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# Attention, 'apprehension' and gerbils searching in patches

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In this paper, we consider the attentional demands associated with detecting and responding to predators, or 'apprehension', and the within-patch search of Allenby's gerbils, *Gerbillus andersoni allenbyi*. We, thus, present a first empirical investigation of the indirect, informational consequences of perceived predation risk. Specifically, we focus on the ability to track the quality of seed patches in sandy habitats. There are two potential effects here; since instantaneous intake rate (or some proxy) is the key parameter of interest to an optimal forager, apprehension can interfere with the estimation of: (1) the number of food items captured, and/or (2) the time taken to capture them (the ability to locate food items). Only (2) will have a consistent effect on patch quality, and we test the hypothesis that increased predation risk reduces gerbil search efficiency. We therefore quantified gerbil search paths in patches of uniform seed distribution that differed in their associated risks of predation by manipulating the presence of barn owls, *Tyto alba*, and light in an aviary. Gerbil search was more random under risky conditions. We discuss the implications of this result for information processing and patch use under predation risk, and the foraging games between gerbils and owls in the Negev Desert.

## Introduction

Predators can have profound effects on their prey, over and above simply increasing mortality rates (for discussions *see* Sih 1987, Lima & Dill 1990). As far as prey behaviour is concerned, much attention has focussed on how foraging decisions are influenced by the risk of predation (Lima & Dill 1990). Investigations here have concentrated on elucidating the 'star-

vation-predation' trade-off. In other words, since finding and consuming food exposes an animal to its predators, a fundamental trade off between the joint risks of starvation and predation is reasoned to underlie many foraging decisions (Houston *et al*. 1993, Cuthill & Houston 1997). The consequences of this trade-off are relatively well understood in a wide range of systems and for most common foraging problems (Cuthill & Houston 1997).

## Attention and apprehension

Predators can also affect the foraging behaviour of their prey in ways that are not related directly to the risk of mortality. One such indirect effect stems from the observation that scanning for predators and/or hiding from perceived attacks (or just being stressed; Mendl 1999) will take attention away from foraging. In an uncertain world, the quality of prey or patch types may be changing continuously due to changes in weather, the behaviour of other animals, and other such factors that are out of the direct control of a foraging animal. Being forced to take attention away from foraging will mean that any information that the forager has about its resources is unlikely to be accurate once foraging resumes. In addition, restricting the foraging time horizon due to predator-associated interruptions reduces the value of learning because there is less opportunity to exploit the information gained and make up for its acquisition costs (Lucas, 1990). These effects, in combination, can have dramatic consequences for foraging efficiency and diet choice in a variable environment (Dall *et al*, 1999). The implications of such indirect effects for patch use, however, have received scant attention, either theoretical or empirical (but *see* J. S. Brown, B. P. Kotler, S. R. X. Dall & A. Bouskila, unpubl.).

Fundamental to most considerations of the effects of predation risk on foraging behaviour is the assumption that foraging and anti-predatory vigilance are mutually exclusive activities (e.g. Pulliam *et al*. 1982, Lima 1987, Packer & Abrams 1990; for a review *see* Bednekoff & Lima 1998): on the one hand, an animal can find and consume food at the expense of detecting potential predators, or it can scan for predators and not forage. In other words, anti-predatory vigilance and foraging are both assumed to require the animal's complete attention. It is becoming increasingly evident, however, that this assumption is commonly violated. Apparently vigilant animals *can* forage (e.g. handle food) and 'head down' foragers *can* detect predatory attacks (Bednekoff & Lima 1998, Lima & Bednekoff 1999). Here we introduce the term anti-predatory 'apprehension' (*see also* J. S. Brown, B. P. Kotler, S. R. X. Dall & A. Bouskila unpubl.) in the spirit of calls for the trade-off to be reconsidered as a continuous one between the efficacy of vigilance, on the one hand, and its cost, on the other (Lima & Bednekoff 1999). We define apprehension as: any reduction in attention to other activities (e.g. foraging) as a result of increasing the allocation of attention to detecting and/or responding to potential predator activity. Thus, applied to a foraging context, anti-predatory apprehension encompasses the observed continuum of attention allocation away from foraging to detecting predators, with 'blind' foraging at one end and overt vigilance at the other.

## Apprehension and patch use by gerbils

We present a first empirical investigation of an indirect effect of predation risk on foraging by utilising the concept of anti-predatory apprehension to understand how predation risk influences the exploitation of food patches by Allenby's gerbils, *Gerbillus andersoni allenbyi* (Kotler *et al*. 1991, 1992, 1993a, 1993b, 1993c, 1994a, 1994b, Kotler 1992, 1997, Brown *et al*. 1994). In particular, we are interested in how reductions in attention to foraging can affect the ability of these gerbils to estimate the instantaneous quality of patches of seeds in their favoured sandy desert habitat (Kotler & Brown 1999)

Functional analyses of patch use suggest that the instantaneous net rate at which food is harvested from a patch is a key decision variable for optimal foragers (e.g. Charnov 1976, Brown

1988). There are, therefore, two main ways that reduced attention to foraging can influence the estimation of patch quality. (1) It can affect the estimation of the time (search effort) taken to find food items. (2) It can affect estimates of the number of food items found (e.g. the ability to 'count'). With food hidden in an unstable substrate, such as seeds in sand, reduced attention to searching will generally increase the chance that a gerbil 'loses its place' and hence the chance that it will re-search areas of a patch. More random search will reduce search efficiency, increase the time between locating food items, and thus *reduce* estimates of patch quality and intake rates. Other effects of reduced foraging attention in such a system are likely to result in a random spread of erroneous patch quality estimates. For example, if distractions from 'counting' the number of seeds eaten cause a gerbil's estimate of this variable to degrade, the direction in which the animal will err depends on the 'run of luck' experienced upon resumption. There is no reason to expect that such runs will be systematically biased in any direction, all else being equal.

In the following experiment, we tested the hypothesis that gerbil search efficiency will decline in artificial patches under increased predation risk. By focussing on the more easily tested of the potential effects of apprehension, it is possible to falsify the idea that predation risk will have a consistent effect on patch quality estimation. Thus, we begin to elucidate the indirect consequences of predation risk on patch use.

## Materials and methods

### Subjects

Foraging trials were performed on 12 wild-caught, male Allenby's gerbils, *G. a. allenbyi*, of undetermined ages, between the 8 and 24 March, 1999. The gerbils were selected randomly from a pool of animals that were captured periodically between 13 February and 16 March 1999. Any animal that was not placed immediately into the experimental arena (see below) was housed individually in the laboratory with *ad libitum* access to food. Each animal had at least five nights to settle into the experimental arena before its first foraging trial, during which time and after each nightly trial it was fed nightly approximately 3 g of uncracked wheat distributed randomly in an aluminium sand-filled tray. During these settling in periods, five hand-reared barn owls, *Tyto alba*, were present in the aviary arena, with its six, evenly spaced, 100 W incandescent lights turned off.

### Experimental arena

The gerbils, in groups of six at a time, were housed individually in $2 \times 2 \times 1$ m wire-mesh pens located in the aviary. The pens were completely covered by shade cloth that excluded the owls when they were present. Each pen was stocked with artificial burrows made of lengths of plastic pipe buried in the substrate with one end exposed and cotton wool nesting material for shelter. Food was located exclusively within a 'patch' that consisted of five litres of sand in a $0.6 \times 0.45 \times 0.025$ m aluminium tray, placed in the centre of each pen. The floors of the pens were also covered with sand to a depth of approximately 0.05 m, under which there were wire-mesh barriers. For each foraging trial, an infrared-sensitive video camera was fitted over the food patch, with its field of view illuminated by infrared lights.

### Procedure

The experiment was of a repeated-measures design, with each gerbil experiencing either owls present in the aviary, or removed to a holding pen, and the aviary lights on or off. The gerbils were exposed to each of the possible combinations of owl presence and illumination on subsequent nights over a four-night period.

The gerbils were allocated randomly to two groups of six individuals. Each group experienced the predation risk manipulations in different orders. The first group was tested from 8 to 11, and the second from 21 to 24 March 1999.

The first group experienced the 'riskiest' manipulations first, while the second group experienced the manipulations in the reverse, from safest to riskiest, order (Table 1). The categorisation of relative risk was based on observations that Allenby's gerbils behave as if the presence of owls is more risky than light in aviary settings (Kotler *et al*. 1991).

In each of the above treatments, the distribution and amount of food was held constant, with ten uncracked wheat seeds distributed uniformly over the 'seed tray' patches. To make the search task realistic, the seeds were buried to a depth of approximately 0.01 m and the sand was smoothed over in order to eliminate any visual cues that the gerbils might use to locate individual seeds. Each animal was deprived of all other food until the end of its nightly trial.

The foraging trials started approximately $^1/_2$ hour after dusk. Each trial lasted for one hour or until the gerbil had shown evidence of foraging on its seed tray. The maximum trial length was two hours. Behaviour was recorded remotely on videocassette, and after each trial the sand in the seed tray was sifted and the number of remaining seeds counted. Each group of six gerbils was thus processed sequentially over the first half of a night, and the order in this sequence that each gerbil was tested was randomised between nights (treatments). The owls, when present, were not fed until after the last gerbil had been videoed. Only those gerbils that foraged on their seed trays during foraging trials under all of the predation risk manipulations were included in the analysis. As a result, only five animals from the Risky-First group and four from the Safe-First group were included. Moreover, some trials had to be extended past the one-hour minimum to get any patch foraging recorded in the Safe-First group. In contrast, in the Risky-First group, all gerbils foraged within an hour in each trial, and an animal was dropped from the analysis only because it died after the first night of experimentation.

## Video analysis

Since the primary goal of this work was to quantify within-patch search behaviour, the video camera was placed so as to obtain the most relevant field of view for this purpose (e.g. Dall & Cuthill 1997a). All footage was hence taken from above the foraging gerbils, and the resolution of the video camera and lighting was insufficient to recognise seed encounter events. We were unable, for this reason, to construct individual gain curves.

The video footage was analysed to record the amount of time that a gerbil spent foraging on the patch (to the nearest 0.01 s) and the number of bouts in which this foraging was performed. A gerbil was classified as foraging if it was walking slowly over the sand, frequently moving its head downwards and side-to-side, and displacing sand. Bouts were delineated by when the animal first stepped onto the seed tray prior to, and when it stepped off after, foraging.

From the original search footage, the position of the head of a foraging gerbil was recorded every second. This 'discretisation' of gerbil search paths was limited to the first minute of cumulative foraging on the seed tray to minimise any 'noise' caused by patch depletion. Searching animals can adjust either their speed, the amount of turning that they do, or both (Benhamou 1992). In order to analyse the effects of treatment on these two components of search separately, the sinuosity index (Bovet & Benhamou, 1988) for each of the trials was calculated in addition to the Euclidean distances moved each time step (search speed). The sinu-

**Table 1.** The orders in which the two groups of gerbils experienced the predation risk manipulations.

| Group | Order of manipulation (changed nightly) |
|---|---|
| Risky First: | Owls, Lights on → Owls, Lights off → No Owls, Lights On → No Owls, Lights off |
| Safe First: | No Owls, Lights off → No Owls, Lights on → Owls, Lights off → Owls, Lights on |

osity index is derived from the distribution of changes in direction per unit space- here radians per $cm^2$. It can range from zero (straight-line movement) to one (random movement = every possible change in direction equally likely). This involved re-discretising each search path so that the position of a gerbil's head every unit length, rather than time, was obtained. We then calculated sinuosity from the resultant distribution of changes in direction over a trial, using the methods described by Bovet and Benhamou (1988). The step length we used for the re-discretisation was 0.05 m.

## Results

### Multivariate analysis

The temporal and spatial components of a search path, and their foraging consequences, cannot be considered totally independent. We therefore adjusted the family-wise error rates (Sokal & Rohlf 1995) by using mixed-model multivariate analyses of variance (MANOVAs), with the order of predation risk manipulation (Risky versus Safe-First) as a between-subjects factor, and owl presence (Present versus Absent) and illumination (Light versus Dark) as within-subjects factors. We included six direct measures of patch use and searching behaviour: mean trial sinuosity, the mean search speed per trial and its variance, the number of seeds eaten per trial, the total time spent in the patch per trial, and the number of foraging bouts per trial. We also used the three non-search measures of foraging (number of seeds eaten, time in patch and the number of bouts) to calculate two further foraging variables: the number of seeds eaten per second (intake rate) and the average number of seconds in a foraging bout, which could not be included in the same analysis. Hence, a separate, equivalent MANOVA was also performed; with the measures of search behaviour and these derived variables as variates.

For the MANOVA that included only the direct measures as variates, a significant three-way interaction between order, owl presence and illumination emerged (Wilks' $\lambda < 0.001, F_{6,2} = 23\ 436.197, P < 0.001$). For the MANOVA that included intake rate and bout length as variates, on the other hand, there were no significant effects of any of the factors, either individually or in interaction (although the order × owl presence × illumination interaction was only marginally non-significant: Wilks' $\lambda = 0.067$, $F_{5,3} = 8.412, P = 0.055$). The equivalent univariate analyses were performed separately to discover which of the variates were responsible for the significant interaction.

With mean sinuosity index as a variate, the equivalent mixed-model analysis of variance (ANOVA) demonstrated that the three-way interaction was significant ($F_{1,7} = 6.551$, $P = 0.038$). However, for all of the other variates in the multivariate model, the three-way interaction was not significant in equivalent ANOVAs (mean search speed: $F_{1,7} = 0.120$, $P = 0.739$; variance in search speed: $F_{1,7} = 0.329$, $P = 0.584$; number of seeds eaten: $F_{1,7} = 2.671$, $P = 0.146$; total time on patch: $F_{1,7} = 0.345$, $P = 0.575$; number of bouts: $F_{1,7} = 1.071, P = 0.335$).

### The three-way interaction and sinuosity

The effects on sinuosity of our manipulations of predation risk differed in their interaction between the two groups of gerbils (Figs. 1 and 2). We therefore describe the interaction between the presence of owls and light on the spatial component of gerbil search for each group separately.

The search paths of the five gerbils that experienced the riskiest manipulations first became less sinuous in the safest (i.e. last) manipulation: when there were no owls in the aviary with the lights off. In contrast, their paths were more sinuous in the presence of any of the manipulated elements of predation risk. However, the presence of owls, light or both together, had little differential influence on the sinuosity of gerbil search paths (Fig. 1).

On the other hand, for the four gerbils that experienced the manipulations of predation risk from safest to riskiest (Table 1), the sinuosity of their within-patch search did not change much as a result of manipulation (Fig. 2). There was,

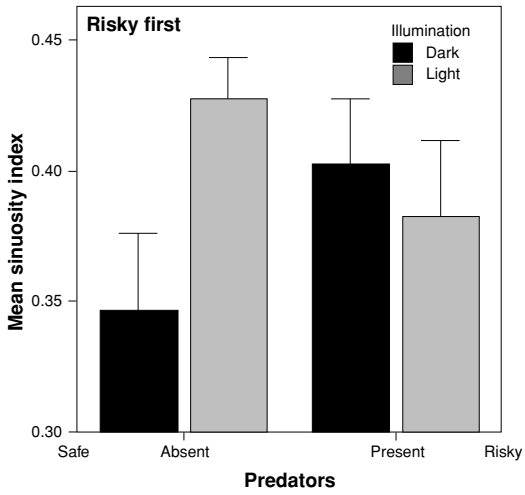



**Fig. 1.** The mean sinuosity index per trial (rad $cm^{-0.5}$ + s.e.m.) of the search paths of Allenby's gerbils when barn owls were present or absent, and aviary lights on or off, manipulated in a factorial manner. This group of five gerbils experienced the manipulations from riskiest (right) to safest (left).

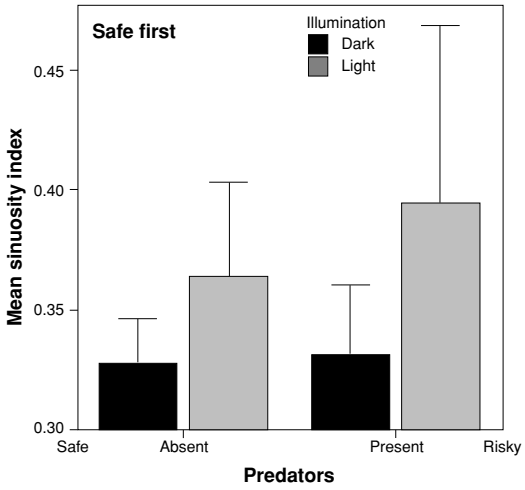



**Fig. 2.** The mean sinuosity index per trial (rad $cm^{-0.5}$ + s.e.m.) of gerbil search paths when barn owls were present or absent, and aviary lights on or off. This group of four gerbils experienced the manipulations from safest (left) to riskiest (right).

however, an apparent trend towards more sinuous search in the light.

## Discussion

### Apprehension and search

The gerbils in our experiment tended to increase the randomness of their within-patch search, as measured by the spread of the distribution of changes in direction per unit search distance (sinuosity index; Bovet & Benhamou 1988), in response to our manipulated increases in their perceived risk of predation. However, the changes in randomness we observed were too small ($\Delta$ sinuosity indices $\leq 0.082$ rad $cm^{-0.5}$; Figs. 1 and 2) to have any significant anti-predatory function, such as making the gerbils harder to catch, other than that derived from apprehension itself. Moreover, this effect of predation risk depended on the order in which the animals experienced the different combinations of manipulated risk factors.

We recorded a clear change in the randomness of the search of the gerbils that experienced the factor combinations from riskiest to safest (the Risky-First group; Table 1); animals searched more randomly under risky conditions than when the owls were absent with the lights off. However, their search did not change in randomness according to which of the risk factors were present, alone or in combination (Fig. 1). Therefore, for these gerbils, just having light and/or owls present causes them to search relatively randomly, but this effect appears to be similar for both light and predator presence. In contrast, there is evidence that moonlight and predator activity affect differentially how much Allenby's gerbils are willing to forage in patches (e.g. Kotler *et al*, 1991). Thus we have evidence that apprehension can influence foraging behaviour independently to the starvation-predation tradeoff.

For those gerbils that experienced the safest environment first (the Safe-First group; Table 1), however, there were no clear influences of either of the risk factors on our measures of foraging behaviour. Nevertheless, the randomness of gerbil search tended to increase under illumination (Fig. 2), in line with hypothetical expectation. One potential reason for the lack of clear effects when the safest manipulations were experienced first could result from perceived

uncertainty in the riskiness of the experimental environment. The results from the Risky-First group of gerbils suggest that *G. a. allenbyi* perceive our safest manipulation as qualitatively different to all of the other manipulated environments, at least as far as search is concerned. Perhaps then, switching from the relatively risky settling-in phase to 'safe' on the first night, and then back again soon afterwards, made the Safe First gerbils too inconsistent in their responses to detect an effect of manipulation statistically, especially given the small sample size (note the large error bars in Fig. 2). On the other hand, the Risky-First group experienced the qualitative change in risk after a longer period of stability, and may therefore have behaved more consistently.

## Apprehension and intake rate?

Our experimental hypothesis that apprehension disrupts the abilities of gerbils to search for seeds in sand is corroborated by the clear increase in search randomness in response to predatory risk we observed in one of our groups of gerbils. Therefore, we also expect that the time between encounters with seeds will increase under risk, all else being equal, since the probability of re-searching areas of the patch becomes relatively high with increased randomness (Charnov *et al*. 1976). Hence, if the gerbils are also attempting to track their instantaneous net rates of intake (harvest rates; Brown, 1988), our results suggest that estimates of this key decision variable will be reduced consistently on lit nights and/or when owls are active locally. Since intake rate estimates must be based on actual intake rates, we would expect to observe reductions in the harvest rates of gerbils in response to increased predation risk. However, neither of the risk factors had a significant effect on intake rates in our experiment, despite an apparent decrease when the lights were on (mean of $0.0163 \pm 0.005$ seeds per second of foraging on the patch) compared to when they were off ($0.0191 \pm 0.004$ seeds $s^{-1}$). This difference was independent of owl presence (in the appropriate ANOVA, $F_{1,7} = 5.208$, $P = 0.056$, for illumination as a factor). Unfortunately, the lack of ability to corroborate our logic conclusively, with the small sample size, is likely to stem from the crudeness of our measure of intake rate. We derived intake rates from the total time spent on the patch and the number of seeds removed during this period. On the one hand, because of the visual resolution of the recordings, it was sometimes difficult to distinguish foraging from other activities on the patch, such as grooming and resting. The latter increased in frequency during a trial, from almost nothing at the beginning, as the value of food decreased and/or food became scarce. On the other hand, by limiting the total number of seeds in a patch to ten for practicality, we also limited the potential variance in numbers removed.

## Some potential implications

Nevertheless then, our results suggest that *G. a. allenbyi* may have consistently reduced harvest rate estimates when elements of risk of the kind we manipulated here are present in their foraging environment. Indeed, Fierer & Kotler (2000) quantified the foraging behaviour of Allenby's gerbils indirectly by comparing the relative densities of seeds remaining in seed trays, before and after foraging using giving up densities, or GUDs (Brown, 1988). In addition, they created micro patches within the seed trays to manipulate the number of 'vague' patch boundaries. The observed GUDs were consistent with a reduction in the gerbils' ability to exploit the micro patches efficiently when risk factors similar to those manipulated here were present. Moreover, the GUDs suggested that the gerbils *reduced* their estimates of patch quality when they were more apprehensive. So, if predator apprehension reduces patch quality estimates for *G. a. allenbyi* foraging for seeds in sandy habitats, as our results and the literature suggest, a number of issues for their efficient foraging under predation risk arise.

### Naïve averagers…

Having consistently reduced estimates of patch quality in risky habitats can result in the underestimation of habitat quality by gerbils, if they

do not also compensate for such biases by devaluing information from risky patches in a systematic manner. In other words, gerbils that are 'naïve averagers' may perceive risky microhabitats as so bad that, even if they become safer periodically, they will never be exploited as their resource qualities merit. Thus, the amount of apprehension that a given risk factor induces, if it differs between competing species, for instance if it changes with body size or morphology, could provide additional, predation-driven mechanisms of species coexistence (e.g. Kotler *et al*. 1994b). Moreover, apprehension-driven underestimation could have implications for the foraging game being played between owls and gerbils in the Negev Desert system (Brown *et al*. 2001). For example, if gerbils underestimate the quality of their seed resources consistently when their main predators, barn owls, are active, their activity levels could be driven down even further than is necessary to trade off food and safety. Thus, foraging would be less profitable for the owls and drive a reduction in their own activity. On the other hand, the game dynamics would be dramatically different if the errors in patch quality estimation were evenly or randomly distributed about the actual qualities, or if patch quality was consistently overestimated. Such dynamics are important determinants of time budgeting and community interactions in this system (Brown *et al*. 2001).

### …or clever discounters?

Alternatively, illumination and predator activity resulting in directionally biased estimates of patch quality could select for gerbils that are 'clever discounters'. The strength of selection depends on both the value of using the risk factors as cues to discount current perceived patch quality as a basis for foraging decisions, and the potential costs of doing so. Following Stephens (1989), discounting will be relatively valuable if failing to do so reduces fitness significantly, and decisions based on discounting differ dramatically from those that do not. On the other hand, the costs of using risk factors such as illumination and owl activity to discount current patch information will depend on how much attending to such cues affects the forager's ability to attend to and track other cues and factors vital to its fitness (*see* Dall & Cuthill 1997b for a discussion of information costs). For Allenby's gerbils, the effects of predator apprehension demonstrated here suggest that the value of being a clever discounter is relatively high while the costs are quite low; naïve averaging would cause safe microhabitats to be overexploited and even temporarily risky ones to be under-exploited, which is fairly maladaptive. Moreover, cueing in on risk factors will be relatively cost-free due to the reallocation of attention to detecting/responding to predators, or apprehension, that predation risk elicits. Further work is needed to test the prediction that gerbils should therefore be clever discounters.

## Conclusions

We have demonstrated that antipredatory apprehension can influence foraging behaviour independently to the starvation-predation trade-off. In doing so, we hope to have also illustrated the value of considering the subtle, informational consequences of predation risk for a complete understanding of predator-prey interactions and information processing in general. In addition, by representing the relative allocation of attention between foraging and predation risk as a continuum, rather than an all-or-nothing phenomenon, we can reconcile traditional treatments of vigilance with observations that vigilant animals *can* forage and foraging animals *can* detect predators (e.g. Lima & Bednekoff 1999). We hope that the concept of anti-predatory apprehension *(see also* J. S. Brown, B. P. Kotler, S. R. X. Dall & A. Bouskila, unpubl.) will be accepted on such merits.

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## References


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

Benhamou, S. 1992: Efficiency of area-concentrated searching behaviour in a continuous patchy environment. — *J. Theor. Biol.* 159: 67–89.

Bovet, P. & Benhamou, S. 1988: Spatial analysis of animals' movements using a correlated random walk model. — *J. Theor. Biol.* 131: 419–433.

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., Kotler, B. P. & Bouskila, A. 2001: Ecology of fear: Foraging games between predators and prey with pulsed resources. — *Ann. Zool. Fennici* 38: 71–87.

Brown, J. S., Kotler, B. P. & Valone, T. J. 1994: Foraging under predation — a comparison of energetic and predation costs in rodent communities of the Negev and Sonoran deserts. — *Austr. J. Zool.* 42: 435–448.

Charnov, E. L. 1976: Optimal foraging, the marginal value theorem. — *Theor. Pop. Biol*, 9: 129–136.

Charnov, E. L., Orians, G. H. & Hyatt, K., 1976: Ecological implications of resource depression. — *Am. Nat.* 110: 247–259.

Cuthill, I. C. & Houston, A. I. 1997: Managing time and energy. — In: Krebs, J. R. & Davies, N. B. (eds.), *Behavioural ecology*. 4th ed.: 97–120. Blackwell Scientific Publications, Oxford.

Dall, S. R. X. & Cuthill, I. C. 1997a: Searching in patches by European starlings, *Sturnus vulgaris*. — *Behav. Proc.* 39: 149–159.

Dall, S. R. X. & Cuthill, I. C. 1997b: The information costs of generalism. — *Oikos* 80: 197–202.

Dall, S. R. X., McNamara, J. M. & Cuthill, I. C. 1999: Interruptions to foraging and learning in a changing environment. — *Anim. Behav.* 57: 233–241.

Fierer, N. & Kotler, B. P. 2000: Evidence for micropatch partitioning and the effects of boundaries on patch use in two species of gerbils. — *J. Func. Ecol.* 14: 176–182.

Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993: General results concerning the trade-off between gaining energy and avoiding predation. — *Phil. Trans. Roy. Soc. Lond., B.* 341: 375–397.

Kotler, B. P. 1992: Behavioural resource depression and decaying perceived risk of predation in two 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. & Brown, J. S. 1999: Mechanisms of coexistence of optimal foragers as determinants of local abundances and distributions of desert granivores. — *J. Mamm.* 80: 361–374.

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

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

Kotler, B. P., Blaustein, L. & Dednam, H. 1993a: The specter of predation — the effects of vipers on the foraging behavior of two gerbilline rodents. — *Isr. J. Zool.* 39: 11–21.

Kotler, B. P., Brown, J. S. & Mitchell, W. A. 1993b: Environmental factors affecting patch use in two species of gerbilline rodents. — *J. Mamm.* 74: 614–620.

Kotler, B. P., Brown, J. S., Slotow, R. H., Goodfriend, W. L. & Strauss, M. 1993c: The influence of snakes on the foraging behavior of gerbils. *Oikos* 67: 309–316.

Kotler, B. P., Ayal, Y. & Subach, A. 1994a: Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. — *Oecol.* 100: 391–396.

Kotler, B. P., Brown, J. S. & Mitchell, W. A. 1994b: The role of predation in shaping the behavior, morphology and community organization of desert rodents. — *Austr. J. Zool.* 42: 449–466.

Lima, S. L. & Bednekoff, P. A. 1999: Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? — *Anim. Behav.* 58: 537–543.

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

Lima, S. L. 1987: Vigilance while feeding and its relation to the risk of predation. — *J. Theor. Biol.* 124: 303–316.

Lucas, J. R. 1990: Time scale and diet choice decisions. — In: Hughes, R. N. (ed.), *Behavioural mechanisms of food selection*. NATO ASI Series Vol. G20: 165–185. Springer-Verlag, Berlin.

Mendl, M. 1999: Performing under pressure: stress and cognitive function. — *Appl. Anim. Behav. Sci.* 65: 221–224.

Packer, C. & Abrams, P. 1990: Should co-operative groups be more vigilant than selfish groups? — *J. Theor. Biol.* 142: 341–357.

Pulliam, H. R., Pyke, G. H. & Caraco, T. 1982: The scanning behavior of juncos: a game-theoretical approach. — *J. Theor. Biol.* 95: 89–103.

Sih, A. 1987: Predators and prey lifestyles: an evolutionary and ecological overview. — In: Kerfoot, W. C. & Sih, A. (ed.), *Predation: direct and indirect impacts on communities*: 203–223. University Press of New England.

Sokal, R. R. & Rohlf, F. J. 1995: *Biometry,* 3rd ed. — W.H. Freeman and company, New York.

Stephens, D. W. 1989: Variance and the value of information. — *Am. Nat.* 134: 128–140.