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Intraspecific competition affects the strength of individual specialization: an optimal diet theory method

Richard Svanbäck[1,2]* and Daniel I. Bolnick[3,4]

[1]*Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden,* [2]*Department of Limnology, Evolutionary Biology Centre, Uppsala University, Norbyv. 20, SE-752 36 Uppsala, Sweden,* [3]*Section of Evolution and Ecology, Center for Population Biology, Storer Hall, University of California, Davis, CA 95616, USA and* [4]*Integrative Biology, University of Texas at Austin, 1 University Station, C0930, Austin, TX 78712-0253, USA*

ABSTRACT

Question: Why would individuals that inhabit the same environment choose to feed on different subsets of the available resources?

Mathematical method: We outline a flexible model that combines phenotypic variation with optimal diet theory and population dynamics. We then apply this model to investigate the role of different types of trade-offs, phenotype diversity and level of competition in determining the degree of individual specialization.

Key assumptions: The foragers in the model are omniscient and maximize energy intake per time unit.

Conclusion: Numerical simulations match empirical observations that changes in population density can alter the degree of individual specialization. Forager density and phenotypic variation affected prey densities, which in turn affected forager diet breadth and fitness (energy income). We propose that this feedback can explain the empirical relationship between forager density and the degree of individual specialization in the forager population.

Keywords: density dependence, frequency dependence, individual specialization, inter-individual variation, intra-population variation, niche breadth.

INTRODUCTION

Many apparently generalist populations are in fact composed of relatively specialized individuals (Bolnick *et al.*, 2003). For example, the Cocos finch, *Pinaroloxias inornata*, uses a broad range of resources including insects, fruits and flower nectar (Werner and Sherry, 1986).

* Address all correspondence to Richard Svanbäck, Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada. E-mail: svanback@zoology.ubc.ca

This diet diversity spans a range of resources normally characteristic of disparate families of birds. In contrast, individual finches tend to specialize on one particular foraging strategy (Werner and Sherry, 1986). Such individual specialization has important implications for both ecological interactions and evolutionary processes, including polymorphism and speciation (Bolnick *et al.*, 2003). However, very little is known about the mechanistic basis for diet variation. In particular, why would a group of conspecific individuals, faced with the same set of available resources, select different diets?

To effectively address the basis of intra-population diet variation, one must first consider the factors determining diet selection of a single individual. This classic topic in individual ecology is most often addressed via optimal diet theory (ODT) (Schoener, 1971; Pulliam, 1974; Werner, 1974), which was developed to explain why an individual forager might select a restricted diet, when a range of potentially profitable resources is available. The theory proposes that an individual selects a particular foraging strategy to maximize some currency related to fitness, such as the rate of energy income. This rate depends on the energetic content of alternative prey, encounter rates, and how effective the forager is at detecting, capturing, handling and digesting the prey. The forager should drop any food type whose energetic value is less than the expected energetic return for foregoing that item to search for more profitable prey. Optimal diet theory has been fairly successful, allowing qualitative and often even quantitative predictions of individuals' diets in many systems (Sih and Christensen, 2001), though it has also been subjected to extensive criticism (Pierce and Ollason, 1987; Bunnell and Harestad, 1990; Ward, 1992; Sih and Christensen, 2001).

By identifying parameters that affect individuals' diet breadth, optimal diet theory provides a framework for thinking about inter-individual variation. If encounter rates, handling times and energetic value really can determine individuals' diets, then individuals that differ in their ability to find, handle or digest alternative prey may have different diets. For instance, diet variation among individuals of the cabbage butterfly, *Pieris rapae*, can be attributed to individuals having search images for different species of flowers, which affects encounter rates (Lewis, 1986). Individual specialization in the medium ground finch, *Geospiza fortis*, is tied to variation in bill morphology that affects individuals' handling times for different seeds (Price, 1987). A given prey type can also have different energetic value for different individual foragers. Yellow-rumped warblers, *Dendroica coronata*, vary in their capacity to digest particular prey as a result of variation in digestive enzyme production (Afik and Karasov, 1995), leading to inter-individual variation in the energetic value of a given prey type.

Optimal diet theory can thus provide a biologically realistic way to model individual specialization, particularly if biomechanical or cognitive models allow one to mechanistically link phenotypic traits to ODT parameters. In contrast, previous theoretical models of niche variation have taken a simple phenomenological approach to individual specialization (Roughgarden, 1972; Taper and Case, 1985; Dieckmann and Doebeli, 1999), in which individuals vary for a continuous trait that determines what subset of the prey axis an individual will consume. The breadth of this subset is either held constant (Dieckmann and Doebeli, 1999; Bolnick and Doebeli, 2003), or is itself allowed to evolve (Taper and Case, 1985). However, neither the phenotype–diet mapping nor the niche width is given a clear biological basis. In contrast, optimal diet theory can explain niche breadth and between-individual differences in terms of biologically measurable traits, and more closely mimics the process by which foragers select their diet.

In this paper, we show that optimal diet theory can explain diet variation when individuals differ in their handling times or attack rates. We outline three distinct patterns of rank-preference variation that could produce individual specialization. We then apply this approach to investigate how resource competition can modify the degree of individual specialization. A number of studies have found that the level of diet variation can vary with the strength of intraspecific competition. For example, in the Eurasian perch, *Perca fluviatilis*, diet variation is more pronounced at higher population densities (Svanbäck and Persson, 2004). The models discussed in this paper can account for this interaction between competition and individual specialization.

MODEL

Diet choice for an individual forager

We modelled a population of foragers in which individuals choose from five possible prey types. Each prey type j has a particular energetic value (e_j) and handling time requirement (h_j). When a forager encounters an individual prey type j, the time spent capturing, consuming and digesting this food item will yield an energy income rate e_j/h_j. Assuming the forager is trying to maximize its energy income per unit time, the forager should prefer prey that yield a higher amount of energy per unit time spent handling. For instance, if

$$\frac{e_1}{h_1} > \frac{e_2}{h_2} > \frac{e_3}{h_3} > \frac{e_4}{h_4} > \frac{e_5}{h_5} \qquad \text{Entrada de energia} \qquad (1)$$

the forager should prefer prey type 1 over prey type 2, prey 2 over 3, and so on – the forager's 'rank preferences'. By 'prefer', we mean that when faced with two types of prey simultaneously, the predator chooses to consume the 'preferred' prey.

Standard optimal foraging models are based on the assumption of maximization of the net rate of energy intake during foraging, which leads to maximization of:

$$\frac{E}{T_s + T_h} \qquad \text{Entrada de energia por tempo de procura e processamento} \qquad (2)$$

where E is the energy intake during a given length of time spent foraging, including both search and handling time, T_s and T_h. Assuming that encounters are linearly related to T_s, and that encounters are linearly related to prey density, then the forager is trying to maximize (Stephens and Krebs, 1986; Krivan, 1996):

$$\frac{\sum_{j=1}^{k} a_j N_j e_j}{1 + \sum_{j=1}^{k} a_j N_j h_j} \qquad (3)$$

where a_j is the forager's efficiency at finding prey type j ('attack rate'), and N_j is the density of prey type j. The number (and identity) of prey types included in an individual's diet will thus depend on the forager's search and handling efficiencies for each prey, prey value and abundance.

Rank preference variation

We suggest that individual specialization occurs when individuals have different optimal diets due to variation in search, handling or digestive abilities. We therefore modelled a population of foragers with three phenotypes ($i \in [1,3]$) that vary in their prey-specific handling times h_{ij}. For simplicity, we assumed that individuals inhabit a homogenous environment, so that all foragers experience the same prey population densities, and all prey have equal energetic value for all foragers ($e_{ij} = 1$ for all i,j). Hence, rank preference depended solely on variation in h_{ij}.

Individual specialization can arise from a number of distinct mechanisms (Bolnick *et al.*, 2003). To account for this variation, we considered three distinct models of rank preference variation: shared preference, competitive refuge and distinct preference (Fig. 1A–C). The handling time values used for the three models are listed in Table 1.

The most obvious basis for diet variation is that individuals have different rank preferences, such that individuals have different 'first-choice' prey (e.g. Bence, 1986; Robinson and Wilson, 1996a,b). Implicit in this model are strong trade-offs, in which the ability to efficiently use one resource comes at the expense of reduced efficiency on other resources. We designated this the 'distinct preference' model, in which forager phenotypes 1 and 3 have different first-ranked prey (1 and 3 have the lowest handling times for prey types 1 and 5, respectively), and phenotype 2 is an intermediate generalist (Fig. 1C).

Modelo de Preferências Distintas

Alternatively, foragers could share some of their top-ranked prey, but have different rankings for less preferred resources (Fig. 1B). This 'refuge model' might occur when a single high-value resource is available to all phenotypes, whereas using lower-value resources requires specialized phenotypic adaptations that are subject to stronger trade-offs (Robinson and Wilson, 1998). Each forager thus has low handling times for prey 1, and a second prey that serves as a refuge from competition with other phenotypes.

Modelo de Refúgio Competitivo

The least intuitive mechanism for individual specialization entails identical rank preferences for all phenotypes ('shared preference' model). Individuals with identical rank preferences may nonetheless vary in the rate at which they accept lower-ranked resources. For instance, both light- and heavy-bill morphs of the seedcracker *Pyrenestes ostrinus* prefer

Modelo de Preferências Compartilhadas

Table 1. Parameter values for handling time (h_{ij}) that were used for illustration purposes in this paper

		Prey species (j)				
Preference	Phenotype (i)	1	2	3	4	5
Shared	1	0.10	0.40	0.70	1.00	1.30
	2	0.40	0.55	0.70	0.85	1.00
	3	0.68	0.69	0.70	0.71	0.72
Refuge	1	0.10	0.40	0.70	1.00	1.30
	2	0.10	1.30	0.40	0.70	1.00
	3	0.10	1.00	1.30	0.40	0.70
Distinct	1	0.10	0.40	0.70	1.00	1.30
	2	0.40	0.55	0.70	0.85	1.00
	3	1.30	1.00	0.70	0.40	0.10

Valores crescentes

Mesma presa preferida

Valores distintos

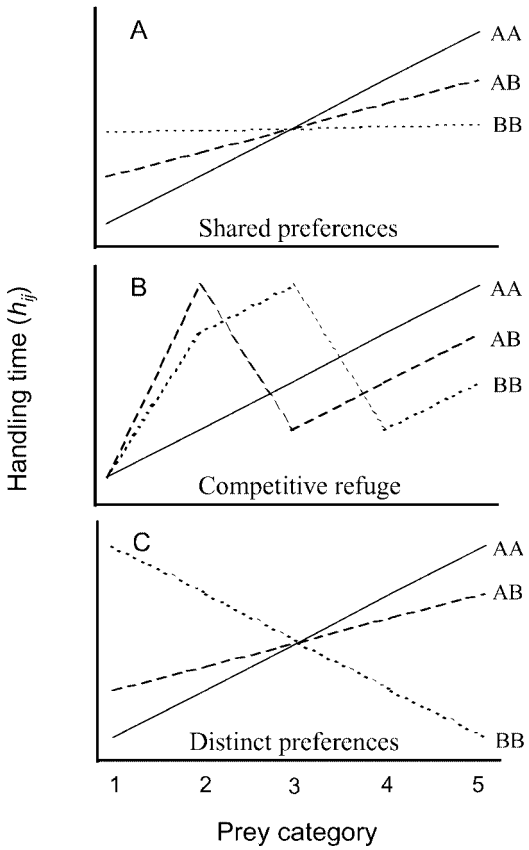

Fig. 1. Illustration of handling time efficiencies for the three phenotypes on the five different prey categories depending on rank preference model. Solid lines represent the handling times of phenotype 1 (genotype AA), dashed lines those of phenotype 2 (genotype AB) and dotted lines those of phenotype 3 (genotype BB). (A) Shared preferences: all phenotypes rank their prey in the same order. (B) Competitive refuge: all phenotypes have the same first-ranked prey but differ in their second-, third-, fourth- and fifth-ranked prey. (C) Distinct preference: phenotypes 1 and 2 have the same rank preference, whereas phenotype 3 ranks the prey in the opposite order.

small sedge seeds, but the heavy-bill morph is better able to switch to larger, harder seeds when small seeds become scarce (Smith, 1990). For the shared preference model, all three phenotypes have identical rank preferences, but vary in how much *e*/*h* differs for alternative prey (Fig. 1A).

It is worth noting that traditional optimal foraging theory cannot explain all instances of individual specialization. We have chosen optimal diet theory and handling time variation because they are consistent with the mechanism underlying individual specialization and resource polymorphism in many systems (for reviews, see Smith and Skúlason, 1996; Bolnick *et al.*, 2003). However, we also appreciate that other mechanisms for individual specialization might be important. For example, diet variation can result from interference competition that precludes some individuals from achieving their optimal diet (e.g. Holbrook and Schmitt, 1992) or when individuals are trying to optimize different currencies (e.g. Grantham *et al.*, 1995; Annett and

Pierotti, 1999). Furthermore, diet variation may result from more complex optimization rules, for instance if foragers vary in their vulnerability or aversion to predation risk. We exclude these mechanisms in our model or simulations, not because we consider them unreasonable, but because optimal diet theory offers a tractable starting point that is consistent with a number of empirical case studies.

Density- and frequency-dependence

For any given model of rank-preference variation, we are interested in knowing to what extent individuals specialize relative to their population as a whole. This will depend on the relative frequencies of the three forager phenotypes, and the prey population density. To model forager phenotype frequencies, we assumed a simple Mendelian one-locus, two-allele system in which phenotype 1 is homozygous for allele A, phenotype 3 is homozygous for allele B, and the functionally intermediate phenotype 2 is the heterozygote. By setting the frequency of allele A we can control the relative frequencies of all three phenotypes with a single parameter, assuming Hardy-Weinberg equilibrium.

While forager densities were set for any given simulation, prey densities were allowed to change dynamically in response to predation pressure until they reached equilibrium, at which point we determined the diet breadth of each phenotype, the degree of individual specialization, and the relative fitness of the three forager phenotypes. In each simulation run, we began at time zero with each of the five prey densities at carrying capacity ($N_j = K_j$ for all j), and determined whether or not a forager i would include a prey type j in its diet. The term I_{ij} is an indicator variable that takes value 0 (1) if forager i excludes (includes) prey j, dictated by equation (3). We then determined a new population density for each prey type based on the change in prey density in response to intraspecific competition and mortality from predation:

$$\frac{\Delta N_j}{\Delta t} = r_j N_j \left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{3} \frac{I_{ij} a_{ij} N_j P_i}{1 + \sum_i I_{ij} a_{ij} h_{ij} N_j} \qquad (4)$$

where r_j and K_j are the prey species' growth rate and carrying capacity, respectively. We iterated this process, determining forager diets given prey density then changing prey density in response to predation pressure, for 1500 prey generations, by which time prey densities invariably had reached an equilibrium level. We assumed a low level of prey immigration to allow decimated prey populations to recover if foragers switched to other prey: if density declined to 0 during an iteration, we set the density to 1 in the following prey generation. PQ?

Simulations

To investigate the effect of density- and frequency-dependent competition on the degree of individual specialization, we varied the prey carrying capacity ($K = 2000$ to 6000 in increments of 1000), the forager population density ($P = 1$ to 1200 in increments of 5), and the frequency of the forager phenotypes (Freq(A) = 0 to 1 in increments of 0.01). This process was repeated for all three models of rank-preference variation. The attack rates (a_{ij}) for each phenotype on the prey were set as 0.08, 0.06, 0.04, 0.02 and 0.01 for prey one

Varrendo os parâmetros

through five, respectively. To ensure that differences among the three preference models were robust, we ran 10 different versions of each preference model, varying the precise values of h_{ij} to alter the relative slopes of the handling time functions for the three phenotypes. The qualitative results were consistent for all variations on a given rank-preference model, so our results and discussion focus on a single set of representative handling time values (Table 1), and the same carrying capacities (K_j = 2000) and growth rates (r_j = 1.2) for all prey types.

Analysis

At the end of each simulation, we recorded the densities of all five prey, the range and identity of prey accepted by each forager phenotype, and the number of each prey actually eaten by a given phenotype. The latter measure was used for two purposes. First, prey consumption was used to calculate the degree of diet overlap among individuals in the population (Bolnick *et al.*, 2002): the extent to which individuals use a subset of the population's total diet. We quantified the proportional similarity (PS_i) between an individual i's resource use distribution and the population's distribution (Schoener, 1968; Feinsinger *et al.*, 1981; Bolnick *et al.*, 2002). The diet overlap between an individual i and the population is:

$$PS_i = 1 - 0.5 \sum_j (p_{ij} - q_j) = \sum_j \min(p_{ij}, q_j) \quad (5)$$

Sobreposição da dieta do indivíduo com a população

where p_{ij} is the frequency of diet category j in individual i's diet, and q_j is the frequency of diet category j in the entire population's diet. For individuals that specialize on a single diet item j, PS_i takes on the value q_j. For individuals that consume resources in the same proportion as the population as a whole, PS_i will equal 1. The overall prevalence of diet overlap (DO) in the population can be expressed by the average PS_i. Note that a high diet overlap ($DO \sim 1$) means a low level of individual diet specialization, whereas a low diet overlap means a high level of individual diet specialization.

Second, we calculated the relative fitness of the three forager phenotypes to test whether frequency-dependent competition leads to stable fitness minima, as has been found in other models (Dieckmann and Doebeli, 1999). Fitness was measured by the expected energy gain:

$$w_i = \sum_{j=1}^{5} \frac{I_{ij} a_{ij} N_j e_j}{1 + I_{ij} a_{ij} h_{ij} N_j} \quad (6)$$

Aptidão do indivíduo, calculada a partir do seu ganho energético esperado

We categorized the shape of the fitness function: directional selection favours phenotype 1 when $w_1 > w_2 > w_3$, and favours phenotype 3 when $w_1 < w_2 < w_3$. Selection is considered disruptive when $w_1 > w_2 < w_3$, stabilizing when $w_1 < w_2 > w_3$, and there is no selection if $w_1 = w_2 = w_3$.

RESULTS

Individual specialization

At low forager densities, resources experienced little predation and so remained at or near their carrying capacities (Fig. 2). This high resource abundance allowed foragers to

Qual seria a diferença de se começar a simulação de uma pop. na metade de K?

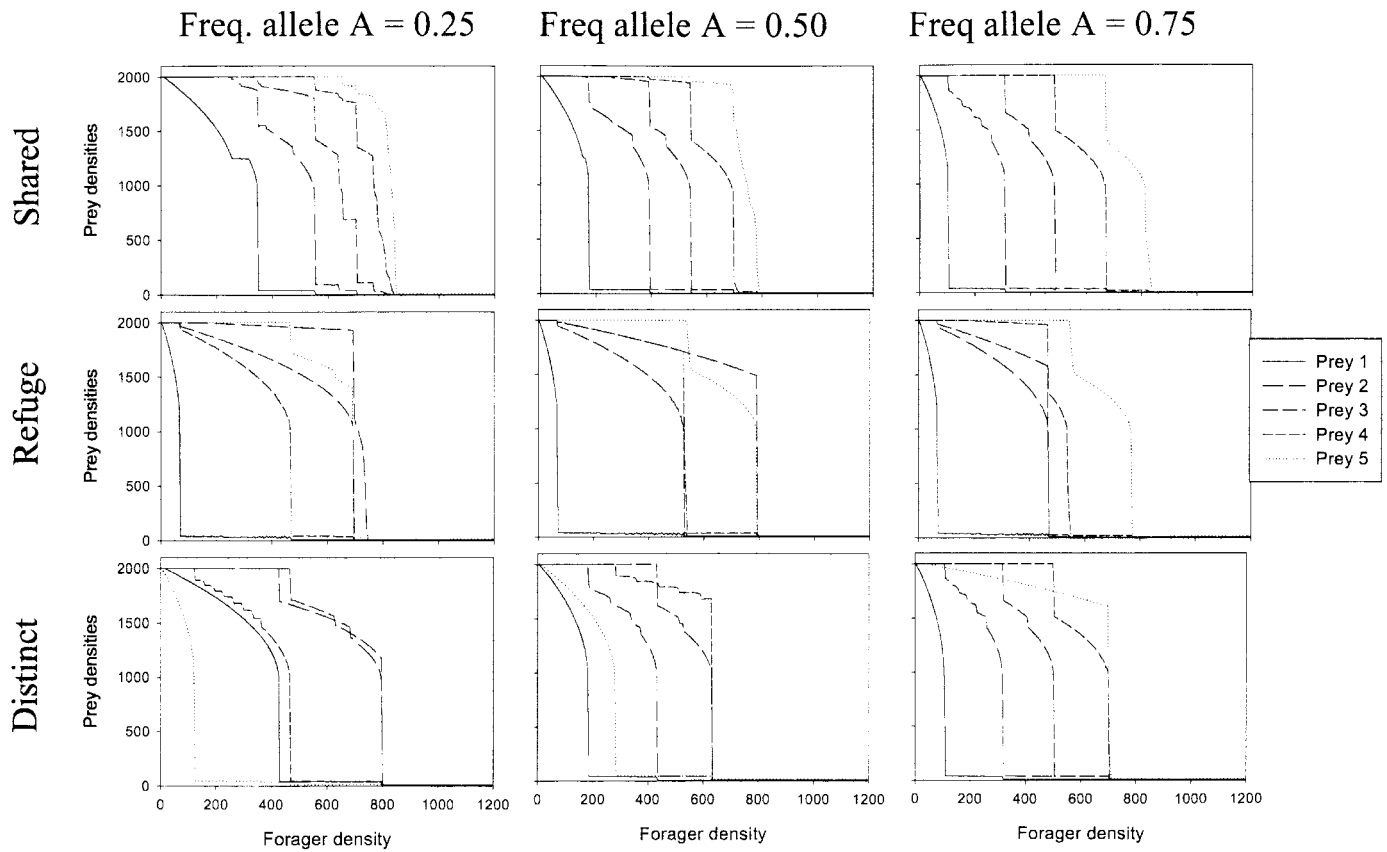

Fig. 2. Equilibrium densities of the five different prey categories for the different preference models depending on the density of foragers. The different frequency distributions are also shown to illustrate the dependency of frequency distribution.

specialize entirely on their top-ranked resource, ignoring all lower-ranked prey. As forager density increased, the first-ranked prey became scarce and secondary prey were added. Intraspecific competition thus tended to increase individual niche width. The degree of diet overlap among individuals changed with density because different phenotypes increased their niche width at different rates. The precise relationship between competition and individual specialization depends on the model of rank-preference variation. We therefore discuss the three preference models separately.

Shared preferences

At low forager densities, all three phenotypes specialized on their shared top-ranked prey. Consequently, there was complete diet overlap between phenotypes ($DO = 1.0$) at low density. At higher forager density, the preferred prey type became increasingly scarce, prompting the predators to begin using their second-ranked prey as well. Further increases in forager density quickly reduced the density of the second-ranked prey, driving the successive addition of more prey types, each of which quickly declined as they were suddenly subject to predation pressure (Fig. 2). Although the three forager phenotypes added prey in the same order, their values of e_i/h_i varied so they added new prey at different points. Phenotype 3 was the first to add new prey items to its diet because the difference between e_1/h_1 and e_2/h_2 was relatively small for that phenotype. This differential rate of prey addition reduced the mean diet overlap in the population because phenotype 1 remained specialized on prey 1, while the other two phenotypes had added other prey types to their diet. Increasing forager density thus leads to stronger individual specialization ($DO < 1.0$). However, this trend reverses at very high forager densities. When all prey are scarce, foragers adopt generalist strategies and diet variation is eliminated (Fig. 3).

Um aumento na densidade de predadores leva a um aumento na EI, até o ponto em que a dens. é mto alta, todos viram generalistas

To understand why this trend is somewhat irregular, consider the horizontal cross-section in Fig. 4 at a constant allele frequency. At low predator densities, there is complete diet overlap ($DO = 1.0$). Increasing competition drives phenotype 3 to add new prey to its diet, reducing diet overlap to about 0.8. Further increases in competition result in phenotype 2 also expanding its diet, increasing mean diet overlap because phenotypes 2 and 3 now overlap more.

Individual specialization is also sensitive to the frequency of forager phenotypes. Diet variation is negligible when the population is dominated by a single phenotype, and maximized when phenotype diversity is high (Fig. 4). This is quite intuitive, as diet variation is impossible in a phenotypically homogenous group of foragers. However, there is also a complex interaction between forager density and phenotype frequency. This arises because changes in one forager's diet breadth alters the availability of prey (and hence diet breadth) of other predators. Furthermore, the impact of a phenotype's diet expansion on mean diet overlap depends on its frequency: rare phenotypes have a negligible impact on the mean diet overlap.

Competitive refuge

Similar to the 'shared preferences' model, individual specialization is absent at low forager densities, increases as competition becomes stronger, and is eliminated again at high forager densities (Fig. 3). The difference is that at intermediate densities, individual specialization is much stronger with the refuge model, with very little diet overlap among the three phenotypes ($DO \sim 0.35$ as opposed to 0.8). This is because each forager adopts a different

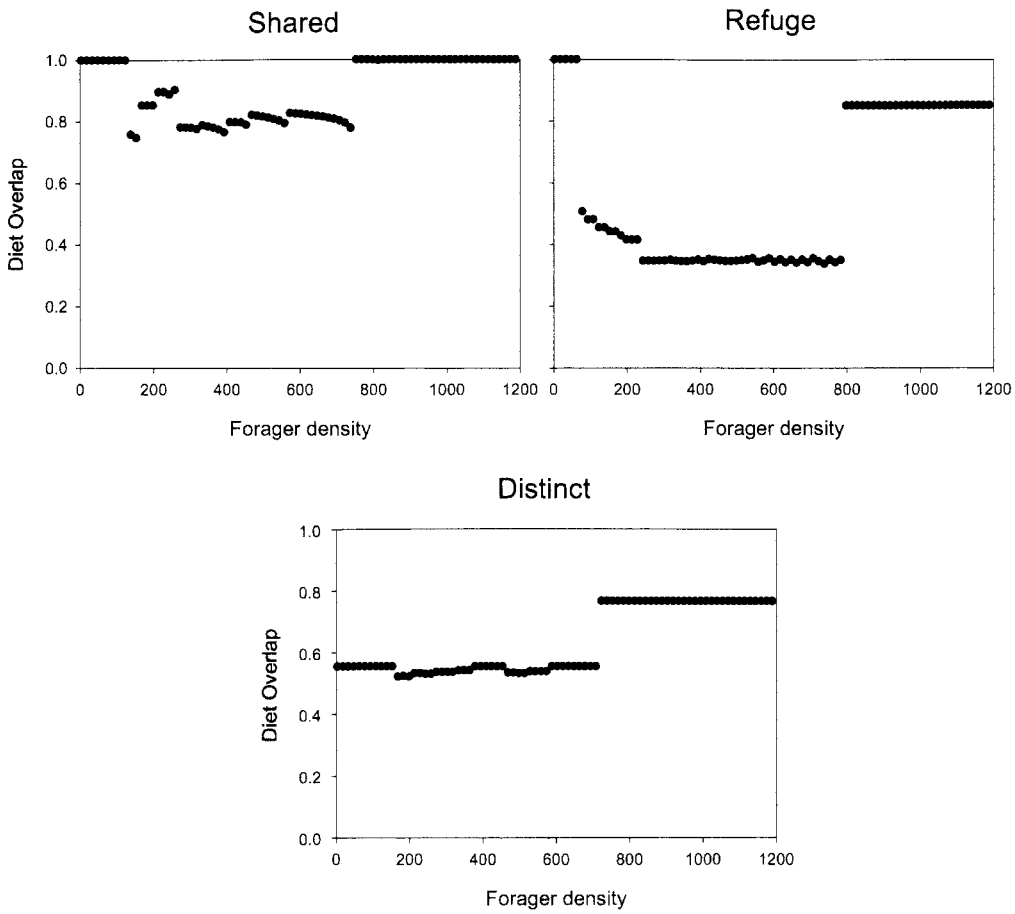

Fig. 3. Density dependence of diet overlap in three preference models. Note that a high value of diet overlap (i.e. close to 1.0) indicates a low level of individual specialization. Data for this figure were produced assuming the three predator phenotypes had frequencies of one-third, and using handling times in Table 1.

second-choice resource, rather than having one phenotype's diet nested within that of another. The population niche breath is thus quite broad (four of five resources consumed), while no single phenotype uses more than two resources. As before, $DO \sim 1.0$ at low density because all phenotypes specialize on the same preferred resource, and at high density because all phenotypes are generalists.

Distinct preferences

Unlike the previous two models, the distinct preference model yields strong individual specialization at low population density (Fig. 3). Phenotypes 1 and 2 specialize on prey 1, while phenotype 3 specializes on prey 5. Increasing competition can reduce diet overlap slightly when the more flexible phenotype 2 adds a new prey type before phenotype 1 does.

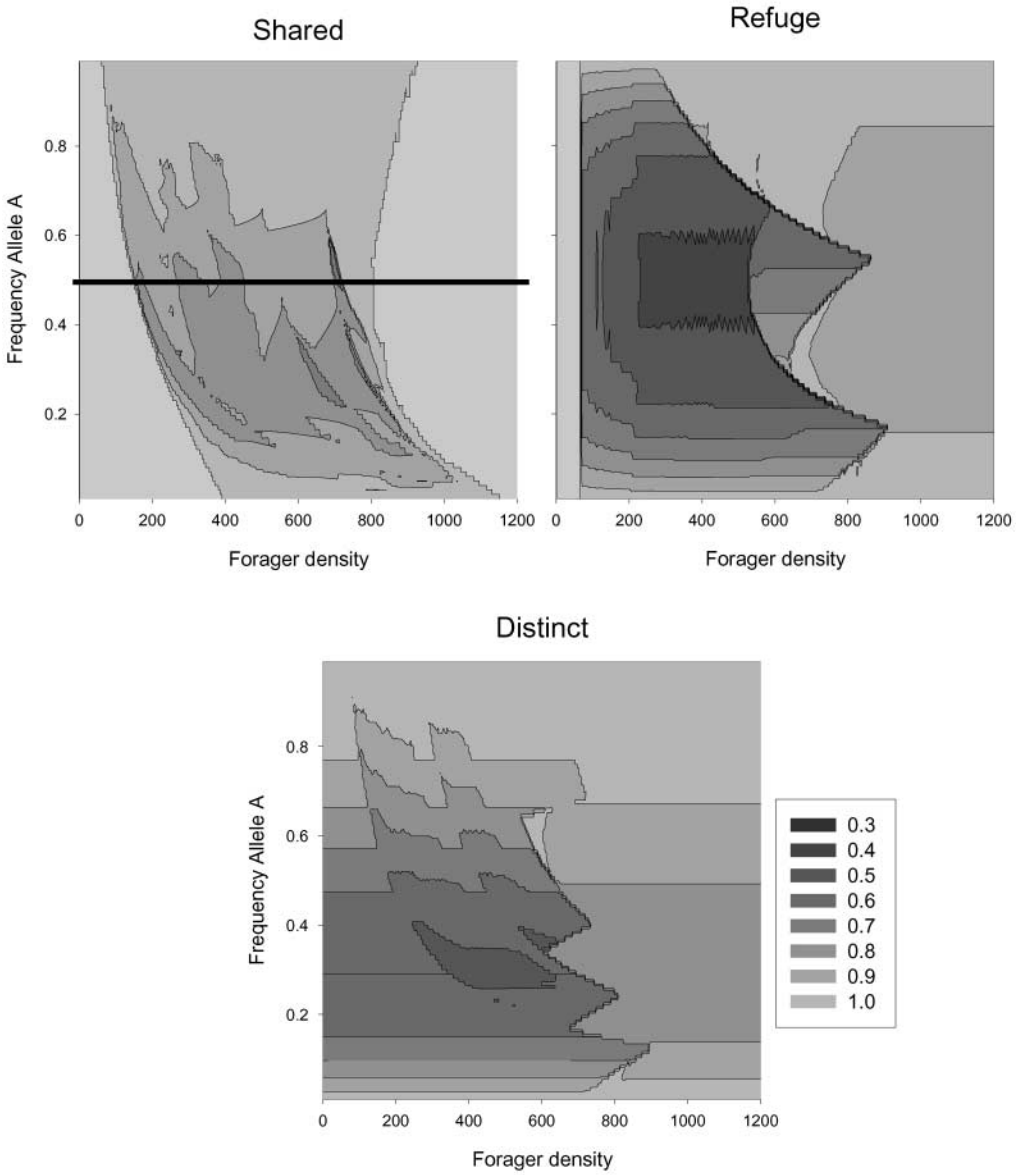

Fig. 4. Index of diet overlap for the different preference models depending on density and frequency distribution of the foragers. Note that a high value (i.e. close to 1) indicates a low level of individual specialization. The dark horizontal line on the shared preferences model represents a transect across densities keeping phenotype frequencies constant (freq(A) = 0.5). See text for discussion.

Individual specialization is thus strongest at low forager densities, declining as competition gets stronger. As before, strong competition drives phenotypes to expand their diets, causing greater overlap between phenotype 3 and the other two forager types.

Fitness landscape

Although we have not modelled forager population dynamics, it is useful to consider how the changes in diet breadth and individual specialization detailed above might alter the forager population. Predator dynamics could be represented by movement along the x-axis in Figs. 4 and 5, while changes in allele frequencies can be represented by movement along the y-axis in Fig. 5. We focus on the latter effect, because diet variation opens up the opportunity for natural selection when phenotypes have different foraging success. Using the energy income of each phenotype at prey-density equilibrium as a measure of fitness (equation 7), we found that the mode of selection was both density- and frequency-dependent. We found five general patterns of selection: directional selection favouring a particular phenotype (1 or 3 – the homozygotes for A or B), disruptive selection reducing phenotype 2 (AB), stabilizing selection favouring the heterozygote, and no selection (all phenotypes have the same fitness). As with diet variation, the fitness landscape depends on the model of handling time trade-offs, and an interaction between population density and phenotype frequencies.

Shared preferences

With shared preferences, selection is predominantly directional, with a large region of parameter space favouring either allele A (dark grey shading in Fig. 5) or allele B (pale grey shading in Fig. 5). Phenotype 1 (AA) has an inherent advantage at both very low and very high densities because we assumed it has the shortest handling time for prey type 1 (preferred by all foragers in low competition, and most readily captured at high competition due to its higher attack rate). Phenotype 3 (BB) can be favoured at intermediate levels of competition, because it is the first to switch to novel prey types, thereby escaping competition. However, this strategy only works when BB is rare, so phenotypes 1 and 3 are both favoured when rare.

Between the two regions of directional selection, there is a narrow window of disruptive selection in which both phenotype AA and BB do better than the heterozygote AB (white shading in Fig. 5). Somewhat surprisingly, the population will tend to converge towards these regions of disruptive selection. To see this, imagine holding the population density constant at $N = 700$ (vertical dark line in Fig. 5). When phenotype AA is rare, directional selection favours allele A, which increases in frequency until it reaches the region of disruptive selection. Conversely, when phenotype AA is abundant, it experiences strong intra-phenotype competition, while phenotype AB and BB can switch to alternative resources. Selection then favours allele B, and freq(A) declines towards the region of disruptive selection. As long as the equilibrium forager population size (not considered in our simulations) is within the range of forager densities for which disruptive selection is possible, the population should converge towards a stable ecological polymorphism. Note that at some forager densities (e.g. $N \sim 900$) there are three possible stable equilibria for allele frequencies, each subject to disruptive selection.

Competitive refuge

Stable fitness minima also appear in the refuge model. At low densities, all foragers feed on the same prey with equal efficiencies and there is no selection (Fig. 5). At higher forager densities when the phenotypes switch to their second-ranked prey, the fitness landscape becomes frequency dependent: both phenotypes 1 and 3 are selected against when they are

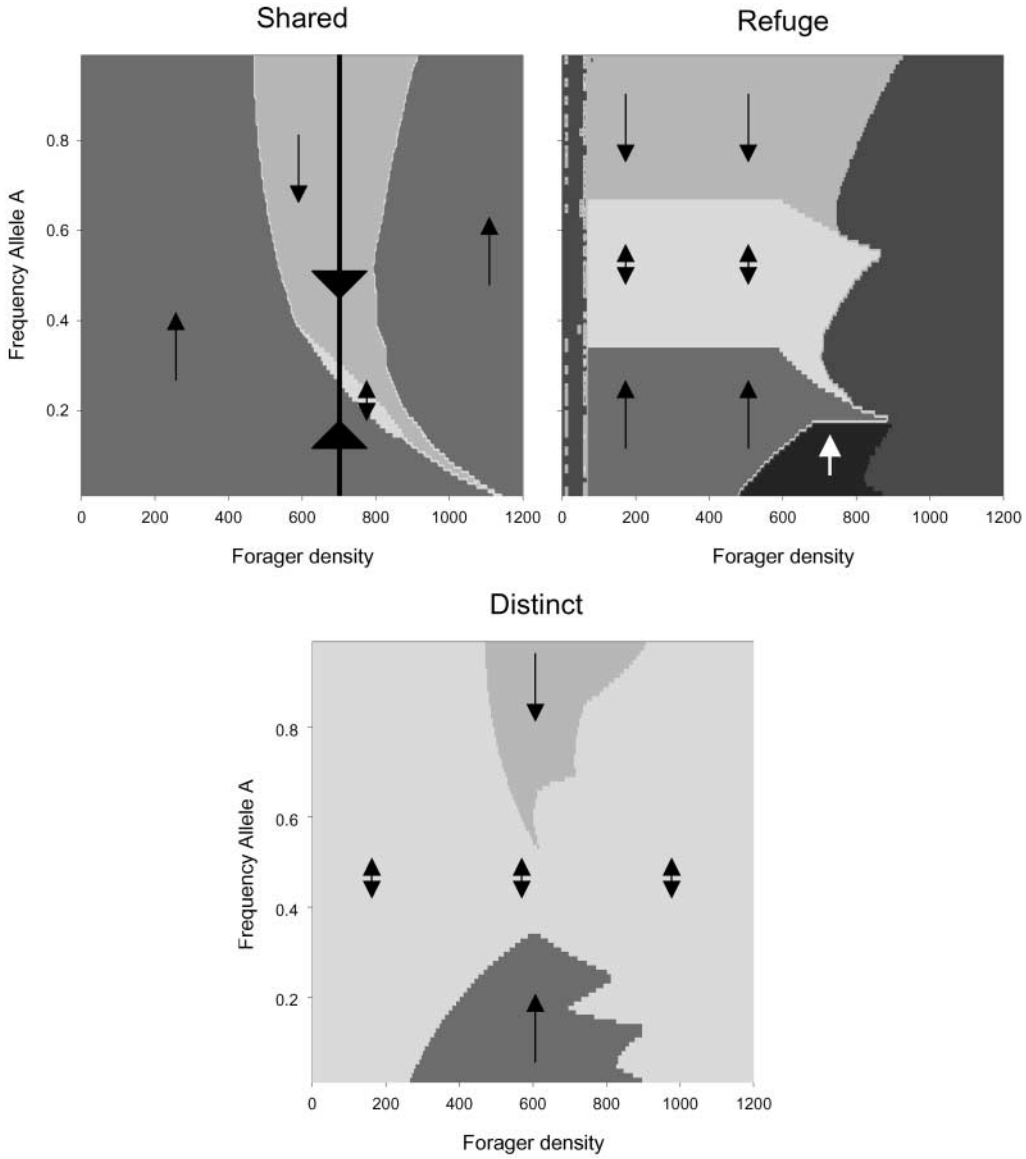

Fig. 5. Fitness landscape for the different preference models depending on density and frequency distribution of the foragers. The different shaded regions signify different directions in the fitness landscape and the directions are indicated by arrows: directional selection favouring phenotype 1 (AA) is marked by upward pointing arrows, directional selection favouring phenotype 2 (BB) is indicated by downward pointing arrows (decreasing freq(A)), and disruptive selection is indicated by double-headed arrows. Stabilizing selection is indicated by an upward pointing white arrow because in the region of stabilizing selection, high heterozygote fitness leads to increasing frequencies of allele A. Regions of parameter space with no selection have no arrows. For shared preference, the vertical cross-section at a density of 700 foragers shows the direction of selection (large arrows). See text for further explanation.

common (Fig. 5), driving allele frequencies towards intermediate values where the population is subjected to disruptive selection. Interestingly, there is a small region of stabilizing selection where phenotype 2 (AB) has the highest fitness (black shading in Fig. 5). However, this region is dynamically unstable: the heterozygote advantage will increase the frequency of allele A, driving the population phenotype distribution first into a region of directional selection before again converging on a stable fitness minimum. At really high densities when all foragers are generalists, they will again have the same energy income and thus there is no selection.

Distinct preferences

Selection is predominantly disruptive under this model. At low population densities, phenotypes 1 and 3 are both highly efficient at using their respective resources, while the heterozygote is a less efficient generalist. Note that this is a consequence of our choice of parameter values for h_{ij} that implicitly incorporated a trade-off in which phenotype 2 is a jack-of-all-trades-but-master-of-none. As population density increases, within-phenotype competition depresses resources and either specialist phenotype (1 or 3) is selected against when it is common, but favoured when rare (Fig. 5). This results in a stable fitness minimum, selection driving allele frequencies towards intermediate allele frequencies where the population is subject to disruptive selection.

DISCUSSION

Diet variation, including individual specialization, ecological sexual dimorphism and discrete polymorphism, is known to occur in a vast array of taxonomic groups and ecological settings (Shine, 1989; Skúlason and Smith, 1995; Smith and Skúlason, 1996; Bolnick *et al.*, 2003). For example, individual specialization has been recorded in nearly 100 species, ranging from gastropods to insects to mammals (Bolnick *et al.*, 2003). In spite of this rich collection of case studies, little is known about the mechanisms underlying diet variation or its ecological and evolutionary implications. One of the barriers to generalizing about individual specialization's implications is that the phenomenon itself may arise from any of a diverse set of biological mechanisms. While most studies of diet variation have focused on morphological variation (Robinson and Wilson, 1994, 1996b; Smith and Skúlason, 1996), it can also arise from behavioural, biochemical, cognitive and social-rank differences (Bolnick *et al.*, 2003). Whatever the source of variation, one rule seems to hold true for most examples: individual specialization occurs when there are efficiency trade-offs between using alternative resources (e.g. Price, 1987; Smith, 1987; Ehlinger, 1990; Schluter, 1995; Svanbäck and Eklöv, 2003; see also review by Bolnick *et al.*, 2003).

This paper presents the first mechanistic model of individual specialization. Rather than designating a simple mapping of phenotypic differences onto diet differences, we have specified a mechanism by which individual foragers choose their diet (optimal diet theory). One can then incorporate many different models of trade-offs to yield diet variation among individuals, so our model is flexible enough to reflect the diverse causes of individual specialization in nature. Since the model is based on empirically measurable quantities – handling times, attack rates, prey density (Schluter, 1995; Robinson, 2000) – it can be adapted to generate predictions for real biological systems. We then used this model to understand the relationship between individual specialization and the strength of intraspecific competition.

Effect of competition

The degree of individual specialization is known to respond to population density in natural systems. In a recent study, Svanbäck and Persson (2004) documented changes in diet variation and population density of the Eurasian perch (*Perca fluviatilis*) over a 9 year period. At low densities all individuals were found in the littoral habitat and had a similar diet. When population density increased, some individuals switched to the pelagic habitat and diet. As a result, increases in population density were accompanied by an expansion of the population's total niche width while within-individual niche width remained small, specialized on a single habitat. The result was that individual specialization tended to increase with increasing intraspecific competition (Svanbäck and Persson, 2004). Similar patterns were observed for different morphs of a tropical seed-eating bird *Pyrenestes ostrinus* (Smith, 1990). The numerical simulations presented here produced results that closely match this empirical result. Both *Perca* and *Pyrenestes* fit our 'shared preference' model where distinct morphs have similar rank preferences, and like the model results they show no diet variation at low density, and more individual specialization at higher densities.

Evidências empíricas para o modelo de preferencias compartilhadas

Other studies have documented quite different responses to population density. In an experimental study of predation and divergent selection on resource use in threespine sticklebacks (*Gasterosteus aculeatus*), Rundle *et al.* (2003) found that resource partitioning was weak at high population densities. This is consistent with any of our models, as extremely strong competition will drive all phenotypes to generalize. Only as predation reduced intraspecific competition did different phenotypes specialize on benthic and limnetic microhabitats. Note that microhabitat partitioning by sticklebacks requires only a slight modification of our model. Individual specialization will also change as a function of competition if different prey are associated with different microhabitat patches, and patch use changes with density.

A study by Schindler *et al.* (1997) failed to show any correlation between forager density and individual diet specialization in the largemouth bass, *Micropterus salmoides*, over a 10 year period. This negative result is not necessarily inconsistent with our model, as the bass density only varied threefold, compared to the 20-fold change documented by Svanbäck and Persson. To see how changing forager densities may (or may not) affect individual specialization, consider the following scenario. Imagine that Schindler's bass are composed of equal numbers of morphs with distinct preferences. Looking at Fig. 4, one can see that at freq(A) = 0.5, diet overlap is the same for forager densities ranging from 0 to nearly 700 individuals. Population cycles staying within this range will therefore have no effect on the strength of individual specialization. In contrast, the same population fluctuations will affect diet overlap at different morph frequencies, or with different trade-off models. One can use the same approach (tracking changes along the x-axis of Fig. 4) to look at the effects of stable predator–prey equilibria, stable limit cycles, or extinction (Fryxell and Lundberg, 1994; Krivan, 1996; Ma *et al.*, 2003) on individual specialization. Similarly, evolutionary dynamics can be expressed as movement along the y-axis of Fig. 4, and will be discussed below.

It is, of course, likely that optimal diet theory will fail to apply to some systems. For instance, pigeons (*Columba livia*) foraged more selectively when feeding with conspecifics than when alone (Inman *et al.*, 1987). Increased competition actually resulted in individual niche restriction, a result that is not expected under any model of optimal foraging. Furthermore, predation risk is another factor that might influence the diet choice of a forager (Stephens and

Krebs, 1986) and this is not included in our ODT model. However, optimal diet theory has proved to be generally useful as both a qualitative and quantitative model of individual diet choices (but see Pierce and Ollason, 1987; Bunnell and Harestad, 1990; Ward, 1992).

Stable fitness minima

Habitat and resource use affect an individual's energy income, mating options and exposure to risk. Niche variation among individuals is therefore likely to be a major source of variation in fitness. In fact, individual specialization plays a central role in a number of models of evolutionary diversification (Turelli *et al.*, 2001). In these models, evolutionary divergence is driven by disruptive selection because phenotypically average individuals experience disproportionately more intense competition than rare phenotypes with access to exclusive resources (Rosenzweig, 1978; Dieckmann and Doebeli, 1999). For this frequency-dependent selection to occur, individuals must compete more strongly with like phenotypes (Dieckmann and Doebeli, 1999). In other words, there must be individual specialization.

The disruptive selection arising from competition among individual specialists is an example of a 'stable fitness minimum' (Abrams *et al.*, 1993). Normally, disruptive selection is unstable, leading to an increase in one allele or the other. However, negative frequency dependence imparts stability because selection changes with allele frequency, driving populations towards regions of disruptive selection. Stable fitness minima serve as a foundation driving phenotypic divergence in models of character release, polymorphism, ecological sexual dimorphism, and sympatric and parapatric speciation (Roughgarden, 1972; Rosenzweig, 1978; Slatkin, 1984; Seger, 1985; Wilson and Turelli, 1986; Doebeli, 1996; Dieckmann and Doebeli, 1999; Drossel and McKane, 2000; Claessen and Dieckmann, 2002; Bolnick and Doebeli, 2003; Doebeli and Dieckmann, 2003).

All three permutations on our model yielded stable fitness minima for at least some range of forager densities. The shared, refuge and distinct preference models all have regions of directional and disruptive selection, but the directional selection tends to drive the phenotype distribution towards areas of disruptive selection. Similar stable fitness minima have been described before using models of quantitative traits (Doebeli, 1996) and discrete allelic traits (Wilson and Turelli, 1986) with very different population dynamic equations. The fact that very different modelling strategies generate stable fitness minima suggests that disruptive selection may be a more robust and general phenomenon than previously appreciated (Bürger, 2002). This generality does not necessarily imply that sympatric speciation follows close behind. Speciation depends on a variety of other conditions such as population structure (Day, 2001), sexual dimorphism (Bolnick and Doebeli, 2003) and genetic potential for powerful assortative mating (Bolnick, 2004b). Furthermore, the model outlined here suggests that stable fitness minima depend on both forager density and the model of trade-offs one assumes.

Disruptive selection due to competition has been demonstrated empirically. For instance, pigeon guillemot (*Cepphus columba*) individuals with more specialized diets (regardless of which prey) had higher fledgling rates than generalist individuals (Golet *et al.*, 2000). Generalized isopods also show lower fitness than their specialized conspecifics in the same environment (Basset and Rossi, 1987). A field experiment with threespine sticklebacks found that trophic morphology, known to be the basis of diet variation, was subject to disruptive selection, and that the strength of the disruptive selection was sensitive to population density (Bolnick, 2004a). The latter result is quite different from the results of another stickleback experiment in which divergent selection was stronger at low population densities (Rundle *et al.*, 2003).

While it might appear at first glance that the two stickleback experiments (Rundle *et al.*, 2003; Bolnick, 2004a) contradict each other, we propose that viewing the results through the lens of our ODT model may reconcile the two studies. First, the range of population densities in the two studies may have been quite different. If Rundle and co-workers' high density was so high that all phenotypes were generalists, decreasing competition would increase individual specialization. In contrast, Bolnick's high density may have fallen in the range of individual specialization, while at low density individuals used the same top-ranked prey. A second possibility is that the laboratory-bred phenotypes, derived from hybridizing benthic and limnetic species, follow a different rank preference model than do natural single-species populations, perhaps because of different trade-off strengths.

Summary

This paper illustrates how it is possible to develop a model of individual specialization that is flexible enough to reflect any of several patterns of trade-offs that can lead to diet variation. We show that different mechanisms of individual specialization can yield different predictions about how diet variation responds to changes in population density, and the resulting fitness landscape.

Our results are, to an important degree, a fairly straightforward consequence of our assumptions (Fig. 1). However, our goal was not to produce surprising or counter-intuitive results, so much as to indicate how an existing model (optimal diet theory) could be slightly modified to explain an empirical observation about individual specialization. As far as we are aware, the relationship between optimal diet theory and individual specialization has not been formally developed, despite being obvious in hindsight. Similarly, the three alternative patterns of trade-offs have not been explicitly distinguished from each other. While each produces individual specialization in a relatively simple manner, they do have distinct effects that make it valuable to distinguish among them. Finally, unlike previous models of diet variation, the model presented here can easily be moulded to fit specific empirical cases. Previous empirical success in parameterizing ODT models makes us confident that this model can both be tested and ultimately used to help understand the ecological and evolutionary causes and consequences of phenotypic variation and individual specialization.

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