VOL. 169, NO. 2 THE AMERICAN NATURALIST FEBRUARY 2007

E-ARTICLE

The Interplay between Behavior and Morphology in the Evolutionary Dynamics of Resource Specialization

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Submitted August 22, 2006; Accepted September 20, 2006; Electronically published December 22, 2006

ABSTRACT: We analyze the consequences of diet choice behavior for the evolutionary dynamics of foraging traits by means of a mathematical model. The model is characterized by the following features. Consumers feed on two different substitutable resources that are distributed in a fine-grained manner. On encounter with a resource item, consumers decide whether to attack it so as to maximize their energy intake. Simultaneously, evolutionary change occurs in morphological traits involved in the foraging process. The assumption here is that evolution is constrained by a trade-off in the consumer's ability to forage on the alternative resources. The model predicts that flexible diet choice behavior can guide the direction of evolutionary change and mediate coexistence of different consumer types. Such polymorphisms can evolve from a monomorphic population at evolutionary branching points and also at points where a small genetic change in a trait can provoke a sharp instantaneous and nongenetic change in choice behavior. In the case of weak trade-offs, the evolutionary dynamics of a dimorphic consumer population can lead to alternative evolutionarily stable communities. The robustness of these predictions is checked with individual-based simulations and by relaxing the assumption of optimally foraging consumers.

Keywords: adaptive dynamics, coexistence, generalist, optimal diet choice, specialist, trade-off.

The fitness of an individual depends on traits that change relatively little during a lifetime and on behavioral patterns that can change on much faster timescales. Waddington pointed out that behavioral patterns can direct the evolution of less labile traits by influencing the strength and direction of selection pressures acting on other aspects of the phenotype (e.g., Waddington 1975; for reviews, see Bateson 1988; Plotkin 1988; Wcislo 1989). This article focuses on the particular case where dietary choice behavior interacts with the evolution of genetically determined foraging traits of a consumer feeding on multiple resources. To illustrate this interaction, we might think of a seed-eating bird species. Selection acts on the bill such that its success in extracting seeds is maximized and the handling time to do so is minimized. The strength and direction of selection is determined by the behavioral diet choice of the individual; if birds accept a variety of different seeds, the bill will form a compromise imposed by conflicting needs. A bill suitable for foraging on small seeds is most likely unsuitable for foraging on large seeds, and if both seed types are included in the diet, the result will be a generalist bill. If a bird chooses only small seeds, selection will favor all morphological adaptations that increase the foraging rate for them, irrespective of how detrimental such adaptations are to the bird's foraging rate for large seeds. This example illustrates how diet choice behavior sets the selection pressure for morphological characteristics. On the other hand, diet choice itself is influenced by the morphological traits of the bird because these traits determine the behavior by which an individual can maximize its energy uptake (Stephens and Krebs 1986). Another complexity arises when consumers regulate the abundance of their resources. In this case, morphological traits and diet choice behavior affect the abundance of resources, while in turn, resource availability determines diet choice behavior and thereby influences the selection pressures acting on morphological traits.

The main goal of this article is to show how behavior can interact with the evolutionary dynamics of morphological traits. As a case in point, the evolution of foraging traits of one consumer species feeding on two different resources is studied. This situation has been analyzed in detail by Rueffler et al. (2006*b*) in a study that built further

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Am. Nat. 2007. Vol. 169, pp. E34–E52.

on a series of models by Lawlor and Maynard Smith (1976), Lundberg and Stenseth (1985), Abrams (1986), and Wilson and Turelli (1986). In all of these models, it is assumed that consumers behave opportunistically; that is, they attack any prey they encounter, regardless of their morphology. Under this assumption, the evolutionary dynamics can be classified with respect to two independent properties: the shape of the trade-off curve and the possibility for selection to be frequency dependent (Rueffler et al. 2006*b*). Trade-off shape is the main determinant of evolution in the frequency-independent case, as introduced by Levins (1962). The curvature of the trade-off determines whether the generalist trait is an endpoint of evolution or is susceptible to invasion by deviating mutants. Frequency dependence, on the other hand, determines whether it is possible for different types to coexist in a protected polymorphism and whether such polymorphisms can emerge at an evolutionary branching point through a series of mutational steps of small effect (Metz et al. 1996; Geritz et al. 1998). Rueffler et al. (2006*b*) show that the presence or absence of frequency-dependent selection depends on the trait that is considered to be evolutionarily variable.

In this article, the constraint of opportunistic consumer behavior is removed, and the composition of a consumer's diet is derived from optimal diet theory (Stephens and Krebs 1986). Our approach is roughly as follows. The first step is to determine the optimal behavior of residents in a morphologically monomorphic population. Subsequently, a mutant type is envisaged that differs in its morphology from the resident population. The behavior of mutant individuals depends on their own morphology and on the abundance of the resources, as determined by the resident type. The joint effects of morphology and behavior determine whether the mutant is going to be successful or will disappear from the population. Given successful invasion of an initially rare mutant, several different configurations occur in practice for the new population dynamical equilibrium. First, the mutant replaces the former resident and shows the same diet choice as its predecessor. Second, the mutant replaces the former resident and shows a diet choice different from that of its predecessor. Third, the mutant coexists with the former resident in a protected dimorphism where both types choose the same resources as the former resident. Fourth, the mutant coexists with the former resident in a protected dimorphism in which the former resident sticks to its behavior while the mutant adopts a behavior different from that of the former resident. By following a series of consecutive mutation events, we can study the dynamic interplay between instantaneously optimized behavior and the evolutionary dynamics of morphological traits.

In order to distinguish between a consumer's ability to use different resources and a consumer's choice behavior with respect to different resources, the terminology of Rosenzweig (1981, 1987) will be adopted here. A consumer that is equally well adapted to utilize a variety of resources is called a "generalist," while a consumer that is specialized in its abilities on a few resources at the cost of being poorly adapted on other resources is called a "specialist." These terms refer to genetically determined foraging traits, whatever their exact nature, that are assumed to change on an evolutionary timescale through the invasion of novel mutants. To simplify matters, in the remainder of this article, we refer to traits of this category as morphological. At the behavioral end, a consumer attacking all encountered prey is called "opportunist," while a choosy consumer is called "selector." These terms refer to diet choice behavior, which is assumed here to be adjusted instantaneously so as to maximize energy intake. We will refer to traits of this second category as behavioral.

The structure of this article is as follows. First, a model of one opportunistic consumer feeding on two discrete resources, based on a model we introduced in an earlier article (Rueffler et al. 2006*b*), is introduced and subsequently extended toward flexible consumer behavior. The resulting evolutionary dynamics of the model with flexible diet choice are compared to those we described previously (Rueffler et al. 2006*b*) and checked with individual-based simulations. Finally, the assumption that consumers behave optimally is dropped by introducing foraging inaccuracy.

The Model

In this section, a population dynamical model of one consumer feeding on two resources is constructed. The resources are assumed to be nutritionally substitutable and homogeneously distributed in space. This model is identical to the one presented in an article by Rueffler et al. (2006*b*), where more details of the model description can be found. Based on the population dynamics of the consumer, an expression for invasion fitness is derived that is used to study the dynamics of both morphological traits and behavior. Table 1 gives an overview of all model parameters.

Population Dynamics

The derivation of the population dynamical model is based on a timescale argument (Schoener 1978; Schaffer 1981; Geritz and Kisdi 2004). The consumer population has nonoverlapping generations and reproduces once per year. The population is censused after juvenile mortality, and consumer densities are assumed to stay constant until the next reproductive event. The dynamics of the resources

Table 1: Notation

Symbol	Definition
α_i	Conversion efficiency of consumed resource into offspring
b_i	Constant resource influx
C_i	Consumer's functional response
d_i	Death rate of resource
e_i	Consumer's search efficiency (area/time step)
f_i	Capture probability for an attacked resource item
N_t	Consumer population density at time step t
p_i	Consumer's probability of attack upon encounter with resource
R_i	Density of resources (1/area)
$t_{\mathrm{m}i}$	Manipulation time (needed for treatment of an already captured resource item)
$t_{\mathrm{p}i}$	Pursuit time (needed to catch an attacked resource item)
s	Search probability (fraction of time spent searching for resources)
θ	Specialization coefficient $\in [0, 1]$ (determines location on the trade-off curve)
w	Invasion fitness
z	Strength of trade-off ($z < 1$, strong; $z = 1$, linear; $z > 1$, weak)

Note: Index i refers to one out of two possible resources.

occur on a much faster timescale, and these dynamics are followed in continuous time within a year. Since the consumer density does not change on this timescale, resource densities reach a within-year equilibrium. First, the dynamics of the consumer are introduced as a function of the as yet unspecified equilibrium densities of the resources. In the second step, the resource dynamics and their equilibrium are derived.

The recurrence equation for the consumer is given by

$$N_{t+1} = (\alpha_1 C_1 + \alpha_2 C_2) N_t, \tag{1}$$

where C_i is the functional response of the consumer for resource i. The factor α_i is the conversion efficiency of consumed resources into offspring. Prey consumption is modeled by applying a two-species version of Holling's disk equation, resulting in a saturating (type II) functional response C_i for each resource i (Case 2000):

$$C_i = \frac{e_i \hat{R}_{it} p_i f_i}{1 + e_1 \hat{R}_{1t} p_1 (t_{\mathrm{p}1} + f_1 t_{\mathrm{m}1}) + e_2 \hat{R}_{2t} p_2 (t_{\mathrm{p}2} + f_2 t_{\mathrm{m}2})}, \tag{2}$$

for $i \in \{1, 2\}$. The number of encountered prey per time step is the product of search efficiency e_i and resource density $\hat{R}_{it}$ in year t. On encounter, the consumer decides to attack the prey with probability p_i. In the article by Rueffler et al. (2006*b*), it was assumed that any prey is attacked upon encounter; that is, $p_1 = 1 = p_2$. In this article, the p values are derived according to optimal diet choice theory; the detailed procedure is described in the next section. The capture probability f_i represents the probability that an attacked prey is actually subdued. The handling time consists of two components: the pursuit time $t_{\mathrm{p}i}$ and the manipulation time $t_{\mathrm{m}i}$. The pursuit time is the time that is needed to get hold of a prey once it is detected. After the prey is caught it might still need a treatment before it can be consumed, and the duration of the treatment is the manipulation time. The denominators of C_1 and C_2 are identical and can be factored out. This factor, to be referred to as search probability

$$s = \frac{1}{1 + e_1 \hat{R}_{1t} p_1 (t_{\mathrm{p}1} + f_1 t_{\mathrm{m}1}) + e_2 \hat{R}_{2t} p_2 (t_{\mathrm{p}2} + f_2 t_{\mathrm{m}2})}, \tag{3}$$

is the fraction per time step spent searching for prey. Equation (1) can now be written as

$$N_{t+1} = s\big(\alpha_1 e_1 p_1 \hat{R}_{1t} f_1 + \alpha_2 e_2 p_2 \hat{R}_{2t} f_2\big) N_t. \tag{4}$$

The resource dynamics within the foraging season in year t are followed on a within-year timescale τ:

$$\frac{dR_{it}}{d\tau} = b_i - d_i R_{it}(\tau) - C_i N_t, \tag{5}$$

for $i \in \{1, 2\}$. We assume that resource production is constant with influx b_i. The death rate is given by d_i. Since constant consumer densities N_t are assumed within years, the following implicit description using equations (2) and (3) of the resource equilibria $\hat{R}_{it}$ can be given:

$$\hat{R}_{it} = \frac{b_i}{d_i + e_i p_i f_i s N_t}. \tag{6}$$

In order to calculate the consumer and resource equilibria, one has to solve equations (4) and (5) simultaneously using equations (2) and (3). This can be done analytically but yields rather lengthy expressions that are not shown here (Mathematica notebook available from corresponding author on request).

Diet Choice

A crucial parameter in this study is the probability of attack by the consumer upon encounter with an item of the *i*th resource, p_i. This parameter has no counterpart in the models of Lawlor and Maynard Smith (1976), Lundberg and Stenseth (1985), Abrams (1986), or Wilson and Turelli (1986). These authors assume that consumers behave opportunistically. In the model of Rueffler et al. (2006*b*), both p values are explicitly set equal to 1. In this article, adaptive consumer behavior is allowed: each individual chooses an optimal diet depending on its morphology and the abundance of the two resources. If consumers have perfect information and make optimal decisions, this procedure gives rise to the zero-one rule; that is, an individual either always or never attacks items of a certain resource (Stephens and Krebs 1986). How does this rule from the individual level extend to the population as a whole (Giraldeau and Caraco 2000)? In principle, it is conceivable that a morphologically monomorphic population consists of a mixture of different feeding types, for example, opportunists and selectors, at frequencies such that the fitness of all foraging strategies is equal. In appendix A we show that, in our model, such a behavioral polymorphism cannot occur in a morphologically monomorphic population. At population dynamical equilibrium, either all individuals are selectors or all individuals are opportunists. In order to distinguish between these different cases, resources are assigned a profitability (Stephens and Krebs 1986). It is defined as the fitness gain a certain resource item entails for the consumer per investment of time:

$$\rho_i = \frac{\alpha_i f_i}{t_{\mathrm{p}i} + f_i t_{\mathrm{m}i}}. \tag{7}$$

If pursuit time $t_{\mathrm{p}i}$ is negligible, profitability simplifies to $\rho_i = \alpha_i / t_{\mathrm{m}i}$. If both the pursuit and the handling time are negligible, attacking a prey is cost-free, resulting in opportunistic consumers. For each individual consumer, it is always beneficial to attack the resource with the higher profitability. The question is whether it pays to attack the lower-ranked resource as well. In appendix A, it is shown that a population of specialists feeding on the more profitable resource j will include the less profitable resource i in its diet when the latter resource could sustain a consumer population on its own (see also Vincent et al. 1996) and that this condition is met when

$$\rho_i > 1. \tag{8}$$

How do consumers behave in a morphologically dimorphic population? This question becomes important when the emergence of rare mutants is considered. Due to its deviating morphology, it might be beneficial for a mutant to also deviate in its behavior. This possibility will influence both a mutant's probability of invasion (see next section) and its scope to coexist with the resident. Here it is assumed that individuals are able to adjust their behavior instantaneously and that it takes no learning period to get perfect knowledge on the environmental condition. Whether a mutant attacks only the resource with the higher profitability or also feeds on the lower-ranked resource depends crucially on the resource abundances it encounters and therefore on the morphological traits and the behavior of the resident (app. A). Once a morphologically dimorphic population has reached its ecological equilibrium, the behavior of each type is again determined by condition (8).

Evolutionary Dynamics

As in Rueffler et al. (2006*b*), the evolutionary dynamics of five different foraging-related traits are studied separately (see table 2). Each trait consists of two resource-specific components. For instance, capture probability can be measured with respect to resource 1 and resource 2, denoted f_1 and f_2. Often we will write such a pair of traits as a vector: $\boldsymbol{f} = (f_1, f_2)$. We assume that evolution proceeds along a trade-off curve that constrains covariation in the two traits (fig. 1). An increase in one resource-specific component is accompanied by a decrease in the other. The trait combinations $\boldsymbol{x} = (x_1, x_2)$, where $\boldsymbol{x} \in \{\boldsymbol{e}, \boldsymbol{f}, \boldsymbol{t}_{\mathrm{p}}, \boldsymbol{t}_{\mathrm{m}}, \boldsymbol{\alpha}\}$, on this curve in the (x_1, x_2)-space are parameterized by a specialization coefficient θ that varies continuously between 0 and 1. For given resource densities, specialization for resource i corresponds to an increase in the functional response $\alpha_i C_i$, that is, to an increase in α_i, e_i, or f_i or to a decrease in $t_{\mathrm{m}i}$ or $t_{\mathrm{p}i}$ (see eq. [1]). Therefore, we have to use different parameterizations. If $\boldsymbol{x} \in \{\boldsymbol{\alpha}, \boldsymbol{e}, \boldsymbol{f}\}$, then $\boldsymbol{x} = [x_{1\max}(1-\theta)^{1/z}, x_{2\max}\theta^{1/z}]$, and if $\boldsymbol{x} \in \{\boldsymbol{t}_{\mathrm{p}}, \boldsymbol{t}_{\mathrm{m}}\}$, then $\boldsymbol{x}(\theta) = [x_{1\max} - x_{1\min}(1-\theta)^{1/z}, x_{2\max} - x_{2\min}\theta^{1/z}]$, where $x_{1\min}$, $x_{1\max}$, $x_{2\min}$, and $x_{2\max}$ are positive constants. These parameterizations are such that $\theta = 0$ corresponds to a

Table 2: Overview of traits considered evolvable

Trait	Behavioral switch
Conversion efficiency $\boldsymbol{\alpha}$	Yes
Search efficiency $\boldsymbol{e}$	No
Capture probability $\boldsymbol{f}$	Yes (if $\boldsymbol{t}_{\mathrm{m}}$ not negligible)
Manipulation time $\boldsymbol{t}_{\mathrm{m}}$	Yes
Pursuit time $\boldsymbol{t}_{\mathrm{p}}$	Yes

Note: Each parameter stands for a vector of two traits coupled by trade-off.

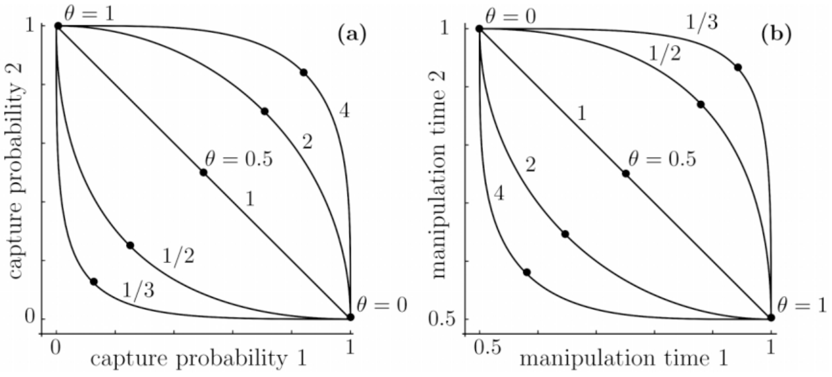


Figure 1: Trade-off in capture probability $\boldsymbol{f}$ (*a*) and manipulation time $\boldsymbol{t}_{\mathrm{m}}$ (*b*). The number next to each curve is the parameter z determining the strength of the trade-off. For capture probability, a weak trade-off ($z > 1$) corresponds to a concave curve, while for manipulation time, a weak trade-off corresponds to a convex curve. The trade-off curve is parameterized such that $\theta = 0$ corresponds to a specialist for resource 1 and $\theta = 1$ corresponds to a specialist for resource 2. Therefore, the two trade-off curves are parameterized in opposite directions. Circles halfway along the trade-off curve correspond to the generalist, with $\theta = 0.5$. Other parameter values: (*a*) $\boldsymbol{f}_{\mathrm{max}} = (1, 1)$; (*b*) $\boldsymbol{t}_{\mathrm{mmax}} = (1, 1)$, $\boldsymbol{t}_{\mathrm{mmin}} = (0.5, 0.5)$.

specialist for resource 1, while $\theta = 1$ corresponds to a specialist for resource 2. The positive parameter z determines the curvature of the trade-off curve. The trade-off curve is linear when $z = 1$. Furthermore, $z > 1$ corresponds to a weak trade-off, while $z < 1$ corresponds to a strong trade-off (fig. 1). In comparison with a linear trade-off curve, generalists with $\theta = 0.5$ have lower (higher) total functional response in case of a strong (weak) trade-off. Throughout this article, both the vector $\boldsymbol{x} = (x_1, x_2)$ and the specialization coefficient θ are used to characterize a pair of resource-specific traits on a trade-off curve.

The possibility that a rare mutant will invade a resident community depends on its invasion fitness w, that is, its long-term average per capita growth rate in an environment where the resource densities are determined by the trait values and the behavior of the resident consumers (e.g., Metz et al. 1992). The growth rate of a mutant depends on its foraging morphology and its behavior. It might therefore be tempting to account explicitly for the effect of both morphology and behavior in the notation of the fitness function by writing $w(\theta', \boldsymbol{p}', \theta, \boldsymbol{p})$. However, this notation would be misleading because it suggests that $\boldsymbol{p}$ is a free parameter that can vary independent of θ. This is not the case for two reasons. First, from inequality (8) we can conclude that the diet composition of a resident consumer population is fully determined by its morphology. In other words, at population dynamical equilibrium of consumers and resources, diet choice is an emergent property of morphology. This implies that also the resource equilibria $\hat{R}_i$ (eq. [6]) are fully determined by the θ value of the resident consumers. Second, from equation (A1) in appendix A, it follows that the diet choice of mutants is determined by their morphology and by the resource densities as set by the resident consumers. Hence, invasion fitness is fully determined by the specialization coefficients of the mutant and the resident. For $\boldsymbol{x} \in \{\boldsymbol{e}, \boldsymbol{f}, \boldsymbol{t}_{\mathrm{p}}, \boldsymbol{t}_{\mathrm{m}}\}$, invasion fitness is given by

$$w(\theta', \theta) = \alpha_1 C_1(\theta', \hat{R}_1(\theta), \hat{R}_2(\theta)) + \alpha_2 C_2(\theta', \hat{R}_1(\theta), \hat{R}_2(\theta)), \tag{9}$$

where C_i is given by equation (2) and $\hat{R}_i(\theta)$ denotes resource equilibria across years set by a consumer with trait value θ. For $\boldsymbol{x} = \boldsymbol{\alpha}$, the α_i's are functions of θ' instead of the C_i's.

We assume that mutations are rare and of small effect. Because of the first assumption, the ecological and evolutionary timescales are separated: a population has reached its ecological equilibrium before a new mutant arises. This approximation is an essential prerequisite for using the toolbox of adaptive dynamics (Metz et al. 1996; Geritz et al. 1998; Waxman and Gavrilets 2005). Both assumptions together assure that the evolutionary dynamics of clonal populations consisting of a single phenotype are equivalent to those of a diploid sexual model with additive genetics (Metz, forthcoming; Van Dooren, forthcoming).

Mutants with $w(\theta', \theta) > 1$ can invade, while mutants with $w(\theta', \theta) < 1$ certainly become extinct. The direction of evolutionary change can be derived from the fitness gradient, that is, the first derivative of the fitness function (eq. [9]) with respect to the mutant's trait evaluated at the resident's trait. Of special interest are trait values θ^* where the fitness gradient equals 0; that is,

$$0 = \left.\frac{\partial w(\theta', \theta^*)}{\partial \theta'}\right|_{\theta' = \theta^*}. \tag{10}$$

These are called evolutionarily singular points by Metz et al. (1996) and Geritz et al. (1998), and they can be classified according to two independent properties: convergence stability and invadability (Geritz et al. 1998; Rueffler et al. 2004). The first property determines whether a singular trait value is approached from nearby (Eshel 1983; Christiansen 1991; Abrams et al. 1993; Geritz et al. 1998), while the second property determines whether any consumer with a different trait value can increase in frequency when initially rare in a population dominated by individuals with θ^* (Maynard Smith 1982). Singular trait values that are both convergence stable and uninvadable are final stops of evolution and were named continuously stable strategies (CSSs) by Eshel and Motro (1981; Eshel 1983), while singular points that lack both properties are evolutionary repellers. A convergence-stable and invadable trait value is called an evolutionary branching point (Metz et al. 1996; Geritz et al. 1998). At these points, selection becomes disruptive and favors increased phenotypic variation (Rueffler et al. 2006*a*).

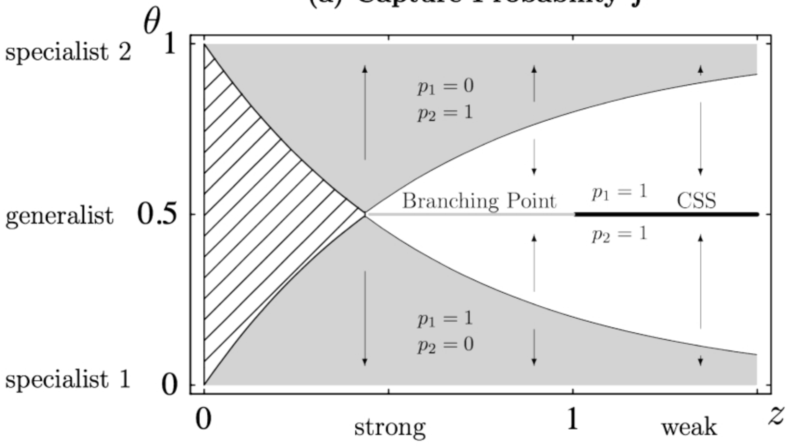
Results

From equation (7) we can see that the profitabilities ρ_i of the resources depend on α_i, f_i, t_{pi}, and t_{mi} but not on the search efficiencies e_i. Profitabilities are independent of search efficiencies because of the assumption made in optimal foraging theory that encounter without attack takes no time and entails no extra cost (Stephens and Krebs 1986). Therefore the frequency of encounter has no influence on the decision to attack a prey. Depending on the values of the other traits, either both resources or only one of them is attacked. If both resources are attacked, evolutionary dynamics for search efficiency are identical to those reported in Rueffler et al. (2006*b*), where diet choice is always opportunistic. If only one resource is attacked, then the consumer population experiences directional selection toward specialization in search efficiency for the chosen prey, independent of the initial condition and the curvature of the trade-off.

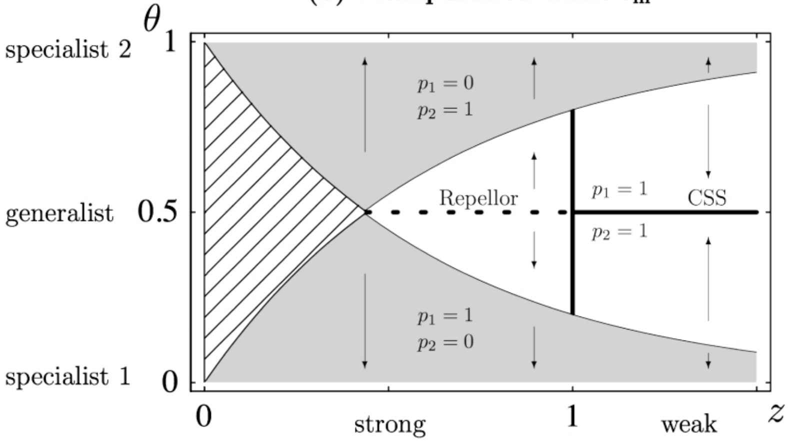
For the four other traits, behavior does depend on the trait values of the consumer and can therefore change as traits evolve. For the remainder of this article we make the assumption that all nonevolving traits and fixed parameters are symmetric with respect to the two resources. Then consumers characterized by $\theta = 0.5$ equalize the profitabilities ($\rho_1 = \rho_2$), and we refer to them as generalists. Asymmetric parameter values do not change the results qualitatively but merely make figures 2–6 less symmetric. On encounter, generalists attack both types of prey. The question is whether consumers that are characterized by $\theta = 0.5$, that is, to whom one resource is more profitable than the other will include the less profitable resource in their diet. From equation (7), we see that the two profitabilities are monotone functions of the trait values and therefore also of the specialization coefficient θ. This means that with increasing specialization, the profitability of one resource continuously increases while the profitability for the other continuously decreases. The less profitable resource is dropped from the diet as soon as its profitability decreases below 1 (eq. [8]). It follows that a consumer behaves as an opportunist in an interval around $\theta = 0.5$, as a selector for resource 1 ($\boldsymbol{p} = (1, 0)$) for values of θ sufficiently close to 0 and as a selector for resource 2 ($\boldsymbol{p} = (0, 1)$) for values of θ sufficiently close to 1. From figure 2 we can see that the region of opportunistic behavior grows with decreasing strength of the trade-off (with increasing values of z). Because weak trade-offs correspond to high profitabilities ρ_i (e_i, f_i, and α_i are increasing functions of z, while t_{pi} and t_{mi} are decreasing functions of z; see fig. 1), they make it more likely that the condition for opportunistic behavior (eq. [8]) is met.

Resident consumers switch from opportunistic to selective behavior when inequality (8) turns into an equality. For such a θ value, the two behavioral alternatives yield exactly the same fitness, and the probability of attacking the less suitable resource can take any value between 0 and 1 without affecting fitness. At these switch points, not only does the behavior of residents change discontinuously but so does that of mutants (fig. 3). Therefore the fitness gradient (eq. [10]) is not defined. These trait values are named "degenerate singular points" here because they are critical points of the fitness function but lack differentiability. The model behavior is special at these degenerate singular points, as described below.

We first discuss the consequences of flexible diet choice behavior for the evolutionary dynamics of monomorphic populations. In the central region of the trait space, where consumers behave opportunistically, the model is identical to our previous model, where diet choice was absent (Rueffler et al. 2006*b*). Hence, the generalist with $\theta = 0.5$ is a CSS for weak trade-offs. In case of strong trade-offs, the generalist is a branching point of the evolutionary dynamics for capture probability $\boldsymbol{f}$ and an evolutionary repeller for conversion efficiency $\boldsymbol{\alpha}$, pursuit time $\boldsymbol{t}_\mathrm{p}$, and manipulation time $\boldsymbol{t}_\mathrm{m}$ (figs. 2, 3). In the boundary region of the trait space where consumers behave selectively, they do not feel any trade-off. In this situation, selection favors further specialization in all traits and independently of the curvature of the trade-off (figs. 2, 3). Hence, any ancestral population of selectively behaving individuals evolves to-



(a) Capture Probability f



(b) Manipulation Time t_m

Figure 2: Bifurcation diagram of singular points with bifurcation parameter z, the parameter determining the strength of the trade-off curve. Phenotypes are represented by the specialization coefficient θ. Arrows give the direction of evolutionary change. Hatched areas indicate parameter combinations corresponding to nonviable populations. White areas indicate opportunistic foraging behavior, while gray areas indicate selective foraging behavior. Results are shown for capture probability $\boldsymbol{f}$ (*a*) and manipulation time $\boldsymbol{t}_{\mathrm{m}}$ (*b*). Results for pursuit time $\boldsymbol{t}_{\mathrm{p}}$ and conversion efficiency α are qualitatively identical to those in *b*. The solid vertical black line in *b* indicates that for $z = 1$, all morphologies corresponding to opportunistic behavior are selectively neutral. Other parameter values: (*a*) $\boldsymbol{t}_{\mathrm{m}} = (0.5, 0.5)$, $\boldsymbol{f}_{\max} = (1, 1)$; (*b*) $\boldsymbol{t}_{\mathrm{m\,min}} = (0.5, 0.5)$, $\boldsymbol{t}_{\mathrm{m\,max}} = (1, 1)$, $\boldsymbol{f} = (1, 1)$; (*a*, *b*) $\boldsymbol{\alpha} = (1, 1)$, $\boldsymbol{e} = (0.05, 0.05)$, $\boldsymbol{t}_{\mathrm{p}} = (0.1, 0.1)$, $\boldsymbol{b} = (5{,}000, 5{,}000)$, $\boldsymbol{d} = (0.1, 0.1)$.

ward complete morphological specialization, and convergence-stable singular points (CSSs and branching points) are not globally attracting anymore but attract only within the interval where the resident consumer behaves opportunistically. As a consequence, the possibility that a polymorphism emerges via an evolutionary branching point depends on initial conditions (figs. 2*a*, 3*a*).

We now turn to the evolutionary dynamics of dimorphic populations. A major result of Rueffler et al. (2006*b*) was that coexistence of different phenotypes is possible when these differ sufficiently in either search efficiency $\boldsymbol{e}$ or capture probability $\boldsymbol{f}$, while phenotypes that differ only in conversion efficiency $\boldsymbol{\alpha}$, pursuit time $\boldsymbol{t}_{\mathrm{p}}$, and manipulation time $\boldsymbol{t}_{\mathrm{m}}$ cannot coexist. In the first case, coexistence is mediated by negative frequency-dependent interactions. Frequency dependence is not present in populations dimorphic for $\boldsymbol{\alpha}$, $\boldsymbol{t}_{\mathrm{p}}$, and $\boldsymbol{t}_{\mathrm{m}}$. In appendix B, we prove that negative frequency dependence is present for any trait whenever the morphologies are sufficiently different for genotypes to differ in their diet choice. Hence, flexible diet choice can mediate coexistence of different phenotypes that could not coexist in the absence of such behavior.

Whether the behavior of a rare mutant type deviates from that of the resident is indicated in the pairwise in-

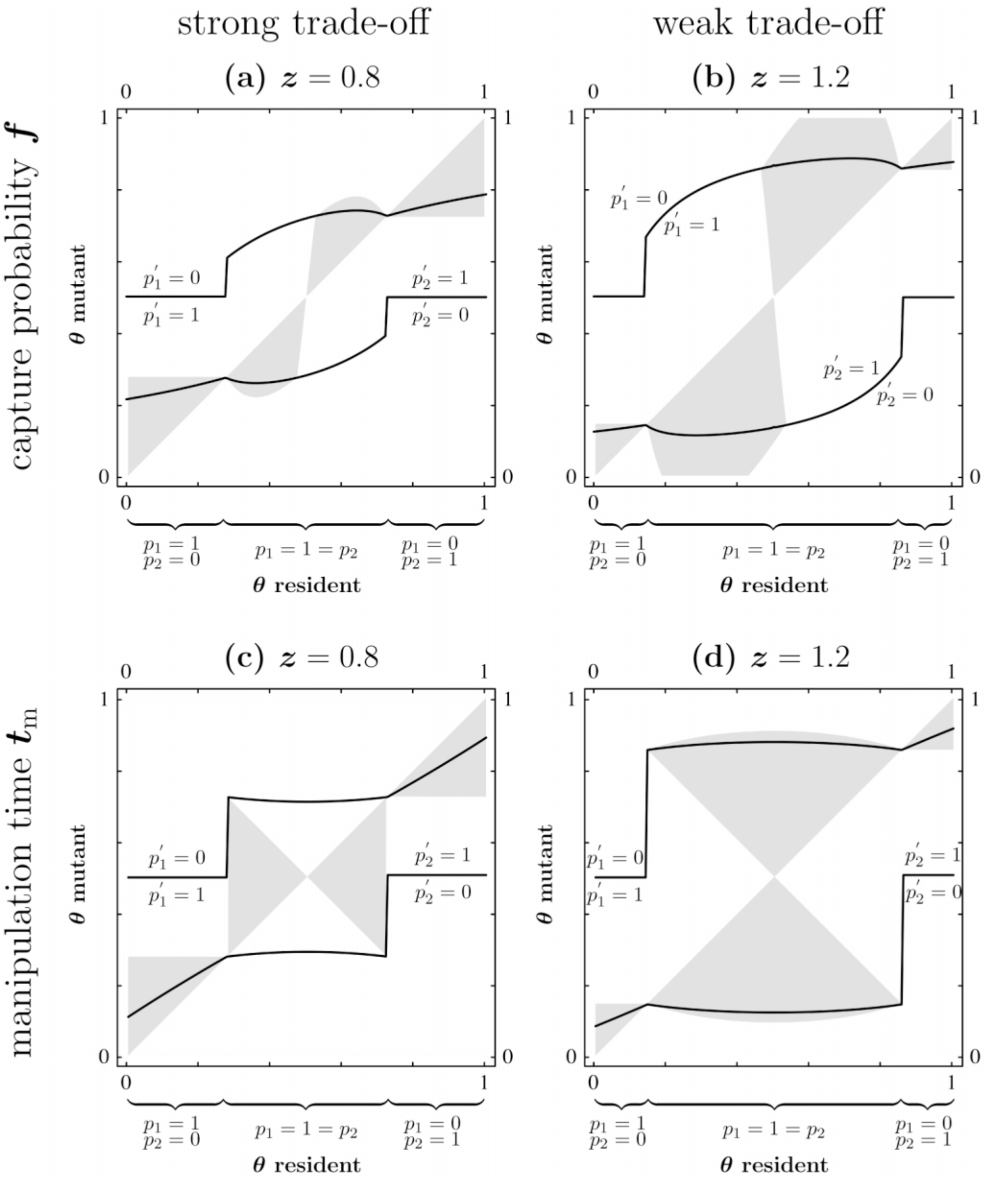


Figure 3: Pairwise invadability plots (PIPs) for capture probability f (a, b) and manipulation time t_m (c, d). White areas indicate combinations of mutants and residents where the mutant is able to invade, while gray areas correspond to combinations where the mutant is doomed to extinction. For each trait, one PIP corresponds to a strong trade-off, with $z = 0.8$ (a, c) while the other corresponds to a weak trade-off with $z = 1.2$ (b, d). Diet choice of residents, $\boldsymbol{p} = (p_1, p_2)$, is indicated at the underbraces at the X-axes. Black lines are mutant choice boundaries that indicate changes in the diet choice of mutants, $\boldsymbol{p}' = (p_1', p_2')$. Other parameter values as in figure 2.

vadability plots (PIPs) of figure 3 by mutant choice boundaries. These lines are defined by an equality in the switching conditions (eq. [A1] in app. A). The two types in a given mutant-resident combination differ in their behavior when a vertical line drawn from the main diagonal at the resident's trait value to the mutant's trait value crosses a mutant choice boundary. After the successful invasion of a mutant, two scenarios have to be distinguished. The individuals of a successful mutant population either stick to their new behavior until the new population dynamical attractor is reached or switch behavior again once their population size has passed a certain threshold. Which scenario applies to a given mutant-resident combination can also be deduced from the mutant choice boundaries. The first happens when the mutant is sufficiently specialized so it would behave selectively if it were the only resident

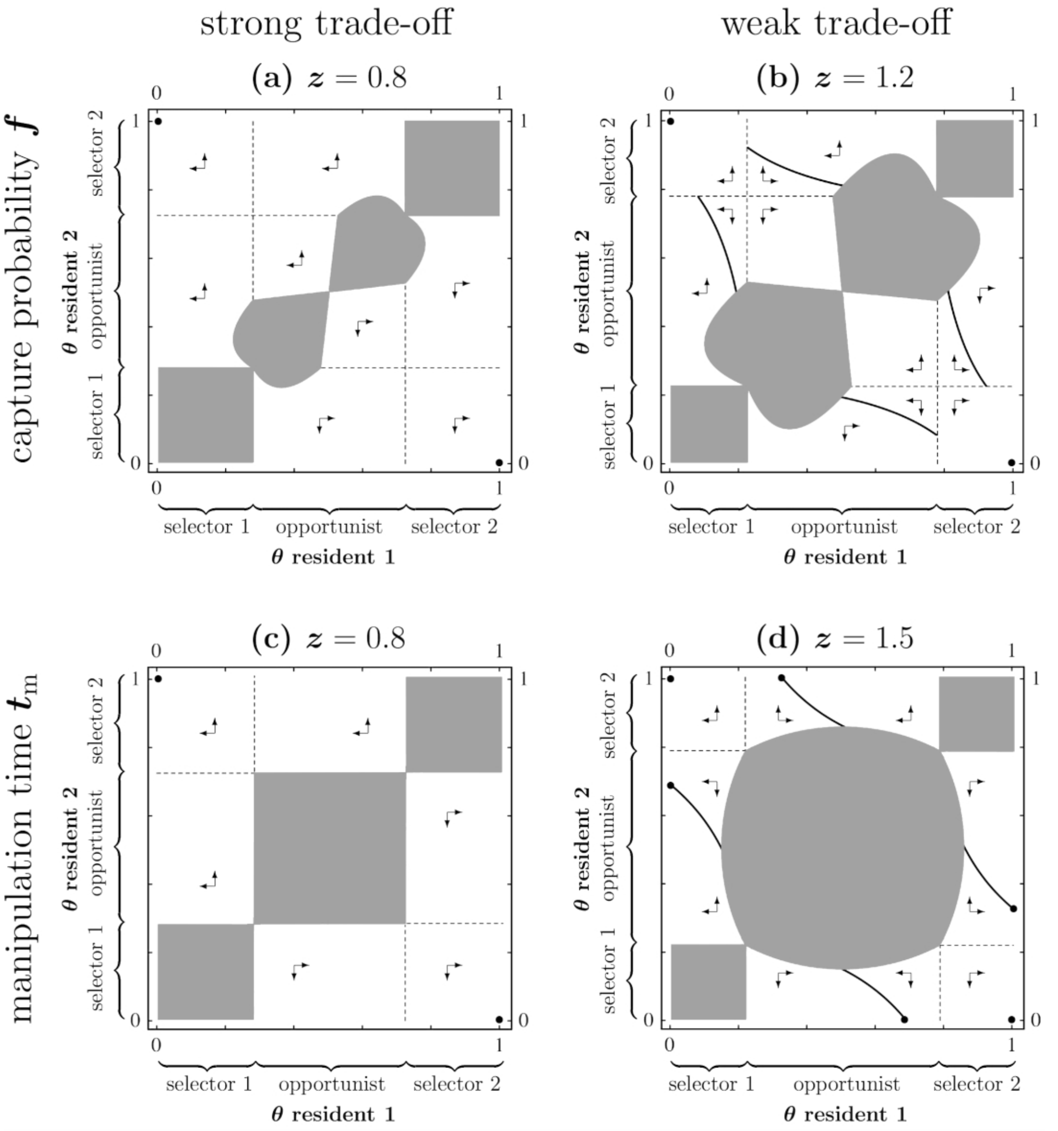


Figure 4: Evolution in dimorphic populations for capture probability f (*a*, *b*) and manipulation time t_m (*c*, *d*) for strong trade-offs with $z = 0.8$ (*a*, *c*) and weak trade-offs with $z = 1.2$ (*b*) and $z = 1.5$ (*d*). Each axis gives the value of the specialization coefficient θ of one consumer type. White areas correspond to phenotype combinations that can coexist in a protected dimorphism. Diet choice at dimorphic population dynamical equilibrium for each type is indicated by the underbraces at each axis. Arrows indicate the direction of selection, and dots indicate evolutionary stable endpoints. Thick lines correspond to stable isoclines, while dashed lines correspond to a change in the diet composition of one of the two types. Other parameter values as in figure 2 except for $\boldsymbol{\alpha} = (0.85, 0.85)$ in *b* and $\boldsymbol{\alpha} = (0.92, 0.92)$ in *d*.

(figs. 3, 4). The latter happens when the mutant trait lies in the region of trait space where trait values correspond to a selector when they are rare and to an opportunist when they are the resident (figs. 3, 4). In this case, a horizontal line drawn from the mutant's trait to the main diagonal crosses a mutant choice boundary again.

Once a population is dimorphic, the further coevolutionary dynamics of the two types can be read from figure 4. The depicted plots show the sets of pairs of phenotypes that are able to coexist in a protected dimorphism. These sets are given by the overlapping parts of the white region of a PIP and its mirror image taken along the main diagonal (for further details, see Metz et al. 1996; Geritz et al. 1998, 1999). Note that the plots in figure 4 are symmetrical with respect to the main diagonal. The two symmetrical parts show the same dynamics but with a reversed

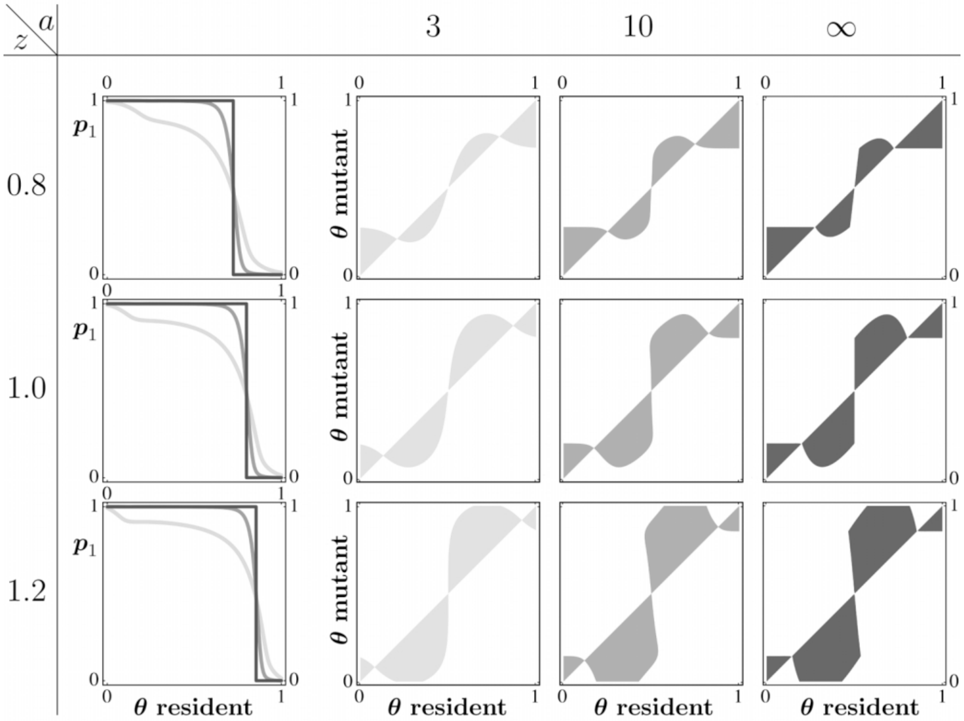


Figure 5: Pairwise invadability plots (PIPs) for capture probability ***f*** for different values of the accuracy parameter a (in columns) and different curvatures for the trade-off, as determined by z (in rows). Figures in the first column show the probability of attack of a resident consumer upon encounter with an item of resource 1 (p_1, on the Y-axis) as a function of the specialization coefficient θ of the resident (X-axis) for $a = 3$, $a = 10$, and $a = \infty$ (darker curves correspond to higher values of a). Curves for p_2 are given by the mirror image of each curve around $\theta = 0.5$. Switch curves in the first figure in a row and PIPs in the same row that are generated with the same value of a are shown in same shade of gray. Note that the sharp drop-off in p_1 occurs for higher values of θ with higher values of z. Other parameter values as in figure 2.

numbering of the two types. The direction of selection acting on two coexisting types, indicated by the arrows in figure 4, can be derived graphically with a geometrical method described in Rueffler et al. (2004) but with taking into account whether a mutant changes behavior.

Polymorphisms can emerge in two different ways. First, in case of capture probability ***f***, a dimorphism can emerge at an evolutionary branching point (figs. 2, 3). In the initial phase after branching, the coexisting types remain opportunists (figs. 4*a*, 7*a*). In the course of further divergence, both types become genetically more specialized, and each type approaches the parameter region where prey selection pays off. When the rate of evolution differs in the two types, one of them turns into a selector while the other is still an opportunist. This results in a population with "nested" behavior, where the diet of the selector consists of a subset of the diet of the opportunist. Both types still experience directional selection toward further specialization, and finally the population will reach a continuously stable coalition with two extreme specialists that are selectors for different resources (fig. 4*a*). To check whether these results are robust against deviations from the assumption of strict mutation limitation, we present some individual-based simulations in figure 7 (see app. C for details). In figure 7*a*, the simulation starts with an opportunistically behaving monomorphic population characterized by $\theta = 0.35$. Initially, evolutionary change occurs in the direction of the generalist. Then phenotypes on opposite sides of the branching point at $\theta = 0.5$ can establish, giving rise to two diverging lineages. The lineage specializing on resource 2 turns into a selector slightly earlier than the other lineage specializing on resource 1 does. Once both types behave selectively, rapid evolution leads to complete specialization.

Second, polymorphisms can emerge when a mutant appears that differs sufficiently from the resident in its morphology and, as a consequence, starts to behave differently. To see this, we have to compare figures 3 and 4. For most mutant-resident combinations where the mutant is able to invade and differs in its behavior from the resident (fig. 3), the two types are able to coexist in a protected polymorphism (fig. 4). In case of strong trade-offs, this route

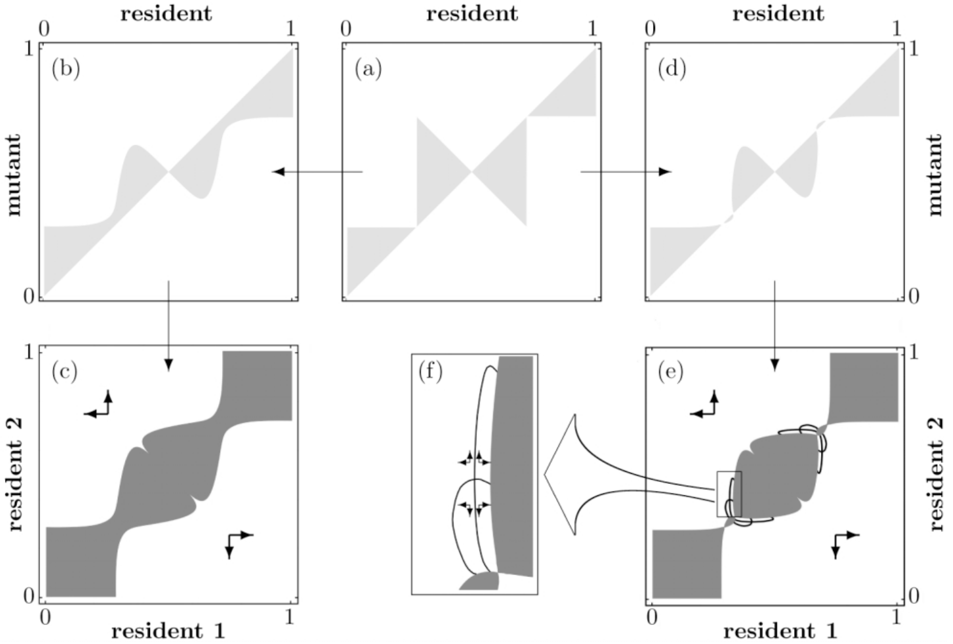


Figure 6: Effect of foraging inaccuracy on the evolution of manipulation time $\boldsymbol{t}_\mathrm{m}$ in monomorphic (*a*, *b*, *d*) and dimorphic (*c*, *e*, *f*) populations. *a*, Example of a pairwise invadability plot (PIP) without foraging inaccuracy ($a = \infty$). This PIP can be generated from two different parameter combinations: (i) $z = 0.56$, $\boldsymbol{t}_\mathrm{p} = (0.05, 0.05)$; and (ii) $z = 0.8$, $\boldsymbol{t}_\mathrm{p} = (0.1, 0.1)$. *b*, *d*, The effect of foraging inaccuracy ($a = 50$) for each of these parameter combinations. For the first set of parameters, the degenerate singular points disappear altogether (*b*). As a consequence, two very similar resident types (close to the main diagonal) can never coexist (*c*). For the second set of parameters, the degenerate singular points unfold into an evolutionary repeller and a continuously stable strategy (*d*). In this case, coexistence of two types close to the main diagonal becomes possible (*e*). However, evolutionary isoclines appear, showing that similar resident types experience convergent selection such that a dimorphic population collapses to become monomorphic again (*e*, *f*). Other parameter values as in figure 2.

to polymorphism also leads to a coalition of two selectors that are each completely specialized on a single resource (fig. 4*a*, 4*c*). With weak trade-offs, an alternative evolutionarily stable coalition exists due to the presence of evolutionarily attracting isoclines (fig. 4*b*, 4*d*). Isoclines are found at the zeroes of the dimorphic fitness gradient (Geritz et al. 1998, 1999):

$$0 = \left.\frac{\partial w(\theta', \theta^1, \theta^2)}{\partial \theta'}\right|_{\theta' = \theta^i}. \tag{11}$$

Superscripts 1 and 2 refer to the two coexisting types of a dimorphic resident community, and isoclines for changes in resident 1 ($i = 1$) and resident 2 ($i = 2$) can exist. However, in our case, a single isocline exists for the opportunists in the region of the phase plane where one type behaves as an opportunist while the other behaves as a selector (fig. 4*b*, 4*d*). In dimorphic populations residing on such an isocline, the opportunist cannot be invaded by any other type while the selector experiences directional selection, just as elsewhere. Whenever the selectors become invaded by a more specialized type, the trait values of the residents no longer reside on the isocline and opportunists become susceptible to invasion by mutants that improve on the resource neglected by the selector. Isoclines attach to the boundary of the set of phenotypes that can coexist vertically above and below and horizontally to the left and to the right of the singular point at $\theta = 0.5$ (fig. 4*b*, 4*d*; Geritz et al. 1999). If the trade-off is sufficiently weak, the isoclines extend to the boundary of the trait space ($z = 1.5$, fig. 4*d*). This boundary point constitutes an alternative evolutionarily stable coalition, where one type is a specialized selector and the other type behaves opportunistically and is morphologically intermediate with a bias toward the resource not taken by the selector. With decreasing values of z, the opportunist in the coalition becomes increasingly specialized on the resource not taken by the selector until it finally pays for the opportunist to become a selector as well ($z = 1.2$; fig. 4*b*). At this point, the coevolutionary dynamics enter the region of the trait space where both types behave selectively, resulting in complete morphological specialization. In figure 7*c*, we demonstrate this outcome with individual-based simula-

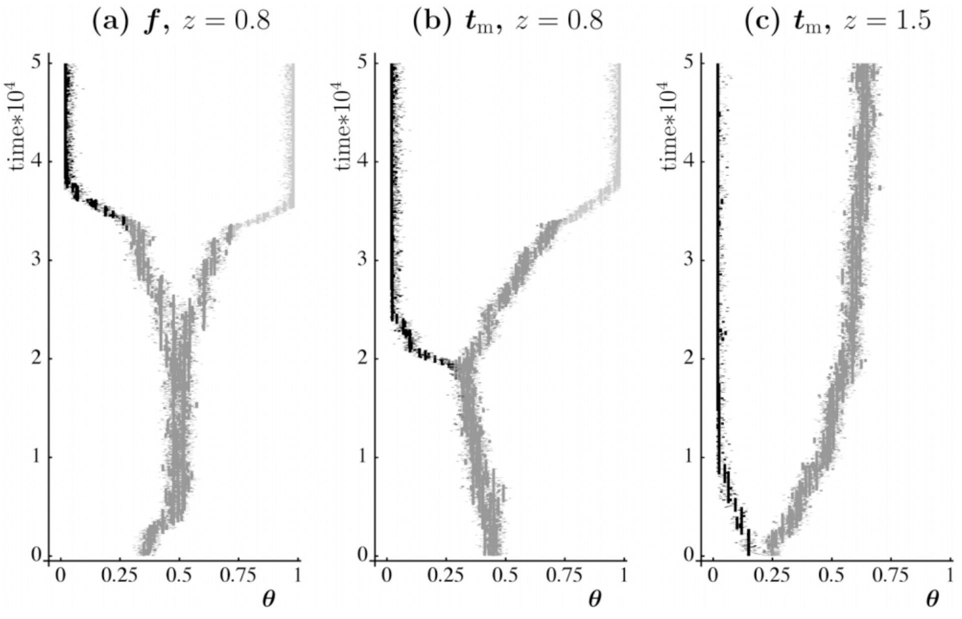


Figure 7: Individual-based simulations of trait distributions for capture probability f (*a*) and manipulation time t_m (*b*, *c*). Different shades of gray indicate behavior: black corresponds to selectors for resource 1, dark gray to opportunists, and light gray to selectors for resource 2. The populations in *a* and *b* are initially monomorphic and characterized by $\theta = 0.35$ (*a*) and $\theta = 0.45$ (*b*). The population in *c* consists of monomorphic population characterized by $\theta = 0.25$ to which 10 immigrants, characterized by $\theta = 0.15$, are added. Parameter values as in figure 4. See appendix C for further details.

tions. Since in the case of weak trade-offs a polymorphism cannot emerge via mutations of small effect, the simulation is initialized by adding 10 immigrants, characterized by $\theta = 0.15$, to a resident consumer population at its ecological equilibrium of 9,100 individuals, characterized by $\theta = 0.25$.

Although no branching point in the sense of the adaptive dynamics literature (Metz et al. 1996; Geritz et al. 1998) exists for α, t_p, and t_m, a polymorphism can nevertheless evolve through a series of mutations of small effect. To see this, consider a scenario with an ancestral type characterized by a value of θ slightly smaller than 0.5. This phenotype behaves opportunistically, and selection favors mutants with smaller θ values, that is, types with a shorter manipulation time for resource 1 (see figs. 2*b*, 3*c*). At some point, evolution has driven the population so close to the degenerate singular point that a mutant with a smaller trait value than the resident drops resource 2 from its diet (fig. 3*c*). Because resident and mutant differ in behavior, they can coexist despite their small morphological difference (fig. 4*c*). Now character displacement between the two phenotypes takes place, and the selector becomes completely specialized for resource 1, while the opportunist evolves in the opposite direction to eventually become a specialist for resource 2. In this scenario, degenerate singular points give rise to dimorphisms through a series of mutations of small effect, a property that was previously known only from evolutionary branching points. This scenario is confirmed by individual-based simulations (fig. 7*b*).

Adding Foraging Inaccuracy

Empirical tests of optimal diet choice theory revealed that prey choice is better described by sigmoid functions than by the step functions reflecting the zero-one rule (Krebs et al. 1977). Deviations from the theoretical predictions of optimal foraging theory can be expected for several reasons. Consumers are likely to have incomplete information about the abundance of resources and imprecise estimates about their profitabilities, that is, about their own performance with respect to the different resources. Here, we investigate the robustness of our results with respect to deviations from the zero-one rule by assuming that consumers do have perfect information but make mistakes in their decisions and that the magnitude of these mistakes increases with decreasing cost of nonoptimal behavior, as determined by the fitness difference between opportunistic and selective behavior. We implement this semimechanistic argument by using the following equation to describe the probability of attack:

$$p_i = \left(1 + \exp\left\{a\left[\frac{\alpha_j e_j \hat{R}_j(\theta) f_j}{1 + e_j \hat{R}_j(\theta)(t_{\mathrm{p}j} + f_j t_{\mathrm{m}j})} - \rho_i\right]\right\}\right)^{-1}. \qquad (12)$$

When p_i is plotted as function of the specialization coefficient θ, we get a sigmoid curve with $p_i = 0.5$ at the trait value where an optimally behaving consumer would switch in its diet choice (fig. 5, *first column*). The foraging accuracy parameter a determines to what extent diet choice deviates from the zero-one rule. If $a \to \infty$, perfect decision-making is approached, and if $a \to 0$, prey choice becomes increasingly random. With the introduction of sigmoid prey switch curves, the mutant choice boundaries in figure 3 and the dashed lines in figure 4, which both reflect the abrupt switch in prey choice of accurately behaving individuals, no longer make sense. The fitness function becomes differentiable at these points, and the kinks in the contour lines of the fitness function get rounded (fig. 5). When the accuracy parameter a decreases, diet choice becomes more and more balanced, and therefore the evolutionary dynamics become more and more similar to that found in the absence of diet choice (Rueffler et al. 2006*b*). In cases with a convergence-stable generalist (CSS or a branching point), the basin of attraction of the generalist grows with decreasing accuracy. This entails shrinking basins of attraction for the two specialists (fig. 5). In case of a repelling generalist, that is, for strong trade-offs in combination with evolving manipulation time $\boldsymbol{t}_{\mathrm{m}}$, pursuit time $\boldsymbol{t}_{\mathrm{p}}$, or conversion efficiency $\boldsymbol{\alpha}$, the situation is more complicated. Two qualitatively different ways exist in which a degenerate singular point can unfold. Figure 6*b* shows the first scenario, in which the degenerate singular points disappear. The generalist strategy immediately becomes globally repelling, as in the case without prey choice. Figure 6*c* shows the second scenario, in which a slight inaccuracy changes the degenerate singular points into a CSS and a repeller.

Overall, the coevolutionary dynamics of two coexisting types do not change qualitatively when foraging inaccuracy is introduced. In all cases, the combination of two highly specialized selectors remains a continuously stable coalition. Also, the location of the evolutionary isocline that occurs in combination with weak trade-offs does not change qualitatively. Hence, the alternative coalition consisting of one opportunist and one selector remains convergence stable when trade-offs are sufficiently weak. Only the emergence of polymorphisms by small mutational steps at degenerate singular points (as described in the previous section) is hampered. That scenario relied on the fact that a mutant that differs only slightly in its morphology from the resident can differ in its behavior from the resident. When foraging inaccuracy causes the degenerate singular point to disappear altogether (fig. 6*b*), mutants have to differ more strongly from the resident in order to enter the area of coexistence, compared to the case without foraging inaccuracy (cf. fig. 4 with fig. 6*c*). When foraging inaccuracy causes the degenerate singular point to give rise to a CSS and a repeller (fig. 6*d*), a small mutational step can still lead into the area of coexistence (fig. 6*e*). However, in this case, two new evolutionary isoclines appear that not only prevent further divergence of the newly established type but even impose convergent selection such that the dimorphic population eventually collapses to become monomorphic again (fig. 6*f*). Only mutants that lie beyond these isoclines can give rise to dimorphisms that undergo disruptive selection.

Discussion

This article focuses on the consequences of behavioral diet choice for the evolution of various foraging traits in a consumer facing two different resources. A mathematical model is analyzed that builds on an existing model for the evolution of morphological characters (Rueffler et al. 2006*b*). In the original model, consumers behave opportunistically and every resource item is attacked upon encounter. In this study, each individual chooses to attack resource items so as to maximize its energy intake.

The results show that the added feature of behavioral flexibility affects various aspects of the evolutionary dynamics. (i) Behavior guides the direction of selection. Only resources that are included in the diet entail a selective force. Consumers that choose few resources will also become specialized in terms of their evolving traits to exploit these resources efficiently. This aspect has been noted earlier (e.g., Stenseth 1984; Abrams 1986; Brown 1990). (ii) A convergence-stable singular point (CSS or branching point) will be approached only when the ancestral population behaves opportunistically. Whenever the ancestral population behaves selectively, directional selection will lead toward specialized morphologies. Therefore, diet choice reduces the likelihood that a population evolves to become a generalist, and whether a population can diversify via a branching point depends on initial conditions. (iii) Successful mutants that differ in their behavior from the resident will in most cases not replace the resident but coexist with it in a protected polymorphism. The emergence of polymorphisms mediated by differential diet choice can occur for a wide range of parameters through the immigration of phenotypes that deviate sufficiently from the resident or through mutations of large effect. However, this mechanism can also create polymorphism in the absence of immigration, with mutational steps constrained to be small. This happens whenever a population evolves toward a degenerate singular point where the less profitable resource becomes so unattractive that a slightly more specialized mutant turns into a selector. This process, which generically gives rise to to polymorphisms through a series of mutations of small effect, has to our knowledge not been described previously. (iv) The incorporation of flexible diet choice enlarges the set of conditions allowing for coexistence. Whenever two types have mutually exclusive diets, coexistence is guaranteed. Furthermore, coexistence is possible when the two types have nested diets, that is, when one type feeds on both resources while the other selects only one of them. For conversion efficiency $\boldsymbol{\alpha}$, pursuit time $\boldsymbol{t}_{\mathrm{p}}$, and manipulation time $\boldsymbol{t}_{\mathrm{m}}$, diet choice is the sole mechanism to mediate coexistence. (v) In models lacking diet choice, the only continuously stable coalition (i.e., attracting and coevolutionarily stable community) consists of two extreme specialists (Lawlor and Maynard Smith 1976; Abrams 1986; Rueffler et al. 2006*b*). In our model, two additional continuously stable coalitions exist, given sufficiently weak trade-offs. These consist of one selecting specialist and one opportunistic intermediate consumer that is biased in its morphology toward the resource that is neglected by the specialist.

Some related models have been analyzed previously but with different emphasis. To our knowledge, Stenseth (1984) was the first to combine the evolutionary dynamics of consumer traits with optimal diet choice theory. Based on qualitative arguments, he concluded that abundant resources that are difficult to handle favor selective specialists, while easy to handle and scarce resources select for opportunistic generalists in case of weak trade-offs and for opportunistic specialists in case of strong trade-offs. Stenseth's model does not incorporate explicit resource dynamics and therefore does not allow for dynamic feedbacks between consumer and resource densities and diet choice behavior. Brown (1990, 1996) considered a consumer in a patchy environment that can specialize in terms of its morphology on different patch types and that can choose which patch type to exploit. He investigated the possible monomorphic and polymorphic evolutionary endpoints that such a system can adopt. Brown's model is special insofar as it allows for a mixture of opportunists and selectors in a morphologically monomorphic population, an impossible constellation in the model analyzed here. At such trait values, the population is prone to become morphologically polymorphic because selectors and opportunists experience very different selection pressures. Vincent et al. (1996) investigated the scope for coexistence of different consumer types in a model that yields a fitness function equivalent to the one analyzed here. Although these authors allow for behavioral diet choice, they dismiss the possibility that this mechanism mediates coexistence. In the model version where Vincent et al. consider mixed substitutable resources, they limit their analysis to the region of the trait space where consumers behave opportunistically. They argue that resources that are not included in the diet cannot be considered a resource because they cannot sustain a consumer population on their own. Our results show that this viewpoint excludes a set of interesting results when populations evolve so resources become excluded from or included in the diet over evolutionary time. More recently, Svanbäck and Bolnick (2005) analyzed a simple population genetic model for the evolution of handling time. These authors show that diet choice can lead to disruptive selection across a wide range of conditions. However, Svanbäck and Bolnick keep consumer dynamics constant and therefore cannot explore the consequences of the feedback between population dynamics, diet choice, and trait evolution. Abrams and a coworker (Abrams 1999; Abrams and Matsuda 2003, 2004) focus on population dynamical systems of one or more consumer types feeding on two prey, where the population dynamics do not reach a stable equilibrium. They show that noninstantaneous diet choice or relatively fast evolutionary changes can cause complex population dynamics and thereby lead to unexpected mean trait values. Abrams (2006) shows that under these conditions, even trimorphisms can readily occur.

Optimal foraging theory predicts that resources with a low profitability are neglected by consumers when resources with a higher profitability are sufficiently abundant (Stephens and Krebs 1986). This prediction is valid at the ecological timescale where resource densities vary in time. The prediction of optimal foraging theory does not apply when consumer and resource populations regulate each other such that they reach stable population dynamical equilibria. In this situation, the resource densities are not free parameters but functions of the evolving consumer traits. This explains why a resource is included in the diet by a resident consumer when the profitability ρ_i is greater than unity (eq. [8]), a condition that depends purely on consumer traits and not on the population dynamics of the resource (eq. [7]). Therefore, if we account for the feedback between consumer and resource densities, the statement of Stenseth (1984) that abundant resources favor selective consumers that subsequently undergo morphological specialization is not relevant. In the model presented here, the ecological timescale does apply during the process of invasion. An initially rare mutant type does not affect the resource densities yet. In this phase, it can be beneficial to feed selectively on the more profitable resource. With increasing frequency of the mutant type, it depletes its preferred resource so that in the end, when it reaches fixation, it may become beneficial to also forage on the less suitable resource.

Our model is based on the assumption of clonal genetics. In the case of rare mutations with small phenotypic effect and random mating, the results apply to monomorphic diploid sexual populations and polygenic traits. In case of polymorphic sexually reproducing populations, the course of evolution cannot be predicted straightforwardly from a clonal model. However, some predictions can still be made. Intermediate heterozygotes will behave as either opportunists or selectors. Whenever such heterozygotes are inferior, disruptive selection favors any mechanism that prevents the production of heterozygotes (Rueffler et al. 2006*a*). Processes such as the evolution of assortative mating or dominance modification lead to two discrete phenotypes, and in this situation, we expect that long-term evolution will lead to the evolutionary endpoints predicted by the clonal model. The condition of heterozygote inferiority in a behaviorally polymorphic population is also given in a model by Svanbäck and Bolnick (2005), where it indeed imposes disruptive selection. The problem of heterozygote inferiority is circumvented altogether when disruptive selection leads to a phenotypic dimorphism that does not require a new genetic polymorphism (Rueffler et al. 2006*a*). In, for example, a sexual dimorphism, a polymorphism emerges from a population with undifferentiated sexes by a mutation in sex-specific genes that are already present. If the two sexes become sufficiently different in terms of their morphology, they will also choose different resources and subsequently undergo further morphological differentiation (Bolnick and Doebeli 2003; Van Dooren et al. 2004).

Our model is based on three different limits. (i) Mutations are rare. This allows for the separation of ecological and evolutionary timescales. (ii) Foraging accuracy is high. This leads to the zero-one rule of diet choice. (iii) Learning is fast so that the optimal behavior is adopted immediately. Of course, none of these limits is a proper description of reality. They are considered primarily because they make the model mathematically tractable. Investigating such limits is generally informative as a guideline for understanding the phenomena we observe in nature, but it is important to explore how violation of the limiting situation alters the model behavior. We show that our results are robust against deviations from the first limit by means of individual-based simulations. In these simulations, evolution is not strictly mutation limited, and new mutants frequently arise before previous ones have gone to fixation. These simulations also account for the effects of drift and of stochastic changes in population size. Deviations from the second limit are investigated by introducing inaccurately foraging consumers. In this case, the steplike prey switch reflecting the zero-one rule is replaced by a sigmoidal switch, and we show that moderate inaccuracies do not change the qualitative model results. The third limit is the one most difficult to explore because it corresponds to a change in behavior during an organism's life span. If individuals need a long learning period before they behave optimally, then the extinction probability of rare mutants might increase. This would slow down the evolutionary dynamics.

In all scenarios considered here, traits evolved one at a time and not simultaneously as in natural systems. The simultaneous evolution of several traits might lead to different predictions. Imagine a scenario where a trait that allows for evolutionary branching, for example, search efficiency $\boldsymbol{e}$, jointly evolves with a trait that does not allow for evolutionary branching, for example, manipulation time $\boldsymbol{t}_\mathrm{m}$. Assume further that no correlation exists between $\boldsymbol{e}$ and $\boldsymbol{t}_\mathrm{m}$ and that, therefore, the trait space can be parameterized in two independent specialization coefficients, one describing the degree of specialization in terms of $\boldsymbol{e}$ and one describing it in terms of $\boldsymbol{t}_\mathrm{m}$. If both trade-offs are strong, then selection in $\boldsymbol{e}$ acts in the direction of the generalist's trait, where a population would subsequently experience disruptive selection, while selection in $\boldsymbol{t}_\mathrm{m}$ acts toward increasing specialization. Under these assumptions, the phenotype that corresponds to a generalist in both $\boldsymbol{e}$ and $\boldsymbol{t}_\mathrm{m}$ turns into a saddle point of the two-dimensional evolutionary dynamics. In this case, polymorphisms can arise in two different ways. If evolution in search efficiency proceeds faster than in manipulation time, then the population will evolve toward the branching point and become dimorphic in search efficiency. On the contrary, if evolutionary change occurs faster for manipulation time than for search efficiency, then the population will evolve toward a degenerate singular point, and the population will become dimorphic in manipulation time as soon as a mutant appears that behaves as selector. In either case, whenever the population is dimorphic in one trait, selection favors a corresponding diversification in the other trait. Eventually the population will consist of two types, a selector for resource 1 with high search efficiency and a low manipulation time for this resource and a selector for resource 2 with the corresponding adaptations in search efficiency and manipulation time. In this example, the evolutionary endpoint does not differ from the one predicted based on the evolution of either trait in isolation. However, the adopted route to this endpoint appears to be sensitive to initial conditions and to details of the mutational process.

To summarize, this article shows that behavioral flexibility in diet choice can influence various aspects of the evolutionary dynamics of morphological consumer traits. Behavior guides natural selection since only resources that are preyed on contribute to the direction of selection a consumer experiences. Furthermore, it is shown that diet choice behavior can mediate coexistence of different consumer types that could not coexist when diet choice is fixed. The effect of flexible diet choice on the emergence of polymorphism is twofold. On the one hand, flexible diet choice decreases the basin of attraction of evolutionary branching points. On the other hand, successful mutants that differ in their diet choice from residents are able to coexist in a protected polymorphism. This mechanism can even generate polymorphisms through a series of mutations of small effect. The dynamics of coevolving consumer populations can lead not only to a community of two selectively behaving specialists but also to a community of a selective specialist and a more intermediate opportunistic phenotype.

Acknowledgments

C.R. was supported by the Research Council for Earth and Life Sciences (ALW), which is subsidized by the Netherlands Organization for Scientific Research (NWO), and by a Discovery Grant to P. Abrams from the Natural Sciences and Engineering Research Council of Canada. T.V.D. was supported by a Dutch NWO-VENI grant. C.R. thanks M. Durinx and F. Jacobs for helpful discussions and P. Abrams for comments.

APPENDIX A

Diet Choice

Each consumer individual always attacks the resource with the higher profitability ρ_i (eq. [7]). Consider the case where $\rho_1 > \rho_2$. A population of selectors for resource 1 can be invaded by opportunistically behaving individuals with the same morphology if

$$\rho_2 > \frac{\alpha_1 e_1 \hat{R}_1(\theta, (1, 0)) f_1}{1 + e_1 \hat{R}_1(\theta, (1, 0))(t_{\mathrm{p}1} + f_1 t_{\mathrm{m}1})}, \tag{A1}$$

where $\hat{R}_i(\theta, (1, 0))$ indicates the equilibrium density of the first resource as it results from consumption by a monomorphic consumer population with trait value θ and behavior $\boldsymbol{p} = (1, 0)$ at its equilibrium $\hat{N}$. The right-hand side of inequality (A1) by definition equals 1 because it describes the the per capita growth rate of a consumer at ecological equilibrium. Hence, condition (A1) simplifies to $\rho_2 > 1$ (eq. [8]). The profitability ρ_i is the limit of the per capita growth rate of a selector for resource i for large resource abundance:

$$\lim_{R_i \to \infty} \frac{\alpha_i e_i R_i f_i}{1 + e_i R_i (t_{\mathrm{p}i} + f_i t_{\mathrm{m}i})} = \frac{\alpha_i f_i}{t_{\mathrm{p}i} + f_i t_{\mathrm{m}i}}.$$

Therefore, inequality (A1) is equivalent to demanding that resource 2 can sustain a viable population on its own, given that the resource is sufficiently abundant. In case condition (A1) is fulfilled, one has to check whether opportunists will replace selectors or both behaviors can coexist, that is, whether the two behavioral strategies can invade each other. Mutual invadability is given when next to condition (A1) the following condition also holds:

$$\rho_2 < \frac{\alpha_1 e_1 \hat{R}_1(\theta, (1, 1)) f_1}{1 + e_1 \hat{R}_1(\theta, (1, 1))(t_{\mathrm{p}1} + f_1 t_{\mathrm{m}1})}. \tag{A2}$$

For this model, we prove that in a morphologically monomorphic population at population dynamical equilibrium all individuals behave either as selectors or as opportunists; that is, the conditions (A1) and (A2) cannot be fulfilled simultaneously. This follows from the fact that if $\rho_1 > \rho_2 > 1$, then the density of resource 1 in the presence of an opportunistic consumer population, $\hat{R}_1(\theta, (1, 1))$, is lower than in the presence of a population that feeds selectively on resource 1, $\hat{R}_1(\theta,(1,0))$, where in each case it is assumed that the consumer population is at its population dynamical equilibrium (Mathematica notebook spelling out the algebraic details available from corresponding author on request).

In order to determine the behavior of mutants the same condition (A1) has to be employed. However, for mutants, the right-hand side of this equation is generally not equal to 1 because the traits governing the mutant's functional response do not equal the traits that determine the abundance of the resources.

APPENDIX B

Frequency-Dependent Selection

In this appendix, we prove that for our model, selection is frequency dependent whenever a population is behaviorally polymorphic, that is, when different genotypes show different diet compositions. In classical population genetics, frequency dependence is defined as a dependence of selection coefficients on allele frequencies. In density-regulated populations, a type with a positive growth rate when rare will have a zero growth rate after fixation, given that the population is at its population dynamical attractor. Hence, under density regulation, invasion fitness depends on frequencies by default, and the classical definition of frequency dependence becomes meaningless. Following Heino et al. (1998), we therefore use the term in a slightly different way, which allows us to distinguish cases where the direction of evolutionary change depends on the frequency of different phenotypes within a density-regulated population.

We refer the reader to Rueffler et al. (2006*b*) and especially appendix B therein for an introduction to the concept of "feedback environment" and the significance of the dimension of the feedback vector $\boldsymbol{I}$. In accordance with Heino et al. (1998) we define selection there as frequency independent when $\dim \boldsymbol{I} = 1$ and as frequency dependent when $\dim \boldsymbol{I} > 1$. In Rueffler et al. (2006*b*), we show that if evolutionary change occurs in $\boldsymbol{\alpha}$, $\boldsymbol{t}_{\mathrm{p}}$, and $\boldsymbol{t}_{\mathrm{m}}$ while the population is monomorphic for $\boldsymbol{e}$ and $\boldsymbol{f}$, then selection is always frequency independent; that is, $\dim \boldsymbol{I} = 1$. On the contrary, if evolution occurs in $\boldsymbol{e}$ or $\boldsymbol{f}$, then $\dim \boldsymbol{I} = 2$, and evolution is frequency dependent. Here, we restrict ourselves to show that in behaviorally dimorphic populations, necessarily $\dim \boldsymbol{I} > 1$. This means that through the effect of diet choice selection becomes frequency dependent in cases where it would be frequency independent in the absence of diet choice.

Assume for the moment that two different genotypes, θ^1 and θ^2, are present in the resident population with corresponding manipulation times $\boldsymbol{t}_{\mathrm{m}}^1 = (t_{\mathrm{m}1}^1, t_{\mathrm{m}2}^1)$ and $\boldsymbol{t}_{\mathrm{m}}^2 = (t_{\mathrm{m}1}^2, t_{\mathrm{m}2}^2)$, respectively. These morphological traits result in the genotype specific behavior $\boldsymbol{p}^1 = (p_1^1, p_2^1)$ and $\boldsymbol{p}^2 = (p_1^2, p_2^2)$, search probabilities s^1 and s^2, and densities $\hat{N}^1$ and $\hat{N}^2$, respectively. Note that superscripts refer to the different types while subscripts refer to resource specific traits. The equations for the resource equilibria (eq. [6]) become

$$\hat{R}_1(\theta^1, \theta^2) = \frac{b_1}{d_1 + e_1 f_1(p_1^1 s^1 \hat{N}^1 + p_1^2 s^2 \hat{N}^2)}$$

and

$$\hat{R}_2(\theta^1, \theta^2) = \frac{b_2}{d_2 + e_2 f_2(p_2^1 s^1 \hat{N}^1 + p_2^2 s^2 \hat{N}^2)}.$$

In these equations, b_i, d_i, e_i, and f_i are assumed to stay constant over evolutionary time. In order to track changes in the resource equilibria while the consumer population is evolving, the following two-dimensional $\boldsymbol{I}$ vector has to be followed: $\boldsymbol{I} = (\sum_{j=1}^{2} p_1^j s^j \hat{N}^j, \sum_{j=1}^{2} p_2^j s^j \hat{N}^j)$. Note that when $\boldsymbol{p}^1 = \boldsymbol{p}^2$, this $\boldsymbol{I}$ vector simplifies to the scalar $\boldsymbol{I} = \sum_{j=1}^{2} s^j \hat{N}^j$. The identical result holds when the population is dimorphic in $\boldsymbol{t}_{\mathrm{p}}$ or $\boldsymbol{\alpha}$. In populations dimorphic in $\boldsymbol{f}$, the feedback environment is given by $\boldsymbol{I} = (\sum_{j=1}^{2} f_1^j p_1^j s^j \hat{N}^j, \sum_{j=1}^{2} f_2^j p_2^j s^j \hat{N}^j)$. The result for a population dimorphic in $\boldsymbol{e}$ is analogous.

APPENDIX C

Individual-Based Simulations

In this appendix, we sketch the algorithm used for the individual-based simulations. Within a generation, we start by determining the within-year resource equilibria. To this end, we use Euler's forward method for solving the ordinary differential equations describing the resource dynamics (eq. [5]). In each step, we advance the solution through an interval of size $h = 2 \times 10^{-3}$. After each increment, the optimal consumer behavior is determined for each genotype present in the population. Based on the resource densities and consumer behavior found after 1,000 steps in the Euler algorithm, the deterministic number of offspring R_0 for each consumer genotype i is calculated as N_{t+1}^i / N_t^i (according to eq. [1]). The actual offspring number per individual is then determined by drawing a random number from a Poisson distribution with mean R_0. Mutations occur with probability $\mu = 1 \times 10^{-4}$ per offspring. Mutant phenotypes are determined by drawing a random number from a normal distribution, truncated to $[0.01, 0.99]$, with the mother's trait value as mean and standard deviation $\sigma = 0.02$. All simulations are initialized with the resident population at its ecological equilibrium, which ranges from 9,000 to 10,000 individuals, depending on the trait value.

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Associate Editor: Luc-Alain Giraldeau
Editor: Michael C. Whitlock