



Quantitative tests of multitrophic ideal free distribution theory



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Ideal free distribution (IFD) theory is often used to explain small-scale spatial distributions of organisms. However, few studies have rigorously tested predictions of IFD models in situations involving multiple species and trophic levels. We fully parameterized and tested predictions of a general interference IFD model for both predators and prey in a tritrophic system: seven-spotted lady beetles (*Coccinella septempunctata* L., Coleoptera: Coccinellidae), pea aphids (*Acyrtosiphon pisum* (Harris), Hemiptera: Aphididae), and tic bean plants (*Vicia faba* L., Fabaceae). We used habitat selection treatments having both predators and prey in the presence and absence of one another. We also performed experiments to quantify the strength of interspecific competition, the functional response of predators and several measures of fitness for the prey. Our results show that whether prey were present or not, predators followed IFD predictions and aggregated most strongly in the patch with the highest-quality resource. Prey in the presence of predators followed the predicted IFD, which was similar to a uniform distribution. However, prey in the absence of predators moved infrequently and were far from ideal free, suggesting that predators instigated habitat selection behaviour. Our results underscore the importance of considering trophic interactions and multiple measures of patch quality in studies of habitat selection. The observed departures from theoretical predictions also usefully suggest promising extensions for future theory and experiments.

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All organisms live in environments that may have spatial variation in factors related to fitness. Accordingly, spatial distributions and habitat selection have a long history of theoretical and empirical study in many disciplines within organismal biology (reviewed in: Tregenza 1995; Lima 2002; Haugen et al. 2006; Krivan et al. 2008; Hammond et al. 2012). Nevertheless, traditionally the vast majority of these studies have focused on analysing how just one or two factors (considered in isolation) impact habitat selection, for example considering how resource quality and competition affect habitat selection by a single species of consumer (Lima 2002). This simplified approach is often utilized for pragmatic reasons: the consideration of additional factors (e.g. more species and their interactions) leads to substantially increased complexity of both theory and experiments. Not surprisingly, theory on simultaneous habitat selection by multiple species has outpaced thorough, quantitative testing.

The ideal free distribution (Fretwell & Lucas 1969; henceforth 'IFD') is frequently used as a theoretical springboard for studies of

habitat selection and small-scale spatial distributions (Ziv et al. 1993; Tregenza 1995; Tregenza et al. 1996a, b; Krivan et al. 2008). In a heterogeneous, patchy environment, an IFD is achieved when the average per capita fitness of consumers is equal across patches. Viewed another way, when a population reaches an IFD, the negative effects of competition between consumers in the same patch are balanced by the positive effects of resources in the patch. Thus, intuitively, at an IFD there will be more consumers in higher-quality patches and fewer consumers in lower-quality patches.

The quantitative relationship predicted between resource quality and consumer density depends upon how competition is modelled. Indeed, two main categories of IFD models have long been distinguished by how they treat competition (Sutherland & Parker 1985, 1992; Parker & Sutherland 1986; Kacelnik et al. 1992; Kennedy & Gray 1993). 'Continuous input' models (also known as 'immediate consumption' models) generally assume purely exploitative competition in a zero sum game. That is, if there are n consumers in a patch of quality R , the payoff to each consumer is simply R/n . Continuous input IFD models give rise to the well-known prediction of 'resource matching' (Milinski 1994). On the other hand, 'interference' IFD models do not assume exploitative competition (Vance 1984; for reviews, see: van der Meer & Ens 1997; Amarasekare 2002, 2003; Hart et al. 2012). Instead, these models can predict a wide variety of spatial distributions, depending upon the strength of competition (Folt & Goldman 1981) within each patch. In general, the degree of

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consumer aggregation in a heterogeneous environment is predicted to correlate positively with food availability and negatively with increasing interference (van der Meer & Ens 1997; more on this below).

Because continuous input models assume a particular form of competition, they are methodologically simpler to test than interference models (i.e. to test a continuous input model, one assumes competition rather than measuring it). Accordingly, quantitative tests of interference IFD models are relatively rare (Flaxman & de Roos 2007). When applied to only one species of consumer, IFD predictions are frequently supported, at least qualitatively. However, when additional variables, such as multispecies interactions, are added to IFD models, spatial distribution equilibria and simultaneous IFDs for all species are not necessarily predicted to exist (Cressman & Krivan 2006; Krivan et al. 2008).

Sih (1998) developed and explored theory treating simultaneous IFDs of mobile predators and mobile prey. His model incorporated (1) foraging success of both species, (2) the strengths of competition within species and (3) variation in the intrinsic qualities of patches (from the perspective of the prey). Sih's (1998) model is a straightforward multitrophic extension of single-species interference IFD models (Tregenza 1995). Indeed, the same or very similar functional forms used by Sih have appeared in a variety of predator–prey IFD models (Krivan 1997; Brown 1998; Heithaus 2001; Alonzo 2002; Morris 2003; Cressman et al. 2004; Jackson et al. 2004; Krivan & Schmitz 2004; see also van Baalen & Sabelis 1993; Rosenheim 2004; Sih 2005). Comparing these different IFD models reveals a prediction about spatial distributions common to most of them, which is frequently referred to as 'leapfrogging': predators should aggregate where prey's food source is of the highest quality, not necessarily where prey density is highest, whereas the prey are often predicted to be more evenly (uniformly) distributed than their predators or their food source (Lima & Dill 1990; Sih 2005; Hammond et al. 2007; Flaxman & Lou 2009). For clarity we note that, as used here, leapfrogging refers to a predicted spatial distribution of organisms, not a specific behaviour or mechanism of habitat selection.

While IFD models comprise some of the most widely applied and accepted models from theoretical ecology (Tregenza 1995; Earn & Johnstone 1997; Jackson et al. 2004), rigorous, empirical testing of them in multitrophic contexts is rare. Empirical testing of habitat selection theory and knowledge of behavioural mechanisms are both crucial for being able to predict responses of populations to changing habitats (Bowler & Benton 2005). To address this gap, a number of recent studies have begun empirically testing leapfrogging and other predictions of general IFD models in multispecies contexts (e.g. Hammond et al. 2007; Dupuch et al. 2009; Luttbeg et al. 2009; Hammond et al. 2012). However, frequently these studies omit experimental measurement of some of the models' parameters, such as quantification of (1) individual fitness across patches of multiple, different qualities, (2) the functional response of predators and (3) the strengths of intraspecific competition in all species involved. As noted above, the latter can have dramatic effects on the spatial distributions predicted by a model; quantitative measurements of competition strengths are thus essential for accurate and rigorous testing of IFD models. In other studies, predators have been restricted to a patch, commonly the highest-quality patch; this potentially creates a greater risk to the foraging prey in certain patches (e.g. Peacor & Werner 2004; Raffel et al. 2010), but prevents real-time, adaptive responses of predators and prey to one another from occurring (since only the prey can engage in active habitat selection; Lima 2002). Furthermore, frequently an inanimate resource of varying quantity but not quality is used (e.g. Hammond et al. 2007; Dupuch et al. 2009). Changing resource amount per se can have very different effects than changing resource quality or density (Flaxman & de Roos 2007).

Our research quantifies all the parameters necessary to test a multitrophic ideal free distribution model with mobile predators, mobile prey, and interference competition within species. Specifically, we parameterize and test the predictions of Sih's (1998) model (which, as noted above, is one general version of a large number of mathematically similar models). After doing so, we also examine potential reasons for departures from the predicted spatial distributions and their importance in predator and prey habitat selection.

THE MODELS

In the basic interference IFD model (see Parker & Sutherland 1986), per capita resource gain in patch i is modelled as

$$W_i = R_i/N_i^x \quad (1)$$

where R_i is the quality of patch i for a consumer in the absence of competition, N_i is the number of consumers in patch i , and x is the coefficient of interference, a measure of the degree of competition between consumers (Hassell & Varley 1969; Sutherland 1983; Tregenza et al. 1996a). (Note: we use 'numbers' of prey and predators rather than 'densities' under the assumption that all patches are the same size. This assumption was indeed met by our experiments.) Small values of the coefficient of interference ($0 < x < 1$) indicate weak to moderate competition, whereas values less than zero indicate Allee effects, and values greater than one indicate harsh competition between individuals. By definition, an IFD is achieved when payoffs are equal across patches, in other words when $W_a = W_b$ for any two patches a and b . From equation (1), the latter will be satisfied when the ratio of consumers in any two patches is such that

$$N_a/N_b = (R_a/R_b)^{1/x} \quad (2)$$

Equation (2) gives the predicted distribution of a single species of consumer feeding on an immobile resource. This is the source of our predictions about prey in treatments below involving only prey and resources (in the absence of predators). We also created a treatment involving predators and resources in the absence of prey. The quality of a patch with no prey (i.e. nothing for predators to consume) is zero to a predator. However, previous experiments showed that predators in the absence of prey were able to detect and respond to the quality of the prey's resource (although the mechanism for this response is not yet clear; Williams & Flaxman 2012). Hence, in treatments without prey, we tested observed predator distributions against two different predictions. First, using the measurement of patch quality from the perspective of the prey, we solved for predicted predator spatial distributions using the single-species IFD model. The rationale here is that, even in the absence of prey, predators should aggregate more strongly to patches that prey find more profitable since, in natural settings, higher-quality patches should be more likely to recruit prey (Flaxman & Lou 2009; Williams & Flaxman 2012). Thus, in the absence of prey, the distribution of adaptively behaving predators that assess the quality of the prey's resource might be expected to follow

$$P_a/P_b = (R_a/R_b)^{1/m} \quad (3)$$

for any two patches, a and b . In equation (3), P_i is the number of predators in patch i , and m is the coefficient of interference for predators. Alternatively, in the absence of prey, predators might be expected to be uniformly distributed ($P_a/P_b = 1$).

Finally, we also conducted experiments in which predators and prey were both present and simultaneously selecting among

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