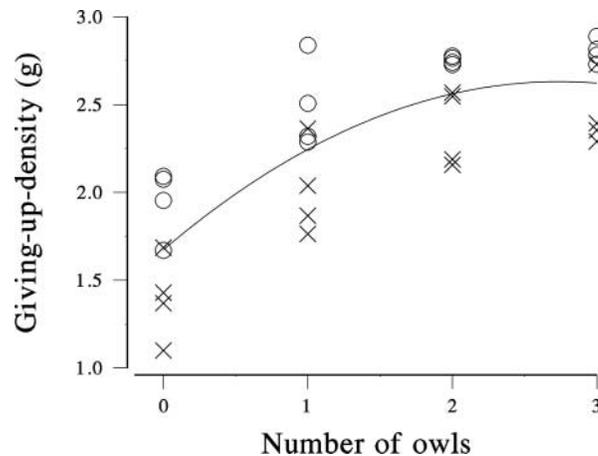

Fig. 1. Giving-up densities as a function of number of owls and microhabitat (x = bush, o = open). We have presented untransformed GUDs for clarity. GUD = 1.96 + (0.32 × #Owls) − (0.13 × (#Owls–1.5)^2); N = 32; d.f. = 2; R^2 = 0.64; P < 0.0001. As the number of owls increased, the GUD increased at a declining rate.

Furthermore, the increase in GUDs with additional predators was asymptotic. The trend of sacrificing harvest for safety also occurred across microhabitats as reflected by greater apprehension and GUDs in the open, where risk is greater (Kotler *et al.*, 1991; Longland and Price, 1991) than under cover. The interactions that we found show that a prey's responses to the risk of predation may depend on the context of the environment. Our GUD results for micro-habitat and moon phase are similar to those of several previous studies (e.g. Kotler *et al.*, 1991, 2002, 2004; Kotler, 1997; Dall *et al.*, 2001).

The increase in GUDs with owl numbers may be asymptotic because predators interfere with one another and decrease each other's attack rate on prey. The number of gerbil deaths (which were few and therefore an unreliable measure of risk) suggests an opposite trend in which danger increases with more owls. In our study system, an increase in the risk of

Table 2. Selectivity (apprehension) GLM statistics: the statistical output for the GLM of GUDs (natural-log-transformed) for the factors listed in the table

Source	d.f.	MS	*F*-ratio	*P*
#Owls	1	0.011	7.85	0.0114
Microhabitat	1	0.008	5.50	0.0301
Moon phase	3	0.002	1.38	0.2797
#Owls × Microhabitat	1	0.001	0.53	0.4775
#Owls × Moon phase	3	0.001	0.75	0.5365
Microhabitat × Moon phase	3	0.008	6.10	0.0044
Error	18	0.001		

Note: #Owls was a continuous variable. Categorical variables were microhabitat (bush or open) and moon phase (new, wax, wane, full).
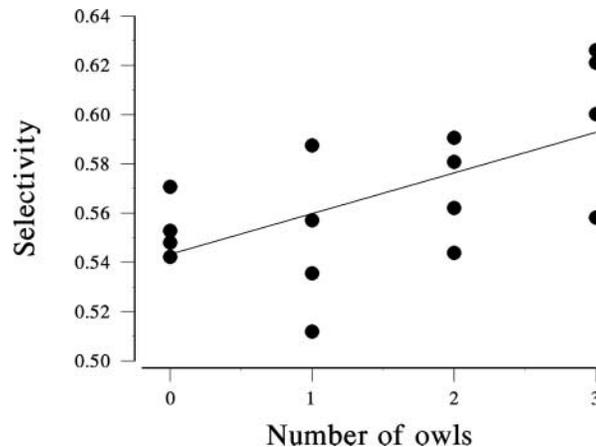

Fig. 2. Number of owls versus the mean selectivity for the full tray (apprehension) for a given night. Values > 0.5 correspond to greater selectivity for the full tray than the bottom tray. Selectivity = $0.54 + 0.02 \times$ #Owls; $N = 16$; d.f. = 1; $R^2 = 0.37$; $P < 0.0120$. Increasing selectivity with increasing owl numbers reveals that gerbils increase their level of apprehensiveness when more owls are present.

predation seems somewhat improbable because barn owls are not known to cooperate while hunting, although non-cooperative facilitation has not been studied in owls. Despite the asymptotic GUD results suggesting the possibility of interference between owls, we do not have adequate data on owl behaviour to evaluate this possibility properly.

The diminishing effect of additional predators on gerbil behaviour may result from the gerbils' inability to assess risk accurately (i.e. an inability to distinguish between multiple predators). For instance, two owls being close to each other or flying at the same time could be perceived by the gerbils as one predator. In such instances, actual risk would increase, but perceived risk of predation would not. There can also be advantages to both under-estimating (Abrams, 1994, 1995) and overestimating (Bouskila and Blumstein, 1992; Bouskila *et al.*, 1995) the risk of predation. If our null model (additive increase in risk) of risk as measured by the number of gerbil deaths is in fact true and the GUD results arise from inaccurate risk

assessment, then it would appear that the gerbils are in fact underestimating risk. Still, we note that the somewhat artificial nature of this study could have resulted in the gerbils' inability to assess risk accurately. Also, we cannot entirely know the role that the gerbils' risk assessment may have played in our results because we do not have a good measure of how risk actually changed with additional predators.

The last possibility for the asymptotic trend in GUDs is that with additional predators gerbils were buying more safety per added unit of apprehension, and so GUDs did not increase linearly. Such a trend could occur if the efficiency of apprehension increased with risk, so that each additional predator became less costly to the prey. We cannot, however, rule out the possibilities that the asymptotic increase in GUDs could result from predator behaviour or from limited perception of prey.

ACKNOWLEDGEMENTS

REFERENCES

Abrams, P.A. 1993. Why predation rate should not be proportional to predator density. *Ecology*, **74**: 726–733.

Abrams, P.A. 1994. Should prey overestimate the risk of predation. *Am. Nat.*, **144**: 317–328.

Abrams, P.A. 1995. Overestimation versus underestimation of predation risk – a reply to Bouskila et al. *Am. Nat.*, **145**: 1020–1024.

Abramsky, Z., Rosenzweig, M.L. and Subach, A. 1997. Gerbils under threat of owl predation: isoclines and isodars. *Oikos*, **78**: 81–90.

Abramsky, Z., Rosenzweig, M.L. and Subach, A. 2002. The costs of apprehensive foraging. *Ecology*, **83**: 1330–1340.

Anholt, B.R., Werner, E. and Skelly, D.K. 2000. Effects of food and predators on the activity of four larval ranid frogs. *Ecology*, **81**: 3509–3521.

Arenz, C.L. and Leger, D.W. 1999. Thirteen-lined ground squirrel (Sciuridae: *Spermophilus tridecemlineatus*) antipredator vigilance: monitoring the sky for aerial predators. *Ethology*, **105**: 807–816.

Bednekoff, P.A. and Lima, S.L. 1998. Randomness, chaos and confusion in the study of antipredator vigilance. *Trends Ecol. Evol.*, **13**: 284–287.

Blumstein, D.T., Daniel, J.C. and Sims, R.A. 2003. Group size but not distance to cover influences agile wallaby (*Macropus agilis*) time allocation. *J. Mammal.*, **84**: 197–204.

Bouskila, A. and Blumstein, D.T. 1992. Rules of thumb for predation hazard assessment – predictions from a dynamic-model. *Am. Nat.*, **139**: 161–176.

Bouskila, A., Blumstein, D.T. and Mangel, M. 1995. Prey under stochastic conditions should probably overestimate predation risk – a reply to Abrams. *Am. Nat.*, **145**: 1015–1019.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.*, **22**: 37–47.

Brown, J.S. and Kotler, B.P. 2007. Foraging and the ecology of fear. In *Foraging* (D. Stephens, R. Ydenberg, and J.S. Brown eds.), pp. 437–483. Chicago, IL: University of Chicago Press.

Chesson, J. 1983. The estimation and analysis of preferences and its relationship to foraging models. *Ecology*, **64**: 1297–1304.

Crowder, L.B., Squires, D.D. and Rice, J.A. 1997. Nonadditive effects of terrestrial and aquatic predators on juvenile estuarine fish. *Ecology*, **78**: 1796–1804.

Dall, S.R.X., Kotler, B.P. and Bouskila, A. 2001. Attention, 'apprehension' and gerbils searching in patches. *Ann. Zool. Fenn.*, **38**: 15–23.

Kie, J.G. 1999. Optimal foraging and risk of predation: effects on behaviour and social structure in ungulates. *J. Mammal.*, **80**: 1114–1129.

Komdeur, J. and Kats, R.K.H. 1999. Predation risk affects trade-off between nest guarding and foraging in Seychelles warblers. *Behav. Ecol.*, **10**: 648–658.

Kotler, B.P. 1992. Behavioral resource depression and decaying perceived risk of predation in species of coexisting gerbils. *Behav. Ecol. Sociobiol.*, **30**: 239–244.

Kotler, B.P. 1997. Patch use by gerbils in a risky environment: manipulating food and safety to test four models. *Oikos*, **78**: 274–282.

Kotler, B.P. and Brown, J.S. 1990. Rates of seed harvest by two species of gerbilline rodents. *J. Mammal.*, **71**: 591–596.

Kotler, B.P., Brown, J.S. and Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology*, **72**: 2249–2260.

Kotler, B.P., Blaustein, L. and Brown, J.S. 1992. Predator facilitation – the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann. Zool. Fenn.*, **29**: 199–206.

Kotler, B.P., Gross, J.E. and Mitchell, W.A. 1994. Applying patch use to assess aspects of foraging behavior in Nubian ibex. *J. Wildl. Manage.*, **58**: 229–307.

Kotler, B.P., Brown, J.S., Oldfield, A., Thorson, J. and Cohen, D. 2001. Foraging substrate and escape substrate: patch use by three species of gerbils. *Ecology*, **82**: 1781–1790.

Kotler, B.P., Brown, J.S., Dall, S.R.X., Gresser, S., Ganey, D. and Bouskila, A. 2002. Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evol. Ecol. Res.*, **4**: 495–518.

Kotler, B.P., Brown, J.S. and Bouskila, A. 2004. Apprehension and time allocation in gerbils: the effects of predator risk and energetic state. *Ecology*, **85**: 917–922.

Lima, S.L. 1992. Life in a multi-predator environment: some considerations for anti-predatory vigilance. *Ann. Zool. Fenn.*, **29**: 217–226.

Lima, S.L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Stud. Behav.*, **27**: 215–290.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.

Lotka, A.J. 1925. *Elements of Physical Biology*. Baltimore, MD: Williams & Wilkins.

Longland, W.S. and Price, M.V. 1991. Direct observations of owls and heteromyid rodents – can predation risk explain microhabitat use? *Ecology*, **72**: 2261–2273.

Molinari-Jobin, A., Molinari, P., Loison, A., Gaillard, J.M. and Breitenmoser, U. 2004. Life cycle period and activity of prey influence their susceptibility to predators. *Ecography*, **27**: 323–329.

Orrock, J.L., Danielson, B.J. and Brinkerhoff, R.J. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behav. Ecol.*, **15**: 433–437.

Peacor, S.D. and Werner, E.E. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl. Acad. Sci. USA*, **98**: 3904–3908.

Relyea, R.A. 2003. How prey respond to combined predators: a review and an empirical test. *Ecology*, **84**: 1827–1839.

Relyea, R.A. 2004. Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. *Ecology*, **85**: 172–179.

Sih, A. 1984. Optimal behavior and density-dependent predation. *Am. Nat.*, **123**: 314–326.

Sih, A., Englund, G. and Wooster, D. 1998. Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.*, **13**: 350–355.

Sikes, R.S., Gannon, W.L. and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.*, **92**: 235–253.

Skalski, G.T. and Gilliam, J.F. 2001. Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology*, **82**: 3083–3092.

Van Buskirk, J. and Arioli, M. 2002. Dosage response of an induced defense: how sensitive are tadpoles to predation risk. *Ecology*, **83**: 1580–1585.

Volterra, V. 1926. Variations and fluctuations of the numbers of individuals in animal species living together. In *Animal Ecology* (R.N. Chapman, ed.), pp. 409–448. New York: McGraw-Hill.

So, gradient descent will fail to converge. At the optimal value of θ (e.g., found by fminunc), we will have $J(\theta) \geq 0$. Because the positive and negative examples cannot be separated using a straight line, linear regression will perform as well as logistic regression on this data. solution. For logistic regression, sometimes gradient descent will converge to a local minimum (and fail to find the global minimum). - This is the reason we prefer more advanced optimization algorithms such as fminunc (conjugate gradient/BFGS/L-BFGS/etc). Since we train one classifier when there are two classes, we train two classifiers when there are three classes (and we do one-vs-all classification). The sigmoid function $g(z)$ is never greater than one (>1). $g(z)=\frac{1}{1+e^{-z}}$. The foraging response of gerbils to a gradient of owl numbers. JRS Juliana, BP Kotler, JS Brown, S Mukherjee, A Bouskila. University of Illinois at Chicago, 2011. 24. 2011. Stress as an adaptation I: Stress hormones are correlated with optimal foraging behaviour of gerbils under the risk of predation. JRS Juliana, BP Kotler, N Wielebnowski, JG Cox. Evolutionary Ecology Research 18 (5), 571-585, 2017. 7. 2017. Optimal foraging behavior and the thermal neutral zone of Peromyscus leucopus during winter: A test using natural and controlled ambient temperatures. JRS Juliana, WA Mitchell. Journal of thermal biology 56, 109-112, 2016. 5. 2016. Using gerbils and trained barn owls, we conducted the first (to our knowledge) field tests of the theory's prediction of mutualism. The behavior of the gerbils confirms its existence. Flights by trained barn owls in 29 trials provided a predation threat. In the absence of owls in flight (56 trials), activity densities were always similar in the two subplots, revealing the intraspecific competition among the gerbils. (Noninteracting individuals should drift aimlessly between the subplots.) In summary, foraging Allenby's gerbils usually disperse as if they were competing with each other. The exception to this behavior occurs at low gerbil densities in the presence of a predation threat. Then they coalesce as if they were mutualists. Great gerbils inhabited the open sandy bottom of the valley covered with scattered shrubs of Haloxylon spp. and Calligonum spp. with average shrub cover of 2.5%. Animals. To trap the gerbils we used wired cage traps (45 14 14.5 cm) baited with fresh leaves of A. halimus (P. obesus) and sunflower seeds (R. opimus). We started observations only if an animal showed no response to our occupation of the observation post by interrupting its activity or by adopting an alert posture. We observed focal individuals for 10-min periods and recorded their activity on to a constantly running tape recorder. To assess multivariate behavioural similarities between categories of gerbils we applied principal components analysis (PCA) to all six normalized.