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Spatial processes can determine the relationship between prey encounter rate and prey density

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Theoretical models frequently assume that the rate at which a searching predator encounters prey increases linearly with prey density. In a recent experiment using great tits searching for winter moth caterpillars, the time to find the first prey item did not decline as quickly with density as the standard theory assumes. Using a spatial simulation model, we show that prey aggregation and/or spatially correlated searching behaviour by the predator can generate a range of relationships, including results that are qualitatively similar to those found in the great tit experiment. We suggest that further experiments are required to determine whether the explanation proposed here is correct, and that theoretical work is needed to determine how this behaviour is likely to influence the ecological and evolutionary dynamics of predator–prey communities.

1. INTRODUCTION

A recent paper published in this journal (Mols *et al.* 2004) reported an intriguing result. In an experimental study using captive great tits searching for winter moth caterpillars, Mols *et al.* (2004) found that the encounter rate (as measured by time to first encounter) did not increase with prey density as rapidly as theory predicts. The authors were unable to offer an explanation for their result. As Mols *et al.* (2004) suggest, the assumption that encounter rate increases directly in proportion to prey density is central to most predator–prey models including the Lotka–Volterra predator–prey model (Lotka 1925) and the Nicholson–Bailey host–parasitoid model (Nicholson 1933). Given the wide use of these models, Mols *et al.*'s (2004) experimental result merits further attention, both in terms of finding a satisfactory explanation and in identifying how robust the predictions of traditional models are to relaxing this core assumption. In this paper, we use a simple simulation model to investigate how time to first encounter depends upon the aggregation of prey and the spatial search strategy employed by the predator. We show that these spatial processes can substantially modify the relationship between prey density and encounter rate, and suggest that they offer a plausible (and testable) explanation for the recent experimental results.

2. THE MODEL

We simulate the searching behaviour of predators that are introduced into a square arena (100 units by 100 units) in which prey are located. The arena is 'wrapped', forming a torus. The prey can be located independently of one another, or can be spatially aggregated. Similarly, the predator may move completely at random as it hunts for prey, or the search may be spatially correlated. We use this framework to establish how the time taken for a predator to encounter its first prey depends upon the number of prey, the aggregation of the prey and the spatial search strategy employed by the predator.

(a) Simulated prey distributions

We use a simple method to generate spatially explicit patterns of prey distributions. The first prey item is placed at a random location within the arena. With probability z, the next prey item is similarly placed at a random location anywhere within the arena, but with probability $1-z$, it is placed at random within a circle of radius r of the previous item. This process is repeated, with each prey item placed close to the previous one with probability $1-z$ until all the prey have been assigned locations. There is no limit to the number of prey items that can occupy the same location. In this paper we only consider results for $r=5.0$, but qualitatively similar results emerge for other relatively low values of r. Figure 1 illustrates the prey distributions that this process simulates, showing different degrees of spatial aggregation.

(b) Simulated search strategies

Once all the prey have been distributed around the arena, a predator is introduced. In the first time-step, the predator is placed at random anywhere within the arena. The predator searches a circle of radius p centred on its position (for all the results shown in this paper $p=5$) and locates prey items within the circle with 100% efficiency. If the predator fails to find a prey item it moves to a new location and searches again. When the predator moves, it does so in a random direction and travels a distance that is determined by drawing a number at random from a continuous uniform distribution between 0 and y. The lower the value of y, the more spatially autocorrelated the search strategy. We also investigate a global search strategy where the predator moves with equal likelihood to any location in the arena. We count the number of moves that it takes the predator to locate its first prey item.

(c) The simulation experiment

We have implemented the model 1000 times for each of 96 different parameter sets, comprising all possible combinations of four different degrees of prey aggregation (including no aggregation), four different predator search strategies (including no spatial autocorrelation) and six prey densities. The effects of prey aggregation, search strategy and prey density, and their interactions on mean time to encounter the first prey within the experiment, were examined by fitting the data to a general linear model (with time and prey density log-transformed).
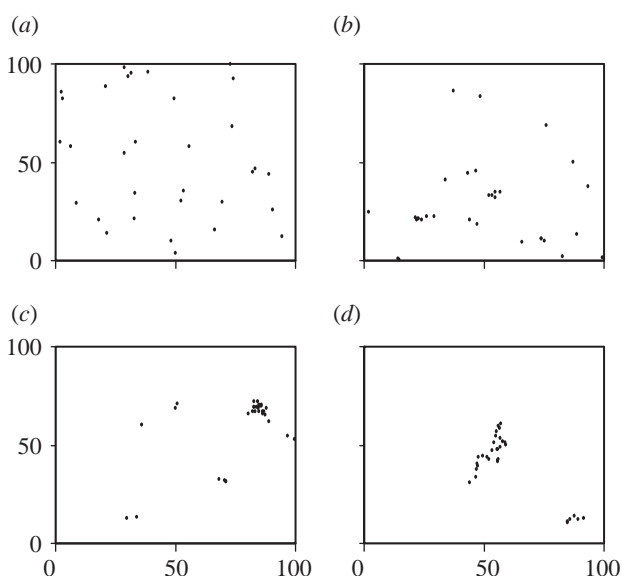
(a)

(b)

(c)

(d)

Figure 1. Example prey distributions with differing levels of aggregation. In (a) $z = 1.0$ (there is no aggregation), in (b) $z = 0.6$, in (c) $z = 0.2$ and in (d) $z = 0.05$. In all cases there are 32 prey on the arena.

3. RESULTS AND DISCUSSION

Both prey aggregation and the search strategy employed by the predator influenced how long it takes a predator to find an item of prey (figure 2). The more aggregated the prey and the more spatially correlated the search pattern of the predator, the longer it took for a first prey item to be located ($F_{3,76} = 507$, $p < 0.001$ and $F_{3,76} = 788$, $p < 0.001$, respectively). There was also a significant interaction between the two ($F_{9,76} = 11$, $p < 0.001$), which acted to amplify the effects of aggregation as the search pattern of the predator became more correlated. These results make intuitive sense. Imagine a situation in which eight larvae are highly aggregated, such that all eight individuals form one relatively small cluster. On average, it will take a predator searching at random locations around the arena far longer to encounter this cluster than it would take it to locate one of eight more widely dispersed individuals (Turner & Pitcher 1986; Krause & Ruxton 2002). This effect is more pronounced for a predator employing a correlated search strategy: a long period of time could be spent in thoroughly searching entirely the wrong section of the arena.

Mols *et al.* (2004) expected that as prey density was doubled, encounter rate would increase by 100%. For great tits searching for winter moth larvae they observed a 72% increase in encounter rate for a doubling of prey density, rather than the 100% that they had predicted. Table 1 presents some results from our simulations that suggest that the rate of increase in encounter rate with prey density is very sensitive to prey aggregation and predator search strategy, and also that it is highly dependent upon prey abundance. For example, when $z = 0.1$ and $y = 10$, a doubling of prey density from 4 to 8 increases the encounter rate by only 25%, whereas doubling the density from 32 to 64 results in a 104% increase. This can be explained by considering how the distribution of prey changes
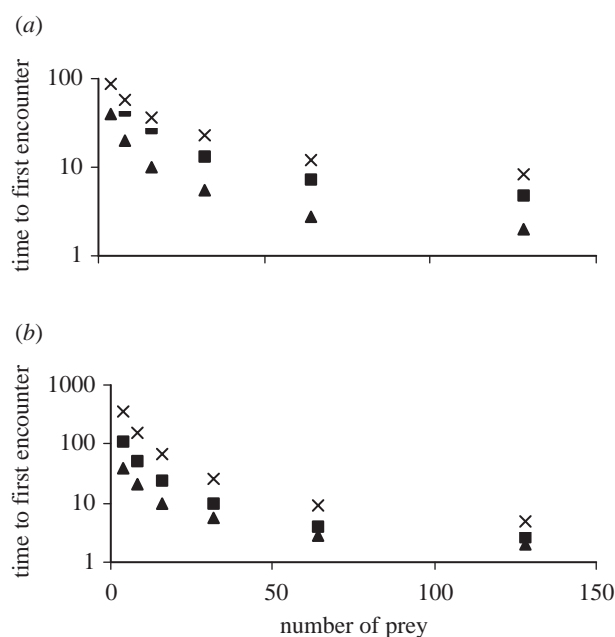
(a)

(b)

Figure 2. Prey aggregation and spatially correlated predator search both increase the time to first prey encounter. (a) The effect of prey aggregation. Triangles depict results for no aggregation ($z = 1.0$), squares for moderate aggregation ($z = 0.2$) and crosses for high aggregation ($z = 0.05$). Here, predator search is not spatially correlated. (b) The effect of predator search strategy. Triangles show the results for no spatial correlation in searching behaviour, squares for moderate correlation ($y = 10$) and crosses for high correlation ($y = 5$). Here, prey are not aggregated.

with density. Doubling the density from 4 to 8 will frequently not result in the formation of any new (spatially distinct) prey clusters, whereas increasing the density from 32 to 64 is likely to result in the formation of several new clusters in different parts of the arena. This effect is felt most sharply by predators whose search strategy is spatially correlated, as they can spend a considerable length of time foraging in one area of the arena when a small number of prey clusters might all be located in quite different areas. The spatial scales over which the prey aggregate and at which the predator performs its search (both held constant at 5 units in our simulation) may also be important determinants of the dynamics of the system.

In this paper, we have used a simple model to demonstrate that the relationship between encounter rate and prey density can be considerably more complex than is frequently assumed. Our results suggest that prey aggregation may be responsible for the relationship observed by Mols *et al.* (2004). Their data record the time to first prey encounter of great tits searching an aviary for winter moth caterpillars, while our data record the time it takes for a hypothetical predator to locate the first hypothetical prey item in an imaginary arena. We have not attempted to simulate the specific experimental system studied by Mols *et al.* (2004), but to do so would be an interesting extension. There are at least two important differences between our general model and the experimental system designed by Mols *et al.* (2004). First, caterpillars were distributed across five apple trees in the experimental system, whereas in our model we have one area of

Table 1. Results of simulations indicating that the rate of increase in encounter rate with prey density is very sensitive to prey aggregation and predator search strategy.
(The impact of doubling prey density on encounter rate depends upon the degree of aggregation, search strategy and prey abundance. The values presented are percentage increases in encounter rate. These results clearly show that encounter rate is not a linear function of prey density. gl. indicates that the predator is employing a global search strategy.)

doubling prey density (from–to)	$z=0.1$, $y=$gl.	$z=1.0$, $y=20$	$z=1.0$, $y=5$	$z=0.1$, $y=10$	$z=0.05$, $y=5$
4–8	49.1	100.4	126.2	25.3	34.5
8–16	84.5	100.8	137.3	52.92	31.1
16–32	80.3	134.6	165.1	91.8	63.0
32–64	94.4	137.5	215.9	104.1	83.7
64–128	76.3	109.4	106.6	81.8	101.7

uniform space in which prey are located. Simulating the experimental system would require a model that included both the arrangement of prey on each tree and the location of the trees relative to one another. Second, edge effects (avoided in our model by modelling the arena as a torus) may in reality be important both for the spatial distribution of prey and for predator foraging behaviour. It would be informative for future studies to combine experimental work that collected data on the spatial pattern of prey distribution (at a finer spatial scale than in Mols *et al.* 2004) and the spatial search strategy of the predators with models fitted to the observational data. Epidemiological modellers have perhaps made further headway in developing techniques that allow spatial population models to be fitted to observational data (see McCallum *et al.* (2001) and references therein) and exploiting some of these approaches might prove fruitful.

A further interesting extension, both within an experimental setting and within the model framework, would be to investigate how time to subsequent encounters depends upon the prey density. For example, how long does it take a predator to locate 4, 8 or 16 prey for varying total prey densities? Within the model, we could see how this depends upon the distribution of prey and the search strategy of the predator. Another interesting area for further work would be to consider how the optimal search strategy depends upon the spatial aggregation of the prey, and how optimal prey distribution (in terms of aggregation behaviour) depends upon the searching behaviour of the predator. Interesting coevolutionary dynamics involving predator and prey behaviour are possible. A further novel extension would be to combine these ideas with those presented by Ruxton (2005), who suggests that when a predator moves into a new area it may spend time determining whether it is itself safe from predators, and generally familiarizing itself with the new environment. It would seem likely that a search strategy that involved longer-distance moves might incur a greater cost in terms of vigilance time, as more often an individual will be moving into an area that it has not recently

experienced. This would lead to a situation in which the optimal search strategy of a predator would depend upon a combination of the spatial distribution of its prey and on the distribution and movement of its own predator species. Recent work at the interface of physics and biology has been exploring the dynamics of interacting many-particle systems (e.g. Bartumeus *et al.* 2002), and reaction–diffusion modelling of two-species systems (e.g. Viswanathan *et al.* 1999; Fulco *et al.* 2001) offers an attractive framework for further theoretical work.

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