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# Increasing search rate over time may cause a slower than expected increase in prey encounter rate with increasing prey density

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**A previous experiment with birds searching for caterpillars in an aviary demonstrated a highly counterintuitive result, that the rate at which a forager encounters prey does not increase linearly with prey density. Here, I demonstrate that if search rate increases over time then this can produce exactly the observed type of behaviour. Further, I argue that declining perception of predation risk over time in the absence of reinforcement, coupled with a trade-off between anti-predator vigilance and searching ability (both widely reported in field and laboratory studies), could generate such a change in search rate over time. Hence, if my hypothesis is correct, the previous experimental results could have considerable generality, and invite reconsideration of our mathematical descriptions of predator–prey interactions.**

**Keywords:** foraging; searching; predation risk; trade-off

## 1. INTRODUCTION

Predator–prey interactions are a key component of almost all ecosystems. Hence, predation has been particularly closely studied by ecologists, and a powerful body of theoretical descriptions of predator–prey interactions has been developed. Such models can be found in any standard text on population biology (e.g. Krebs 2001; Townsend *et al.* 2003; Neal 2004). As Mols *et al.* (2004) pointed out, embedded in almost all models of predator–prey interactions is the assumption that the rate at which a searching predator encounters prey increases linearly with prey density. This seems a reasonable assumption, and can be justified by analogy with physicists' models of collisions between randomly moving molecules (e.g. Denny & Gaines 2000). This search rate assumption is so plausible that it has not been subjected to purpose-designed empirical testing until the results reported by Mols *et al.* (2004). They found that for great tits (*Parus major*) searching a large aviary for previously released winter moth (*Operophtera brumata* L.) caterpillars, the time to find the first prey item did not decline as quickly with increasing prey density as was predicted by theory. The authors did not speculate on why this effect occurred. This lack of a postulated underlying mechanism stands in contrast to another counterintuitive result that they also report: that the rate of prey detection was dependent not only on the current density of the prey population, but also on the extent of previous depletion. Mols *et al.* (2004) conclude that 'both these effects are likely to have major consequences for the outcome of predator–prey interactions' (p. 85). In view of the potential importance of these results, it is vital that the mechanisms underlying both of them are identified so as to allow the likely generality of the results to be judged. Here, I present a suggested mechanism for the previously unexplained result of Mols *et al.* (2004) together with discussion of both its likely generality and how my hypothesis could be tested empirically.

## 2. HYPOTHESIZED MECHANISM

My hypothesis is that when first released into the aviary, the rate at which the great tit searches the environment for food is initially low, but that this rate increases as time passes. The reason for the increase in search rate over time could come from one or a combination of different mechanisms. For example, it is very plausible that initially the great tit is wary of its new environment, which may contain predatory threats to it, but over time (with nothing to reinforce it) this concern about predators will decline. If, as has commonly been documented (e.g. Krebs & Davies 1993), there is a trade-off between anti-predatory vigilance and food-searching behaviour, then this could lead to an increase over time in the rate at which the environment is searched for food (as anti-predatory vigilance declines). Alternatively or additionally, there is ample evidence of individuals improving in their facility in a task with practice, and it could be that as the bird 'gets to know its environment better' it is able to search it more rapidly. Whatever the underlying reason for it, §3 presents a very simple mechanistic model, which demonstrates that an increase in search rate with time can produce the type of results observed by Mols *et al.* (2004). Although Mols *et al.* (2004) discounted 'time spent in other activities' from their values of search time, in practice this would not provide an effective means of factoring the effect described here out of experimental results, since identifying whether a bird is searching its environment for food, or for predators, or for both will generally be difficult to determine with certainty.

## 3. THE MODEL

We imagine an idealized environment consisting of $N$ individual microhabitats (hereafter called sites), each of which has a probability $\rho$ of containing a food item. The expected number of food items in the environment ($n$) is given by $N\rho$, and so $\rho$ can be considered a measure of the density of prey items available. We assume that the predator visits sites at a rate $V$ that is a function of the time spent in the environment $t$; specifically, we will assume the following functional form:

$$V(t) = V_{\min} + (V_{\max} - V_{\min})(1 - \exp(-\alpha t)). \qquad (3.1)$$

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That is, the initial visiting rate is $V_{\min}$; this increases over time (with rate of increase determined by parameter $\alpha$) until the visiting rate saturates at a higher value $V_{\max}$. We assume that the predator selects sites to visit randomly with replacement from the entire set of $N$ microhabitats. That is, we assume the predator has no memory of where it has visited before. Although this assumption greatly simplifies the model, the key result is not contingent on it. If the probability of any microhabitat containing a food item is $\rho$, then on average $(1/\rho)$ sites will have to be visited before a food item is found. Ruxton & Glasbey (1995) demonstrated that if our predator visits a site on $v$ occasions, with each site chosen at random (with replacement) from the whole environment, then the number of distinct sites visited ($v_{\rm d}$) is well approximated (when $v$ is not too small) by the relation originally derived by Dvoretzky & Erdos (1950):

$$v_{\rm d} = \frac{\pi v}{\ln(v)}. \tag{3.2}$$

Thus, to calculate the time taken to find the first food item when the density of food items is $\rho$, we first evaluate the number of site visits ($v^*$), by solving

$$\frac{\pi v^*}{\ln(v^*)} = \frac{1}{\rho}. \tag{3.3}$$

We then calculate the time taken to visit this number of sites ($T$) by solving

$$\int_0^T V(t)\mathrm{d}t = v^*. \tag{3.4}$$

Since equation (3.3) must be solved numerically, we present the results for $T$ as a function of $\rho$ for a purely demonstratory set of parameter values as the solid line in figure 1. Also plotted in this figure (as the dashed line) are the predictions of the theory based on the assumption that as we increase the density of prey (increase $\rho$), then the rate of encounter should increase linearly with $\rho$ and so the time to find the first prey item should vary as $(1/\rho)$. In fact, we find that, when the search rate increases over time, the time to find the first prey item does decline with increasing $\rho$ but more slowly than the classical $(1/\rho)$ theory would predict, exactly as Mols *et al.* (2004) observed.

The result presented in figure 1 does not critically depend on the exact parameter values. The effect described will be seen provided that food is sparse ($\rho$ is low), the change in search rate over time is sufficiently large (i.e. $V_{\max} - V_{\min}$ is large enough), and the decay constant ($\alpha$) is such that the search rate changes on similar time-scales to the time-scales on which prey are found.

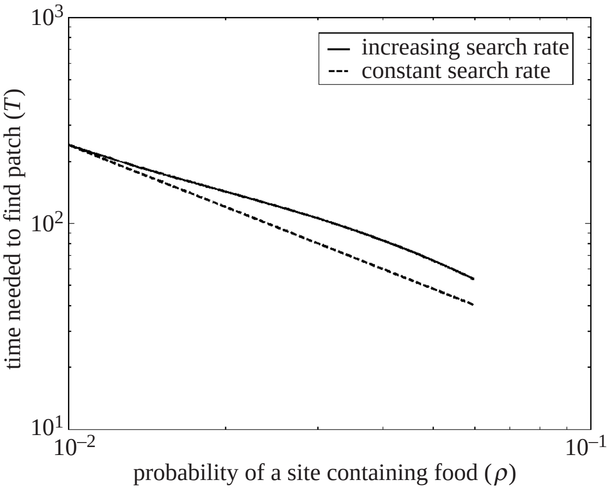

Figure 1. The solid line represents the average time taken to find food ($T$) as a function of prey density (the probability that a microhabitat will contain a food item: $\rho$) calculated, assuming an increasing search rate, from equations (3.3) and (3.4). The dashed line is derived from the theory that rate of food discovery increases linearly with $\rho$ and so $T$ should vary as $(1/\rho)$; this is scaled to agree with the solid line for the lowest $\rho$-value considered. Other parameter values: $V_{\max}=5$, $V_{\min}=1$, $\alpha=0.05$.

## 4. CONCLUSION

Mols *et al.* (2004) demonstrated a counterintuitive result: that the rate at which a forager encounters prey does not increase linearly with prey density. Since such linearity lies at the heart of almost all models of predator–prey interactions, this result could be influential if the mechanism behind it is general. Here, I demonstrate that an increase in search rate over time can produce exactly the type of behaviour reported by Mols *et al.* (2004). Further, I speculate that declining concern about predation over time in the absence of reinforcement, coupled with a trade-off between anti-predator vigilance and searching ability (both widely reported in field and laboratory studies), could generate such a change in search rate over time. Hence, if my hypothesis is correct, the results of Mols *et al.* (2004) could have great generality and invite reconsideration of our mathematical descriptions of predator–prey interactions.

Further, the hypothesis of changing search rate over time should be open to relatively straightforward testing; all that is required is a log of the times at which a predator searches discrete microhabitats within its environment as a function of time since it was introduced into the environment. If the specific formulation of this paper is used, then the model parameters ($V_{\min}$, $V_{\max}$ and $\alpha$) would have to be found by numerically intensive model-fitting techniques, because equations for them cannot be expressed in closed form. An alternative approach would be to use a similar proportional hazard model to that used by Mols *et al.* (2004); the mechanism described here predicts that the fitted baseline function should increase over time. Insectivorous birds in an aviary, as used by Mols *et al.* (2004), would be an entirely suitable study system, although the environment would have to be designed so that there are clearly differentiated microhabitats within that environment in which food can be hidden, and the predator can investigate only one of these microhabitats at a time. However, designing such a foraging environment should not be overly challenging, and examples of such an experimental set-up already exist (e.g. Templeton & Giraldeau 1995, 1996). The importance of this mechanism in the natural world is likely to vary with the movement patterns of the searcher. Where the searcher makes relatively frequent long-distance movements between discrete foraging areas, it will often enter an environment in which it does not have recent experience of (for example) predatory threat, and so the effect described here is likely to be strong. Insectivorous birds, such as the great tits used by Mols *et al.* (2004), are likely to provide good examples of this type of foraging behaviour. For a searcher whose movement is more gradual, without discrete larger-scale movements, the effect should be less strong, since frequent changes in knowledge of the local environment will be much less marked. Insectivorous mammals, such as shrews, are likely to provide examples of this type of foraging behaviour.

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