Central assumptions of predator–prey models fail in a semi-natural experimental system

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The relationship between the encounter rate of predators with prey and the density of this prey is fundamental to models of predator–prey interactions. The relationship determines, among other variables, the rate at which prey patches are depleted, and hence the impact of predator populations on their prey, and the optimal spatial distribution of foraging effort. Two central assumptions that are made in many models are that encounter rate is directly proportional to prey density and that it is independent of the proportion of prey already removed, other than via the decreased density. We show here, using captive great tits searching for winter moth caterpillars in their natural hiding positions, that neither of these assumptions hold. Encounter rate increased less than directly in proportion to prey density, and it depended not only on the current density of prey, but also on the proportion of prey already removed by previous foragers. Both of these effects are likely to have major consequences for the outcome of predator–prey interactions.

Keywords: search time; depletion; great tit; foraging

1. INTRODUCTION

Predator–prey interactions are common components of all ecological communities. The rate at which predators encounter prey is central to such interactions and has consequences on an ecological time-scale through its influence on population dynamics as well as on an evolutionary time-scale through its influence on optimal foraging strategies. Two assumptions are commonly made concerning the relationship between encounter rate and prey density. The first is that overall encounter rate is the sum of the encounter rates for individual prey items, and hence that encounter rate increases directly in proportion to prey density. This assumption is embodied in many classical models including the Lotka–Volterra predator–prey model (Lotka 1925) and the Nicholson–Bailey parasitoid–host model (Nicholson 1933) among population models, and the optimal diet model (Pyke *et al.* 1977; Stephens & Krebs 1986) among optimal foraging models. A second commonly made assumption is that encounter rate only depends on the current density of prey, and is unaffected by the proportion of prey already removed by

previous predators. This implicitly assumes that there is no heterogeneity in the likelihood of being found for individual prey items. We carried out an experiment on captive great tits foraging on different densities of winter moth caterpillars in their natural hiding positions on small apple trees to test whether these assumptions hold. We tested the first assumption by allowing individual great tits to forage on previously unexploited patches with an experimentally created range of prey densities. We tested the second assumption by allowing individual great tits to forage on patches that had previously been exploited by other great tits.

2. METHODS

We used 17 male and 14 female great tits (*Parus major*), housed individually in 0.9 m × 0.4 m × 0.5 m cages connected via sliding doors to one of two observation rooms (4.2 m × 2.5 m × 2.3 m). The birds were let in and out of the observation room without handling, and had access to various types of food and water in their cages (Verbeek *et al.* 1994) but no live insects were fed to them during the experimental period.

Winter moth (*Operophtera brumata* L.) caterpillars (larval stage L5, weight 63.2 mg (± 11.0 s.d.)) were placed in a Poisson distribution over groups of five 2-year-old potted apple trees (variety Jonagold) 1 day before these were used in the experiment. This allowed the larvae to build their natural shelters. Directly after the experiment, the trees were searched three times by different experimenters to check that the intended number of prey had been present during the experiment. If less caterpillars were found than was expected, it was assumed that they had been missing from the beginning of the test and densities were corrected in the analysis. Unexploited sets of five trees had densities of 2, 4, 8, 16 and 32 caterpillars. Depleted patches were created by allowing other individuals to forage successively on the same set of trees, each being allowed to remove up to four caterpillars. When a bird failed to find four caterpillars, additional caterpillars were removed either by a non-experimental bird (8.2% of removed caterpillars) or by the observers (16.6%). This design resulted in five current densities for unexploited patches and 11 combinations of current density and level of depletion for partially exploited patches.

Before the experiment, great tits were trained on four occasions on initial densities of 26, 30, 34 or 38 caterpillars offered in a random sequence. In the experiment we used a randomized Latin Square to determine the sequence in which the 16 tested combinations of current prey density and level of depletion (including previously unexploited patches) were offered to the different individuals. Each of the 31 great tits searched 15 out of the 16 different combinations; the last series of combinations could not be tested due to a lack of winter moths. In total 465 observations were made. The observation period started when the bird entered the room and ended when four caterpillars had been found (or one caterpillar at densities of two or four), a total period of 30 min had elapsed, or the bird had stopped searching for 30 s. ‘Search time’ was the time after the bird landed on the first tree until finding the first caterpillar minus the time spent on other activities. Date of testing, time of day, experience of the bird, observation room and observer (C.M.M.M., K.v.O. or L.M.A.W.) did not affect the recorded search time (all $p > 0.15$).

Search times were analysed using proportional hazard models (Kalbfleisch & Prentice 1980), which can incorporate censored data such as ours. We fitted the model $h(t) = h_0(t) \exp(\beta \ln(d))$, where $\ln(d)$ is the natural log of the prey density, β its coefficient, $h(t)$ the hazard at time t , and $h_0(t)$ the baseline function. The baseline function is time dependent and therefore accounts for, for example, birds not foraging for the first seconds at the start of a trial. We tested whether encounter rate (hazard) is proportional to density by testing whether β departs from 1 for the trials involving only unexploited patches. To test for the effect of the level of depletion on encounter rate we used observations from all trials and included the level of depletion [$1 - (\text{actual density}/\text{initial density})$] (which varies from 0 in unexploited patches to 0.875 in the most depleted patches used in the experiment) in the analysis.

3. RESULTS

When great tits searched on unexploited patches we found that encounter rate increased ($\chi^2_1 = 64.6$, $p < 0.0001$; table 1a; and hence search time for the first prey decreased; figure 1) with increasing prey density, but

Table 1. Proportional hazard model of the time to find the first prey (search time).

((a) A test as to whether encounter rate (hazard) is directly proportional to prey density (unexploited patches only). The observed coefficient of $\ln$ density, β (0.7807, s.e. = 0.1056) is significantly smaller than the predicted β of 1 ($t_{138} = 2.08$, $p < 0.04$). Encounter rate did not differ significantly between individuals ($\chi^2_{30} = 42.58$, $p = 0.06$) or sexes ($\chi^2_1 = 1.80$, $p = 0.18$), nor was there a significant interaction between $\log_e$ prey density and sex ($\chi^2_1 = 3.07$, $p = 0.08$). (b) A test as to whether search time is affected by the level of depletion [$1 - (\text{current density}/\text{initial density})$] (unexploited and partially depleted patches). Search time did not differ between individuals ($\chi^2_{30} = 37.29$, $p = 0.17$), nor were there significant interactions between $\ln$ prey density and sex ($\chi^2_1 = 2.40$, $p = 0.12$) or depletion and sex ($\chi^2_1 = 0.004$, $p = 0.96$).

variable	χ^2	d.f.	p	β (s.e.)
(a) unexploited patches ($n = 140$; 9 censored, 6.43%)				
$\ln$ (prey density)	64.6	1	< 0.0001	0.781 (0.106)
(b) unexploited and partially depleted patches ($n = 453$; 80 censored, 17.6%)				
$\ln$ (prey density)	104.3	1	< 0.001	0.891 (0.092)
depletion	5.1	1	0.024	-1.246 (0.545)
$\ln$ (prey density) $\times$ depletion	4.1	1	0.042	-0.490 (0.272)
sex	9.8	1	0.002	-0.337 (0.106)

Figure 1. Median time to find the first prey ('search time': Kaplan–Meier estimate with s.e.) in relation to prey density on previously unexploited patches. The solid line is calculated from the proportional hazard model with $\beta = 0.7807$ (see table 1a); the dashed line is the predicted line when search time is directly inversely proportional to prey density.

that this decrease was significantly less than directly proportional to density ($t_{138} = 2.08$, $p < 0.04$). When prey density is doubled, encounter rate increases only by 72% (not 100%). This causes the search time to be 58% ($1 \times 1.72^{-1} = 0.58$ instead of $1 \times 2^{-1} = 0.50$) of the search time at the original prey density. This is a reduction of 42% instead of the expected 50%.

When great tits foraged on both unexploited trees and trees where other great tits had previously removed prey (see § 2), we again find an effect of prey density ($\chi^2_1 = 104.3$, $p < 0.0001$), but also a very clear effect of the level of depletion (both as a main effect, $\chi^2_1 = 5.10$, $p = 0.024$, and in interaction with prey density, $\chi^2_1 = 4.13$, $p = 0.042$; table 1b). Encounter rate decreased, and hence search time increased, considerably with

increasing depletion levels (figure 2). Thus, when density decreases due to exploitation by other predators, encounter rate decreases much more than expected from the decrease in density alone. For example, the expected search time to find the first out of four caterpillars is almost five times higher when these are the survivors from an initial density of 32 than when they constitute the entire initial group of four prey. This effect of depletion is stronger at higher current prey densities (a significant interaction between depletion and prey density; table 1b).

4. DISCUSSION

We show clearly that encounter rate increases less than directly in proportion to prey density and decreases considerably with increasing levels of depletion. This latter effect has often been ignored and decreases in capture rate (assuming random search) within a patch have been attributed to decreases in prey abundance only (Cowie & Krebs 1979). We do not know why encounter rate does not increase as quickly as expected with prey density in our experiment. If there is competition between winter moth larvae for resting places where they are well hidden, we would expect the opposite effect. An increase in searching rate by the great tits at high prey densities would also produce the opposite effect, but in any case is not expected in our experimental results because we analysed only the search times for the first prey, when foraging great tits had no information about the current prey density. Our second finding, the effect of depletion on prey availability, has been addressed by Charnov *et al.* (1976) who gave three explanations. Prey may change their behaviour (behavioural depression) or their position (microhabitat depression) such that they become more difficult to encounter or capture, or the prey that is easiest to find are taken first because of heterogeneity in either the prey or environment. The prey items in our experiment were confined to their self-built shelters, so behavioural and microhabitat depression is unlikely. We therefore attribute the effect of previous exploitation in our experiment to heterogeneity in encounter rates, with the easiest prey to find being removed first, leading to a decrease in the average encounter rate of the individual remaining prey.

The effects that we found may have a profound effect

Figure 2. Median time to find the first prey ('search time'; Kaplan–Meier estimate with s.e.) in relation to the level of depletion for three current prey densities (dots, four prey; triangles, eight prey; squares, 16 prey) for (a) female and (b) male great tits. Lines are calculated from the proportional hazard model (see table 1b for covariates and their estimated coefficients).

on predator–prey interactions in natural environments, particularly because prey often have a clumped distribution, and exploitation is often initially concentrated in the high-density patches (Sutherland 1996). The effects found in our experiment can lead to a paradoxical situation in partly depleted environments, where patches with a relatively low current density, but little previous exploitation, may offer the best foraging opportunities. The reduced encounter rate in partially exploited patches will also effectively create refugia from predation. Some recent models of predator–prey interactions do take into account heterogeneity in encounter rates between prey (Anderson & May 1991; Sibly *et al.* 2002) but this is often limited to easily recognizable classes of prey such as age, size or sex. The fact that we have found effects of previous exploitation when both the prey size distribution and environment are more homogeneous than in most natural situations, and that we have found an unexplained departure from direct proportionality between encounter rate and the density of previously unexploited prey, warns us against uncritical acceptance of the plausible assumptions of classical predator–prey models, even in seemingly uniform environments.

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