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Consumer–resource matching in a food chain when both predators and prey are free to move

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The classical theory of the ideal free distribution (IFD) predicts that the spatial distribution of consumers should follow the distribution of the resources they depend on. Here, we study consumer–resource matching in a community context. Our model for the community is a food chain with three levels. We study whether the primary consumers are able to match resources both under predation risk and in its absence. Both prey and predators have varying degrees of knowledge of the global and local resource distribution. We present two versions of the model. In the "resource maximising" model, the consumers consider the availability of their resource only. In the "balancing" model, individual consumers minimise predation risk per unit of resource that they can gain access to. We show that both models can lead to perfect matching of consumers on resources and predators on consumers, assuming that individuals have full knowledge of the whole environment. However, when the consumers' information and freedom of movement are greater than those of the predators, then the predators generally undermatch the consumers. In the opposite case, we observe overmatching and high consumer movement rates. Furthermore, undermatching of predators on consumers tends to induce overmatching of consumers on resources.

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The idea that the distribution of consumers should roughly match the distribution of their resources is an intuitive and widely held concept in ecology. The ideal free distribution (IFD, Fretwell and Lucas 1970, Fretwell 1972) provides the theoretical framework that underpins this concept; in simplest terms it predicts that areas with more resources should contain more consumers. The generality and widespread acceptance of this theory is reflected in the many papers and books that provide empirical support for it (reviewed by Tregenza 1995). However, some of these empirical studies have brought to light several repeatedly observed deviations from the basic theory. In each case, ecologists have offered modifications to the classical theory that attempt to explain the observed departures from the IFD. Three of these non-mutually-exclusive problems are of direct interest to us here.

First, in many cases, more consumers are found on the poorer patches than is predicted by IFD, a phenomenon termed "undermatching" (Abrahams 1989, Grand and Grant 1994a, 1994b, Gray and Kennedy 1994). Possible explanations include limited knowledge of the environment (Abrahams 1986, Kennedy and Gray 1993, Ranta et al. 1999), competitive asymmetries among individuals

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(Sutherland 1996), restricted movement or dispersal between patches, habitats or other landscape elements (Åström 1994) and population dynamical effects (Schwinning and Rosenzweig 1990, Kacelnik et al. 1992, Fryxell and Lundberg 1997, Ranta and Kaitala 2000).

Second, many experiments have reported continued movement of individuals between patches after an equilibrium state has been achieved (Milinski 1984, Abrahams 1989, Grand and Grant 1994a, b). The existence and strength of such movements cannot be effectively explained using the classical model in its simplest form; the underlying movements are not considered by it. Superficially, continued movements about an equilibrium point appear to have no great importance in the application of the IFD. However, Hugie and Grand (1998, 2003) and Ruxton and Humphries (1999, 2003) have recently shown that consideration of propensities to move for other non-IFD reasons such as sampling error or predator sightings can have a profound effect on the outcome of an IFD system.

Third, the very basic idea that resources and consumers should even be expected to match under biologically realistic circumstances has recently been questioned (Ranta et al. 1999, 2000). This latter problem has received comparatively little attention.

The mismatch between IFD theory and empirical observations may be that the theory considers a very simple trophic arrangement, whereas most populations are embedded in food webs of greater or lesser complexity. We have generated a dynamic model that considers a simple but biologically realistic linear food chain with three levels. The primary producers (e.g. plants) are fixed and cannot move between patches. Primary consumers (e.g. herbivores) are free to move between patches both to maximise their intake rates of the primary producers and in another version to simultaneously minimise their risk of predation from the secondary consumers. For further consideration of the foraging–predation trade-off, see Grand (2002), Krivan and Sirot (2002), and Krivan (2003). The secondary consumers (e.g. predators) are similarly free to move in order to maximise their intake rates of the primary consumers. Furthermore we independently vary the primary and secondary consumer's knowledge of the global and local resource distribution. Specifically we are interested in varying the extent of the system that they can draw information about intake rates from, and how spatial structure of the primary producers affects the distribution of both predators and consumers. Berec and Krivan (2000), provide an analytical solution to optimal foraging theory that includes consideration of partial preferences and limited perception. We examine this novel approach to the IFD in the context of the problems outlined above.

Model description

We consider three species forming a simple linear food chain: resources (R) are preyed upon by consumers (C), which are themselves prey for predators (P). These three species exist in an environment consisting of a ring of L identical discrete habitats, which we will call patches. At the start of a simulation, the resource level on each patch is drawn independently from a uniform distribution between zero and one. These original resource levels persist unchanged throughout the simulation. In contrast, we allow consumers and predators to move between patches. Hence, although the total numbers of consumers and predators in the whole system remains constant, their distributions across the environment can vary over time. At the start of a simulation, individuals of both types are each independently assigned to one of the habitat patches at random, with all patches having equal probability of selection. The simulation then consists of a fixed number of movement events or updating rounds.

The system works as follows. Predators quantify the suitability of their current situation by dividing the number of consumers on their current patch (c_i) by the number of predators (p_i). They estimate the consequences of moving by calculating the simple mean of the uptake rate of all individuals in their current patch and in all the patches up to some constant number of positions (w_p) either side of the current patch. If this mean (μ) is greater than c_i/p_i, then the individual will move with probability

$$\frac{\mu - \frac{c_i}{p_i}}{\mu}$$

Thus, the greater the disparity between their current situation and how others nearby are doing, the more likely an individual is to move. Because 'fitness' is calculated as a proportion of resources to consumers, the case of perfect matching to resources can be taken to be the null hypothesis (this occurs for the IFD equilibrium $p_i/p_j = c_i/c_j = r_i/r_j$ between all patches). Therefore, any departures from this outcome observed in our simulation results must arise due to the constraints we have introduced. If an individual moves, then its new patch is determined randomly from the subset of patches (including its current one) that it used to estimate the performance of others. Each of these patches is equally likely to be selected. Movement works in an analogous fashion for consumers, although we use another parameter w_c to describe the size of consumers' sampling window and use different measures of habitat suitability (below). One movement round consists of simultaneous evaluation of propensities for all individuals to move, across all patches followed by the appropriate

updating of local patch populations. This process is then repeated for the duration of each simulation.

We consider two versions of the model. In the "resource maximising" version, the consumers consider only the availability of resource for them: i.e. simply the local resource number divided by the local consumer number. In the "balancing" version, individuals try to minimise their risk of predation hazard (defined as local predator number divided by local consumer number) per unit of resource that they can gain access to (defined as local resource level divided by local consumer number). This simplifies to minimising local predator number divided by local resource level, which is equivalent to maximising local resource level divided by local predator number.

We measure the match between the distributions of two species by plotting the fraction of the total population of one species for each patch against the fraction of the other species. We then examine the gradient of the linear regression line through these points. A gradient of one indicates perfect IFD matching, less than one indicates undermatching, and greater than one, overmatching. We fit these regression lines using reduced major axis (Fowler and Cohen 1991). We report averages and standard deviations for 50 rounds after discarding transient behaviour in Fig. 2. The transient period was removed by examining the variation of the gradient across all patches in the consumer species. The temporal average of this measure for the last 50 movement rounds was recorded after every 100 movement rounds. If this value changed by less than 1% from one set of 50 rounds to the next, the program was stopped and results recorded.

It is important to remember that our model does not include the population dynamics of the resources or consumers. Our results are therefore descriptive of short-term or behavioural time-scales. Because no "deaths" occur in our model it is appropriate to consider our predators to be "risk predators" that are capable of mediating behavioural responses in the consumers. Bolker et al. (2003) provide a recent review of such responses in both real and theoretical situations.

Results

First, consider the case where the information and movement windows for both consumers and predators are identical and equal to the whole of the system. We wish to compare the two versions of the model. One would expect that the resource maximising model would lead to perfect matching of consumers on resources and predators on consumers, and this is what we find (Fig. 1). One would also expect perfect matching to be achieved in the balancing model. In this model, although consumers seek to maximise local resource level divided

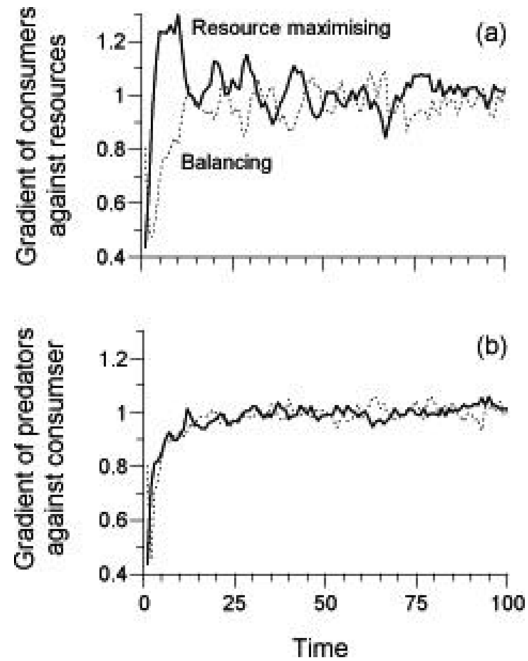

Fig. 1. Plots of the gradients as defined in the model description section (with standard deviations) against time for (a) consumers against resources and (b) predators against consumers for both the resource maximising and balancing models (note: includes the transient period). Parameter values: $C = 600$, $P = 600$, $L = 23$, $w_c = 11$, $w_p = 11$.

by predator number rather than consumer number, we would expect the predator population distribution to mimic that of the consumers, thus the two currencies for the consumers ought be equivalent. Indeed, we again find that the final equilibrium shows perfect matching (Fig. 1). Figure 1 also illustrates the perpetually dynamic nature of our model, with individuals moving after equilibrium has been achieved; i.e. the system does not settle down to a static, level line. Instead the system is tightly held within a narrow range of values, through which the populations move.

We now explore the consequences for the balancing model of decreasing the size of the information and movement windows for one or other species. That is, we wish to restrict the extent of the system that an individual possesses knowledge about. The effect of keeping the consumers' window large and reducing the predators' window on the resulting distribution is shown in Fig. 2a. For medium sized windows, predators are still able to track the consumer population effectively, and we see perfect matching. However, if the window is very much reduced, then because of their limited knowledge and mobility, during the transient phase, the predators generally undermatch the consumers. Thus, because high resource level patches have fewer predators than perfect matching to their consumer numbers would predict, this attracts more consumers to these patches, leading to overmatching of consumers on resources.

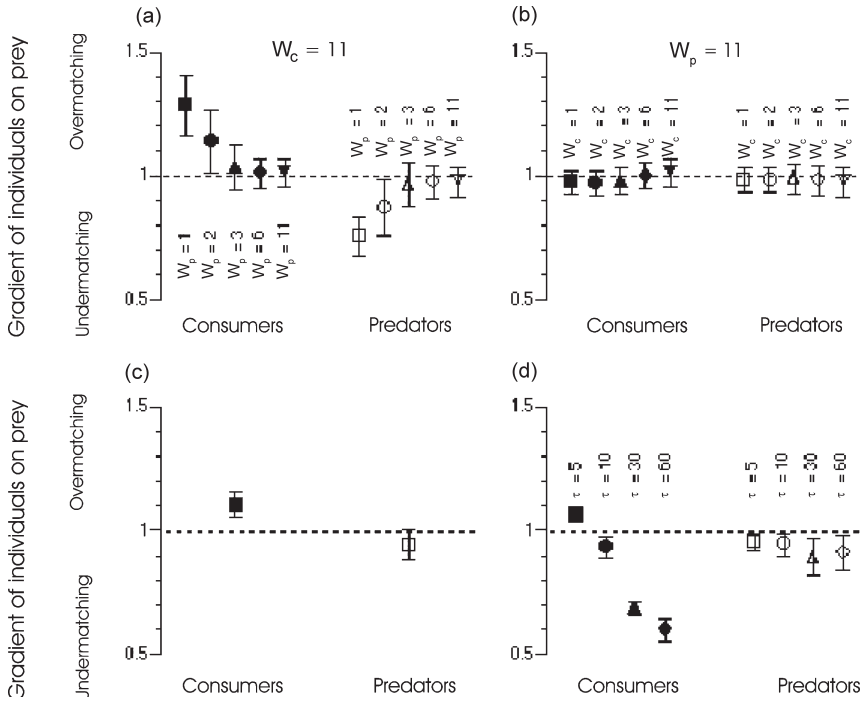

Fig. 2. Plots of the mean gradients (with standard deviations) of consumers against resources (solid symbols) and predators against consumers (open symbols) for (a) several values of w_p as given (parameter values: C = 600, P = 600, L = 23, $w_c = 11$) and (b) of w_c as given (C = 600, P = 600, L = 23, $w_p = 11$). Panel (c) gives the gradients of consumers against resources and predators against consumers for a very low value of w_c (C = 600, P = 600, L = 60, $w_p = 29$, $w_c = 1$). In panel (d) the consumer and predator gradients are given for four different spatially structured resource distribution (C = 600, P = 600, L = 60, $w_p = 29$, $w_c = 1$).

The reverse situation, where we have a large window for predators but a small one for consumers, leads to a rather different situation. The net result is very good matching even when the consumers' window is small (Fig. 2b). The actual dynamics of the system are that the consumers' lack of knowledge and mobility tends to lead to overmatching of resources, and high movement rates. These high movement rates make it difficult for predators to perfectly match consumers, even with their large window. This undermatching of predators on consumers tends to induce overmatching of consumers on resources. However, this is not always the case, and in extreme situations when the consumer's window is very small in comparison to that of the predator, we generally find overmatching of the consumers to resources and undermatching of predators to consumers (Fig. 2c).

The situations we have considered so far, where the resource levels on neighbouring patches are not correlated, is one where the ill-effects of a limited knowledge and mobility window are minimised. We now consider a situation where there is spatial structure in these resource levels. Specifically, we assume that resource levels across the system vary by setting the resource level in patch i to be

$$r_i = (1 + \sin(2\pi i/\tau))/2$$

for some positive constant τ. The larger τ the more gradually resource levels change in space. As we would expect, when τ is low, we recover the situation in Fig. 2c, with overmatching of consumers to resources and undermatching of predators to consumers (Fig. 2d). However, as τ increases, the limitations of the consumes' small window size become more and more pronounced, leading to stronger and stronger undermatching of consumers to resources.

Discussion

The system described by our model demonstrates the often observed characteristic that is a continuous movement of individuals, after an apparent equilibrium is achieved-as in the non-IFD models (Hugie and Grand 1998, 2003, Ruxton and Humphries 1999, 2003). This occurs in our trophic system as the predators chase the herbivores around the habitat. Although the overall effect is similar, our perpetual system is maintained by IFD movements only. Thus, consideration of non-IFD movements is not necessary to explain perpetual movements.

Our results confirm and extend the already known effects of limited knowledge about the resource environment on the distribution of consumers. If the consumers have poor estimates of the global resource distribution and/or limited possibilities to use that knowledge because their movement is restricted (e.g. the w_p parameter in our model), then the general consequence is undermatching. There is ample empirical evidence to support this conclusion (Abrahams 1986, Kennedy and Gray 1993, Tregenza 1995, Sutherland 1996) and strong theoretical reasons for it (Ranta et al. 1999 for a recent analysis), especially if one allows

for consumer-resource population dynamics (Bernstein et al. 1999). If the consumers possess full knowledge of the resource distribution and move freely, then the IFD (perfect matching) is also reached when population dynamics are permitted (Fryxell and Lundberg 1993, Krivan 1997, Bernstein et al. 1999). However, the consequences for population stability seem to depend strongly on assumptions about migration rules and how freely both consumers and their resources can move between patches. Fryxell and Lundberg (1993) showed that constrained consumer migration in a system with sedentary resources leads to population stability. In contrast, Bernstein et al. (1999) concluded that unconstrained mobility of both predators and prey results in both an IFD and stability. Furthermore, Krivan (1997) has shown that populations are persistent when both predators and prey (single populations of each) follow an IFD distribution in a two-patch system. Because our model does not consider population dynamics it is hard to make direct comparisons between these two approaches.

The system we have studied is much simpler, and hence more general and strategic, and does not include changes in global abundance of the populations. It is, however, richer in that the size of the information window varies between predators and prey, and it contrasts random and spatially auto-correlated resource distributions. We also allow the middle trophic level in the community to employ alternative fitness maximising rules (maximising resource acquisition only, or balancing resource intake and risk of predation). A wider range of possible outcomes emerges. Not only do we find undermatching, or, when the information windows are equal across trophic levels, perfect resource matching (IFD), but also overmatching. This means that poor patches are used less than expected and good ones more than expected. Hence, we can rather easily have situations when prey err (in relation to the IFD expectation of exact matching), but in opposite directions. Predators however tend to undermatch their resources, or follow them closely depending on their information and movement capabilities. Resource matching is thus contingent not only on the spatial structure of the environment and how well individuals can gain knowledge about it, but also on community structure.

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