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Asymmetric competition, body size, and foraging tactics: testing the ideal free distribution in two competing fish species

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ABSTRACT

Question: Do habitat preferences of two competing fish species correspond to the two-species ideal free distribution (IFD)?

Prediction: Consumer distributions across habitats will match the distribution of resource supply rates.

Organisms: A mixture of white cloud mountain minnow *Tanichthys albonubes* and giant danio *Danio aequipinnatus*. The choice of allopatric species avoids confounding the factors of common evolutionary history and can reveal competition patterns that follow biological invasions.

Methods: Record habitat preferences of the two competing fish species in an aquarium with two feeding sites. Develop the two-species IFD model and compare the data to its predictions.

Results: In the presence of conspecifics alone, individuals of each species conform to Parker's matching rule, distributing themselves according to the ratio of the food supply rates. When both species are present, the minnow distribution still follows the matching rule but the danio selects the feeding site with the lower food supply rate disproportionately more often than when it is alone. Hence, while intraspecific competition does not affect feeding site preferences in either of the species, interspecific competition between minnows and danios is asymmetric; the minnow is the dominant competitor. We trace the asymmetry to species-specific foraging tactics. Minnows stay much closer to a feeding site and reach food items twice as quickly as danios. Our model, based solely on exploitative competition, does not fit these observations. Instead, interference between species appears to drive the asymmetric competition and make Parker's matching rule generalized to a two-species environment inadequate.

Keywords: allopatric species, asymmetric competition, body size, habitat preference, ideal free distribution, interference.

INTRODUCTION

Interspecific competition for a limiting resource is a common phenomenon in nature. It can affect diverse population-level characteristics such as patterns of habitat selection

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(Křivan and Sirot, 2002; Salewski *et al.*, 2003; Cressman *et al.*, 2004; Young, 2004), geographic distribution (Thulin, 2003), activity (Agostinho, 2003), and niche overlap (Young, 2004; Friggens and Brown, 2005), among others.

The ideal free distribution [IFD (Fretwell and Lucas, 1970)] is a theoretical construct that describes the distribution of a single species in a patchy environment, assuming omniscient adaptive animals that move freely and instantaneously between patches. Maximizing their feeding rates, these 'ideal free' animals distribute such that no single individual can unilaterally increase its fitness by changing its habitat selection strategy. Assuming animals consume resources immediately upon supply (a way of invoking a fierce competition for a limiting resource), Parker (1978) derived the 'matching rule'. It states that the consumer distribution across patches 'matches' the distribution of resource supply rates. This prediction, despite somewhat idealized model assumptions, passed an experimental scrutiny (for a critical review, see Kennedy and Gray, 1993). The IFD concept now applies also to situations where resources undergo population dynamics (Lessells, 1995; Křivan, 2003), thus covering a complex feedback between consumer preferences and resource population dynamics: consumer preferences influence resource dynamics, which, in turn, affect consumer preferences.

Most work on the IFD has concerned a single species. The concept has also been extended to two-species environments (Lawlor and Maynard Smith, 1976; Brown, 1990, 1998; Possingham, 1992; Grand and Dill, 1999; Grand, 2002; Guthrie and Moorhead, 2002; Křivan and Sirot, 2002). This is by no means a straightforward task, as it requires the definition of evolutionary stability for two or more species (Cressman *et al.*, 2004). The two-species IFD is usually visualized through isolegs, the lines separating regions in the two-dimensional consumer phase space in which they show qualitatively different feeding preferences (Rosenzweig, 1979, 1981, 1991). Křivan and Sirot (2002) and Cressman *et al.* (2004) listed a catalogue of isolegs for two species that either compete for a common resource or are in a predator–prey relationship.

Despite this extensive theoretical research, empirical studies exploring simultaneous habitat selection by two or more competing species are scarce (Pimm *et al.*, 1985; Abramsky *et al.*, 1990; Young, 2004). As resources were not under control in these studies, their population dynamics are not known and, in particular, Parker's assumption on immediate resource consumption does not apply. The currently available observational evidence on two-species habitat selection thus disables any direct comparison with existing model predictions.

In this article, we generalize Parker's matching rule to a two-species environment and test predictions of the extended model against data collected from a competition experiment on two allopatric fish species, white cloud mountain minnow *Tanichthys albonubes* and giant danio *Danio aequipinnatus*. We also discuss to what extent species-specific behavioural patterns (i.e. foraging tactics) affect competition outcomes and potential differences between data and theory.

METHODS

Study species and experimental design

Whereas minnows occur naturally in China and Vietnam and reach an adult average length of 4 cm, danios inhabit Sri Lankan waters and grow to 10 cm in length. Although sympatric species with a common and long evolutionary history have standardly been used in interspecific competition studies (Abramsky *et al.*, 1990; Young, 2004), we believe using geographically isolated species might be an advantage for a number of reasons (see Discussion).

Our experimental design is analogous to that of the classic experiment carried out by Milinski (1979), using sticklebacks to test for the single-species IFD, and the conceptual framework discussed by Milinski (1988). We deposited 25 individuals of each fish species in a 120-litre tank equipped with a foam filter and plants. Every day, we switched the light (two fluorescent 60-W tubes) on at 07.00 h and off at 19.00 h. In this tank, we fed fish (flake food) once a day, about one hour after the end of each test. Habitat selection trials took place in a 70-litre tank (60 cm long, 27 cm wide, 40 cm high) equipped with a foam filter and one fluorescent tube (60 W). To minimize disturbance by the observer, we covered the lateral and rear sides of the tank with black polyethylene.

Before the start of each test (09.00 h), we switched the filter off and light on. Also, we transferred a selected number of individuals of each species from the repository tank to the experimental tank and placed two individuals of defrosted *Daphnia* sp. of roughly equal size into each of 90 small plastic caps (about 2.5 ml). Following a 30 min habituation period, we switched on a digital camera (JVC GR-D70) and dropped the food into the tank at a constant frequency, one cap every 4 s (altogether 60 caps) on a randomly selected side of the tank and one cap every 8 s (altogether 30 caps) on the other side. During these foraging bouts, fish did not show any signs of satiation. Using all caps, we returned fish to the repository tank.

The whole experiment consisted of 16 trials with different combinations of fish numbers in each trial (3, 6, 9, and 12 minnows combined with 3, 6, 9, and 12 danio individuals). We thus adopted a fully factorial response surface design (Inouye, 2001). Each trial consisted of five replicates. The sequence of trials was randomized, and all five replicates were conducted in one block. To test for the single-species IFD, we also conducted additional trials with each fish species alone (3, 6, 9, and 12 individuals).

We processed the video-recordings as follows. Two seconds after we offered the first cap with food and then every 4 s after that (that is, in the middle of the two consecutive offerings of the food in the more rewarding habitat), we recorded fish numbers in each half of the experimental tank.

To get an insight into potential differences in foraging tactics between the two fish species, we conducted an additional set of trials in which we used only one fish, either alone (single-fish trial) or with six individuals of the other species (supplemented-fish trial), in each replicate. In these trials, we measured two characteristics. First, we measured the time the focal fish needed to catch the (first) food item after the caps with two *Daphnia* individuals were provided simultaneously from both sides of the tank (now at equal frequency of one cap every 4 s). Second, we measured the reaction distance of the fish (i.e. the distance at which the fish clearly responded to a food supply) from the feeding site it took the (first) food item from. We replicated these trials five times with individuals of each fish species (different individuals and 30 feeding bouts in each replicate).

Models

Here we re-derive Parker's single-species matching rule and then generalize it to a two-species environment. Predictions of these models will serve as null hypotheses against which we can test our empirical observations.

The single-species IFD

Let the two habitats 1 and 2 have resource densities R_1 and R_2 respectively, and assume that these resources enter the habitats at fixed rates r_1 and r_2 respectively. Let the overall consumer density be C and consumers be allowed to move freely between the habitats with negligible travel time spent in between. If the habitats differ only in the resource supply rate, resource densities change as follows:

$$\begin{aligned}\frac{\mathrm{d}R_1}{\mathrm{d}t} &= r_1 - \lambda R_1 u_1 C \\ \frac{\mathrm{d}R_2}{\mathrm{d}t} &= r_2 - \lambda R_2 u_2 C\end{aligned} \tag{1}$$

Here, u_i is the proportion of consumers currently in habitat i and λ is the habitat- and consumer-density-independent cropping rate. At the individual level, u_i describes the preference of a consumer for habitat i, given as the probability of actually being in this habitat, or the fraction of time the consumer spends in it. For adaptive consumers, u_i changes as resources vary. Since the travel time between habitats is assumed to be negligible, $u_1 + u_2 = 1$.

The optimal habitat selection strategy maximizing the per capita food intake rate is as follows. If one resource is more abundant than the other, all individuals should remain in the habitat with larger R_i. As a consequence, the resource level in the other habitat increases (linearly) until resources in both habitats equalize. Assuming that the resource supply rate in habitat 1 is higher than in habitat 2 ($r_1 > r_2$), Appendix 1 shows that resource densities equalize at $R_1 = R_2 = (r_1 + r_2)/(\lambda C)$ and the proportion of consumers in habitat $i(= 1,2)$ at this equilibrium is

$$u_i = r_i/(r_1 + r_2) \tag{2}$$

This implies Parker's matching rule: $u_1/u_2 = r_1/r_2$.

The IFD for two competing species

Now we extend the previous analysis to the case of two competing consumer species. Their overall densities are denoted by M (for minnows) and D (for danios). In a two-species environment, model (1) becomes

$$\begin{aligned}\frac{\mathrm{d}R_1}{\mathrm{d}t} &= r_1 - \lambda_M R_1 u_1 M - \lambda_D R_1 v_1 D \\ \frac{\mathrm{d}R_2}{\mathrm{d}t} &= r_2 - \lambda_M R_2 u_2 M - \lambda_D R_2 v_2 D\end{aligned} \tag{3}$$

where λ_M and λ_D are habitat- and consumer-density-independent resource cropping rates. Controls u_i and v_i ($i = 1, 2$, $u_1 + u_2 = v_1 + v_2 = 1$) describe preferences of species M and D for habitat i, respectively. Hence, this model assumes that competition for resources is only exploitative – that is, the two species interact only through the shared resource. By sharing one resource, each species decreases the level of this resource, which decreases the resource intake rate of the other species.

Simultaneous maximization of the species-specific, per capita food intake rates ($\lambda_M R_1 u_1 + \lambda_M R_2 u_2$ for species M and $\lambda_D R_1 v_1 + \lambda_D R_2 v_2$ for species D) predicts that, analogously to the single-species case, individuals of both species should remain in habitat 1 if $R_1 > R_2$ or in habitat 2 if the opposite inequality holds. These rules likewise cause resources in both habitats to equalize, with the resource equilibrium (Appendix 2)

$R_1 = R_2 = (r_1 + r_2)/(\lambda_M M + \lambda_D D)$. The distribution of the two species at this equilibrium satisfies

$$\left(u_1 - \frac{r_1}{r_1 + r_2}\right) M\lambda_M + \left(v_1 - \frac{r_1}{r_1 + r_2}\right) D\lambda_D = 0 \tag{4}$$

This formula generalizes Parker's single-species matching rule to a two-species environment. Indeed, for M or D equal to 0, we get the single-species IFD (2). When together, the distribution of either species can deviate from its single-species IFD. Yet, an increase of one species in a patch above its single-species distribution must be balanced by a proportional decrease of the second species in the same patch so that equation (4) holds. Contrary to the single-species case, however, formula (4) does not allow us to compute the two-species IFD uniquely. Instead, any combination of u_1 and v_1 that satisfies (4) defines the distribution through which individuals of each species maximize their per capita food intake rate. Indeed, the four scenarios sketched in Milinski (1988) of how six 'large' and six 'small' individuals may distribute themselves over two feeding sites with a 2:1 food supply rate accrue from (4) as a special case, assuming $D = M$ and $\lambda_D = 2\lambda_M$.

Statistical analyses

For the statistical analyses, we used only data collected in the second half of each replicate, as the distribution of both fish species had settled by then and remained steady after that (see also Milinski, 1979; Grand, 1997). We conducted all statistical calculations in Statistica 6.0 (StatSoft, Inc. 2000).

We tested for the effects of intra- and interspecific competition on feeding decisions (habitat selection) in fish using a two-step procedure. First, we used analysis of variance (ANOVA) to test for uniformity of individual habitat preferences across appropriate experimental trials (i.e. different combinations of minnow and danio numbers in two-species trials and different combinations of numbers of the focal species in single-species trials).

The second step consisted of pooling the data we used in the first step whenever species habitat preferences did not differ across the trials, and testing a deviation of the mean of the pooled data from the theoretically predicted single-species IFD using the two-tailed Student's *t*-test. When the species distribution differed across trials, we used multiple regression to assess potential trends in individual habitat preferences, with minnow number, danio number, and their product as independent variables.

Finally, we used nested ANOVA to compare differences between individuals, species, and trials in the time to catch the food item and in the reaction distance from the feeding patch the food item was taken from. We also tested for a correlation between these two quantities.

RESULTS

Habitat preferences

When alone, each species demonstrated uniform habitat preferences, irrespective of the number of conspecifics (minnow: $F_{3,16} = 0.081$, $P = 0.97$; danio: $F_{3,16} = 1$, $P = 0.42$; Fig. 1). Given the actual food supply rates $r_1 = 0.5$ and $r_2 = 0.25$ items per second, Parker's matching rule (2) predicts distribution of fish between feeding sites 1 and 2 in a 2:1 ratio.

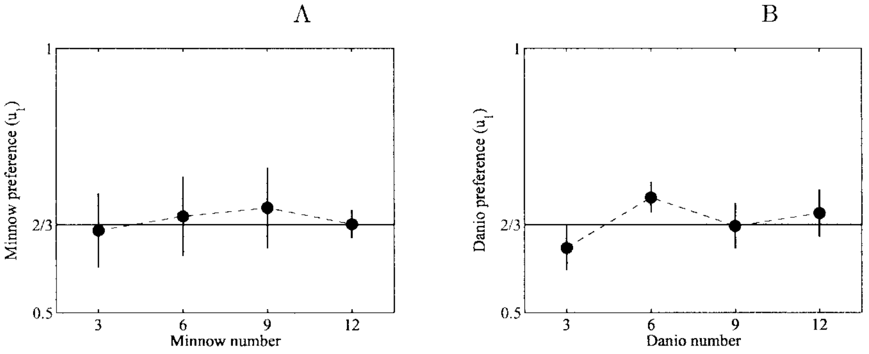

Fig. 1. Single-species habitat selection. Preferences for the more rewarding habitat 1 in minnows (A) and danios (B) (mean ± standard error). The solid line is the single-species IFD (2), corresponding to the distribution matching the ratio 2 : 1 of food supply rates.

Deviations of means of data, pooled across all single-species trials (separately for minnows and danios), from the expected preference 2/3 in the more rewarding habitat 1 were not significant (minnow: mean = 0.68, $t = 0.3$, $P = 0.38$; danio: mean = 0.67, $t = 0.3$, $P = 0.38$; Fig. 1). Each species thus followed the theoretically predicted single-species IFD when feeding alone.

When minnows and danios competed for food in two-species experiments, the minnow preferences stayed uniform over all 16 trials ($F_{15,64} = 0.95$, $P = 0.47$) and followed the ratio of food supply rates (mean = 0.66, $t = -0.0055$, $P = 0.5$; Fig. 2, upper panels). In contrast, danio preferences varied significantly for different combinations of danio and minnow numbers ($F_{15,64} = 1.88$, $P = 0.042$; Fig. 2, lower panels). Therefore, the presence of minnows caused the distribution of danios to deviate from the single-species IFD (2).

Not affected by its own abundance in the tank, danio preferences for the more rewarding patch 1 showed a decreasing trend with increasing minnow density (Table 1; Fig. 2, lower panels). In other words, the more minnows were present in the environment, the fraction of danios (relative to the single-species IFD) that tended to feed in the less rewarding feeding site 2 increased.

To summarize, we conclude that intraspecific competition did not play a role in determining feeding site preferences of minnows and danios, that preferences of each species studied in isolation followed predictions of the adaptive consumer-based IFD theory, and that the interspecific competition between minnows and danios was asymmetric, with minnows the dominant competitor.

Foraging tactics

Generally, minnows changed habitats less often and spent more time close to a feeding site. Danios, on the other hand, frequently moved away from feeding sites upon capturing a food item and switched the feeding sites quite often during any single foraging bout.

In the single-fish trial, the time to catch the first food item upon providing two *Daphnia* simultaneously from both tank sides (0.8 ± 0.024 s for minnow and 2 ± 0.059 s for danio) did not differ among individuals within each species, but differed between the species (Table 2A). Similarly, the reaction distance from the feeding site the food item was taken

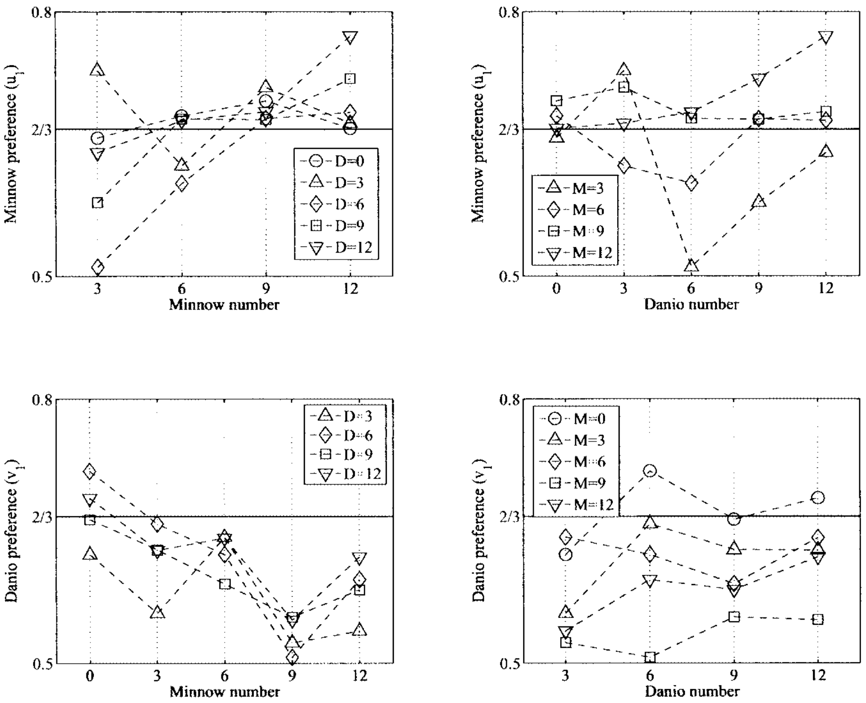

Fig. 2. Two-species habitat selection. Preferences for the more rewarding habitat 1 in minnows (upper panels) and danios (lower panels) as a function of minnow numbers (left-hand panels) and danio numbers (right-hand panels). The solid line denotes the single-species IFD (2), corresponding to the distribution matching the ratio 2 : 1 of food supply rates. Various lines correspond to various numbers of danios (left-hand panels) or minnows (right-hand panels). For the sake of clarity, standard errors are not shown.

Table 1. Results of multiple regression on danio preferences for the patch with the higher food supply rate (patch 1) in the two-species experimental trials

Parameter	Estimate	Standard error	t_{16}	P
Intercept	0.634	0.0402	15.79	<0.0001
Minnow density	−0.00998	0.00546	−1.83	0.086
Danio density	0.00338	0.00489	0.69	0.50
Minnow × danio	0.00016	0.000665	0.24	0.81

Note: Adjusted $R^2 = 0.44$.

from (6.65 ± 0.36 cm for minnows and 14.11 ± 0.39 cm for danios) did not differ among conspecifics, but differed between the species (Table 2B). In addition, these two quantities were strongly correlated ($r = 0.447$, $F_{298,298} = 74.456$, $P < 0.0001$), suggesting that swimming speed did not differ between the species. Neither the time to catch the food item nor the reaction distance differed in any fish species between the single-fish and supplemented-fish trials (Table 3).

Table 2. Results of nested ANOVA on two characteristics of foraging tactics in the single-fish trial: (A) the time to catch the (first) food item, (B) the reaction distance from the feeding site the (first) food item was taken from

Effect	Log-likelihood	d.f.	χ^2	P
A. Time				
Within-species effect	132.96	8	9.18	0.33
Between-species effect	128.37	1	270.65	<0.0001
B. Distance				
Within-species effect	−33.82	8	5.28	0.73
Between-species effect	−36.46	1	131.67	<0.0001

Table 3. Results of nested ANOVA on two characteristics of foraging tactics, comparing the single-fish and supplemented-fish trials: (A) the time to catch the (first) food item, (B) the reaction distance from the feeding site the (first) food item was taken from

Effect	Log-likelihood	d.f.	χ^2	P
A. Time (only bouts in which a focal species consumed a food item)				
Within-species, between-trial effect	−732.63	2	4.67	0.097
Between-species effect	−734.96	1	105.076	<0.0001
B. Distance (all bouts)				
Within-species, between-trial effect	−1732.81	2	3.07	0.22
Between-species effect	−1734.34	1	287.44	<0.0001

Most importantly, the fish species differed in their efficiency to capture prey when competing with one another. In five replicates of the supplemented-fish trial, the minnow individuals missed their food (i.e. were too late to capture any food item that was in the meantime consumed by danios) in 18 of 150 cases (3.6 ± 0.4 cases per replicate), whereas danios missed it in 85 of 150 cases (17.2 ± 1.3 cases per replicate), a difference that is highly significant ($P < 0.0001$).

To summarize, foraging tactics, though not affected by the presence or absence of the other species in the two characteristics we measured, decreased the foraging efficiency of danios in competition with minnows to a significantly greater extent than vice versa. This suggests that interspecific competition is not merely exploitative but its asymmetry is apparently a consequence of a sort of interference.

Competitive ability and the two-species IFD

We showed that minnows followed the single-species IFD regardless of the presence or absence of danios. In this case, $u_1 = r_1/(r_1 + r_2)$ and (4) reduces to $(v_1 - 2/3)D\lambda_D = 0$. For any fixed D and λ_D, this is true only if danios follow the single-species IFD as well, which does not correspond to our observations. In particular, formula (4) does not predict decreasing preferences of danios for the more rewarding habitat 1 with increasing minnow density (Fig. 2, bottom-left).

Although our design does not allow us to estimate precisely cropping rates λ_M and λ_D, the results on foraging tactics prove that $\lambda_D/\lambda_M < 1$. Figure 3 shows the location of the observed species preferences relative to the surface defined by the two-species IFD (4) with $\lambda_D/\lambda_M = 1$. Visual inspection of Fig. 3 shows an inadequacy of (4) for describing the observed habitat preferences of minnows and danios. Decreasing λ_D/λ_M below 1 only reduces the correspondence between data and theory by a fraction, quantified by the sum of squares of deviations of the measured preferences from the model-based surface (not shown).

We conclude that our two-species generalization of Parker's matching rule is not in general agreement with our experimental observations because, while the former considers only exploitative competition, fish distribution is in part driven by interference.

DISCUSSION

In this article, we have studied habitat preferences of two competing fish species in an environment composed of two feeding sites, both empirically and via simple mathematical models, and come up with three main results.

First, when each species was fed separately, individual preferences for one or the other feeding site matched perfectly the predictions of the single-species IFD model. This observation is not new, but adds two new species to the suite of those that were already shown to behave that way (Kennedy and Gray, 1993), thereby adding a value to the basic principles of IFD theory. We note that the parameter a used by Kennedy and Gray to assess precision of the fit takes here the values 1.064 and 1.048 for minnows and danios, respectively. These values

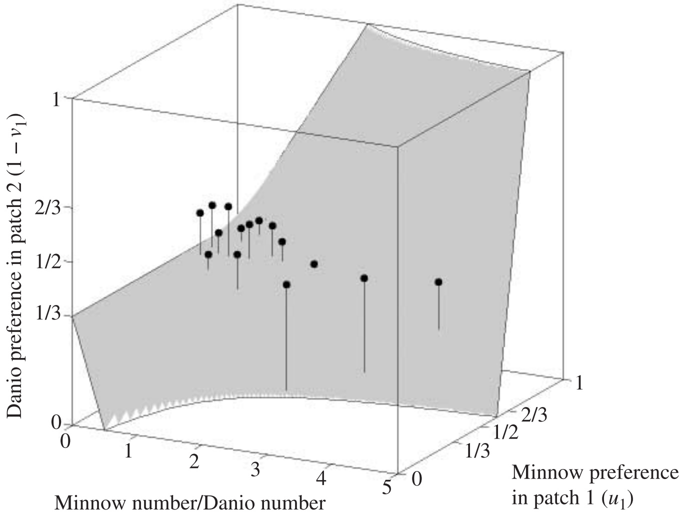

Fig. 3. Danio preferences for the less rewarding habitat 2 as a function of minnow preferences for the more rewarding habitat 1 and the ratio of minnows to danios. Black dots represent the observed habitat preferences of the two species, while the two-species IFD (4) with $\lambda_D/\lambda_M = 1$ defines the surface.

are among the closest ever observed to the expected value of 1. Unfortunately, we do not have adequate data to estimate their second parameter *c*, also expected to be 1 for the adaptively foraging consumers.

Second, the two-species experiments demonstrated that the much smaller white cloud mountain minnow *T. albonubes* was the dominant species. While following the single-species IFD, it affected feeding preferences of the larger giant danio *D. aequipinnatus*. In particular, a preference of danios for the patch with the higher food supply rate was observed (statistically) independent of its own density in the tank, but showed a decreasing trend with increasing minnow numbers. Hence, in the presence of minnows, danios used the less rewarding feeding site significantly more often than in their absence. Contrary to this observation, larger-bodied species are usually competitively dominant (Pimm *et al.*, 1985; Abramsky *et al.*, 1990; Smith *et al.*, 2004; Young, 2004). For example, Abramsky *et al.* (1990) observed that a few individuals of the heavier *Gerbillus pyramidum* changed the preferences of *G. allenbyi* when the latter was common, while the reverse interspecific effect was not that strong. Similarly, coho salmon *Oncorhynchus kisutch*, having a size advantage, increased the proportion of steelhead trout *O. mykiss* in the less favourable habitat, whereas steelhead had little effect on habitat selection by coho (Young, 2004). We thus show that size (weight) is not always the factor responsible for the competitive asymmetry, with the larger-bodied species the winner.

What did make the two species different to the extent that their competition is asymmetric? Recall that minnows remained closer to the food patches. Given both species have a similar swimming speed (the time to reach a food item was more than twice as quick for minnows than for danios and the reaction distance from the feeding site the food item was taken from was about half of that observed for danios), this made minnows competitively superior. Indeed, when we provided food from both feeding sites at equal frequency, single minnow individuals unsuccessfully competed for food in significantly less cases than vice versa (18 of 150 cases for minnows, 85 of 150 cases for danios). Minnows distributed more or less equally between the sites (not shown) and danios thus had no chance of escaping from such strong competition by preferentially feeding in one or the other patch.

Another interesting question is why did danio preferences for the more rewarding patch decrease with increasing minnow numbers and eventually tend to 50% preference for each patch. The dynamic IFD theory predicts that resource levels across all patches should equalize once consumers achieve an IFD (Křivan, 1997). As one species (minnow) dominates competition it should distribute according to the single-species IFD. This equalizes resources, making the patches equally profitable for the subordinate species (danio) that should now distribute homogeneously (i.e. in a 50 : 50 ratio). Alternatively, as minnow abundance increases, so does the difference in the minnow numbers in the two patches. Since danios are competitively inferior and their consumption rate decreases with increasing minnow numbers, their preference for the less rewarding patch (and hence deviation from the single-species IFD) could steadily increase, until there are negligible differences in profitability between patches from the perspective of danios. As a consequence, danios may choose each of the patches with equal (50%) preference.

Third, whereas the single-species IFD model (based on exploitative competition only) succeeded in explaining our observations, its direct extension to a two-species environment did not. This is because interference between the two species was strong enough to contradict the model predictions. We suggest that the assumption of consumer-density-independence of the cropping rates is likely not to be valid in our case. The success of danios in obtaining food in the presence of six minnow individuals decreased by 57% compared with the case of no minnows present, and presumably decreases further with minnow density, eventually reaching nil success (the more minnows in the feeding site, the less chance danios have to reach the site in time and find a food item). The two-species IFD thus appears to depend generally on the detailed foraging behaviour of each species, behaviour that defines a mechanistic basis of interference.

Milinski (1988) presented a conceptual framework for interspecific competition in a patchy environment in which there exists a within-species variability in body size or, more generally, competitive ability, exemplified by, for example, larger/more experienced adults and smaller/less experienced juveniles. This framework applies well to multiple-species competitive communities in which individual species differ in their foraging tactics only quantitatively. In terms of our two-species model, this means that cropping rates are consumer-density-independent, but can differ in different habitats. In terms of our two-species experimental system, this would mean that both danios and minnows share the same time to reach a food item and/or the reaction distance from the feeding site the food item was taken from. As this is not the case in our system, we conclude that the two fish species differ in their foraging tactics qualitatively (cropping rates are likely functions of one or both consumer densities). This between-species difference is a plausible explanation of the two-species model inadequacy as well as of the observation that the smaller species largely outcompetes the larger one. The framework of Milinski (1988), who did not take these differences into account, may thus be overly simple to cover a whole range of two-species competitive scenarios.

Sympatric species, a standard choice in two-species competition studies (e.g. Abramsky *et al.*, 1990; Young, 2004), share a long evolutionary history. Such a history, however, is likely to result in most cases in a kind of niche differentiation, whether spatial, temporal or dietary (Tilman, 1982). Although invaluable for understanding general principles of competition, the results of laboratory studies that 'force' species to share a diet in time and space have only limited value for understanding specific natural communities.

Allopatric species, by definition, live in geographically distinct areas, but this is often not the case today. Biological invasions or unwanted introductions of non-native species are more common today than in our distant or more recent past (Vitousek *et al.*, 1997). In addition, their impact has virtually always been negative (e.g. Kiesecker, 2003). Since behaviourally naive with respect to one another, invading species are likely to adopt a different species niche. Competitive studies of allopatric species conducted in the laboratory may thus resemble much more what is actually going on between such species in nature. Though our results would have been certainly more compelling if there actually were an invasive species problem involving the introduction of one of the studied species into the other's historic range, we feel that studies confronting any two allopatric species may reveal patterns confounded by evolution if two sympatric species are used instead. Living together for a sufficiently long time in a resource-limited and patchy environment, danios might eventually change their foraging tactics to operate nearer to the foraging sites and possibly even reverse the outcome of competition, simply by 'covering the space around the hole'. On the other hand, before this can happen, the inferior tactics of a resident species may result in its complete extirpation once it is not able to face the challenge set by foraging tactics of an invading species. Studies of interactions between formerly allopatric species will thus certainly gain in importance, with ramifications for both conservation and evolutionary biology.

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APPENDIX 1: DERIVATION OF FORMULA (2)

If the two habitats are equally profitable ($R_1 = R_2$), then we have $\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t$. Substituting for derivatives on the right-hand sides of equation (1), realizing that $u_2 = 1 - u_1$, and solving for unknown u_1, we get

$$u_1 = \frac{r_1 - r_2 + \lambda R_1 C}{2\lambda R_1 C} \tag{A1}$$

Substituting this expression to (1) and solving for the resource equilibrium ($\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t = 0$) gives

$$R_1 = R_2 = \frac{r_1 + r_2}{\lambda C} \tag{A2}$$

Finally, by substituting (A2) to (A1), the proportion of consumers in habitat $i(= 1, 2)$ at this equilibrium is $u_i = r_i/(r_1 + r_2)$.

APPENDIX 2: DERIVATION OF FORMULA (4)

When a trajectory of model (3) moves along the line $R_1 = R_2$, then it must satisfy $\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t$. Substituting for derivatives on the right-hand sides of equation (3) and solving for unknown u_1 and v_1, then substituting the result to (3) and solving $\mathrm{d}R_1/\mathrm{d}t = 0$ or $\mathrm{d}R_2/\mathrm{d}t = 0$ (to get a resource equilibrium), we have

$$R_1 = R_2 = \frac{r_1 + r_2}{\lambda_M M + \lambda_D D}$$

Substituting this formula back to $\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t$ leads to expression (4).