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

Abstract

In this paper the consequences of diet choice behavior for the evolutionary dynamics of foraging traits are analyzed by means of a mathematical model. The model is characterized by the following features: Consumers are feeding on two different substitutable resources that are distributed in a fine grained manner. They decide upon encounter with a resource whether they attack it or not. This decision is made according to the assumptions of optimal foraging theory. At the same time, evolution occurs in either of five different traits involved in the foraging process. For each trait, a trade-off exists between the consumer’s abilities to forage on the alternative resources. The model predicts that flexible diet choice behavior can guide the direction of evolutionary change in a foraging trait and that flexible behavior can mediate the coexistence of different consumer types where coexistence would not be possible otherwise. 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 non-genetic change in choice behavior. In the case of weak trade-offs, the evolutionary dynamics of a dimorphic consumer population can lead to alternative evolutionary stable communities. These predictions seem to be robust against moderate deviations from the assumption of optimally foraging consumers.

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Introduction

The fitness of an individual depends both on genetically determined traits that can change on an evolutionary time scale and on behavioral patterns that can change on much shorter time scales, without genetic variation. Waddington pointed out that individuals, by their behavior, can influence the strength and direction of selection pressures acting on other aspects of their phenotype (e.g. Waddington, 1975). In this way behavioral patterns can direct the evolution of other traits, a topic reviewed by Bateson (1988), Plotkin (1988) and Wcislo (1989). This paper 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 would be maximized and the handling time to do so would be minimized. The strength and direction of selection is determined by the behavioral diet choice of the individual: If birds accept a wide variety of different seeds, the bill will form a compromise imposed by conflicting needs. A bill suitable for foraging on small soft seeds is most likely unsuitable for foraging on large hard seeds and if both types are included in the diet, this will result in a generalist bill. If a bird solely chooses small seeds, selection will favor all morphological adaptations that increase the foraging rate for them. Importantly, this will happen irrespective of how detrimental such adaptations are on the birds foraging rate for the large seeds. This example illustrates how diet choice sets the selection pressure for morphological characteristics of the bill. On the other hand, diet choice itself is influenced by the morphological traits of the bird because they determine how an individual can, given some time constraint, maximize its energy uptake (Stephens and Krebs, 1986). An additional complexity arises when consumers are important in regulating the abundance of their resources. In this case morphological traits and diet choice behavior will determine the abundance of resources while resource availability simultaneously determines diet choice behavior and thereby influences the selection pressures acting on morphological traits.

In order to distinguish between a consumer’s ability to use different resources and a consumers 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, be they morphological, physiological or behavioral, and are assumed to change on an evolutionary time scale through invasion of mutants and fixation events. To simplify matters, we will refer to traits of this category as morphological in the remainder of this paper. On the other hand, 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 such that energy intake is maximized. We will
refer to traits of this second category as behavioral.

The main goal of this paper 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 in chapter 3, in a study that built on
a series of models by Lawlor and Maynard Smith (1976), Lundberg and Stenseth
(1985), Abrams (1986) and Wilson and Turelli (1986). In all these models it is
assumed that the consumer behaves opportunistically, i.e., it attacks any prey it
encounters, regardless of its morphological adaptation. 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 (chapter 3). Trade-off shape is the main determinant of
evolution in the frequency-independent theory, as initiated by Levins (1962). The
curvature of the trade-off determines whether the generalist trait is an endpoint of
evolution once it dominates, or whether it is susceptible to invasion by deviating
mutants. Frequency-dependence, on the other hand, determines whether it is
possible that different types coexist in a protected polymorphism and whether such
a polymorphism can emerge through a series of mutational steps of small effect
at an evolutionary branching point (Metz et al., 1996a; Geritz et al., 1998). In
chapter 3) we show that the presence or absence of frequency-dependent selection
depends on the trait that is considered to be the evolutionarily variable.

In this paper the constraint of opportunistic consumer behavior is removed.
The composition of the consumer’s diet is derived from optimal diet theory
(Stephens and Krebs, 1986). The approach employed here, 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. The
joint effects of morphology and behavior decides whether the mutant is going
to be successful or whether it will disappear from the population. After the
successful invasion of an initially rare mutant several different outcomes are
possible: (1) the mutant goes to fixation while showing the same behavior as
the former resident, (2) the mutant goes to fixation and shows a different behavior
when compared to the former resident, (3) the mutant coexists with the former
resident in a protected dimorphism where both types behave identically, and
(4) the mutant coexists with the former resident in a protected dimorphism in
which both types behave differently. By following a series of consecutive mutation
events the dynamic interplay between instantaneously optimized behavior and the
evolutionary dynamics of morphological traits can be studied.
Some related models have been analyzed previously but with different emphasis. To our knowledge, Stenseth (1984) was the first to combine frequency-dependent evolutionary dynamics with instantaneous consumer choice dynamics. 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. Abrams (1986) remarked that strongly asymmetric handling times are expected to cause exclusion of one resource from the diet with specialization for the remaining resource as a consequence but did not give this idea a quantitative treatment. Brown analyzed this idea in detail, but within a different ecological system (Brown, 1990, 1996). He considered a consumer in a patchy environment that can specialize in terms of its morphology on one patch type or the other and that can choose which patch type to exploit. He focuses on the different monomorphic and polymorphic evolutionary endpoints that such a system can adopt and his results corroborate the predictions of Stenseth (1984). Vincent et al. (1996) investigated the scope for coexistence of different consumers when consumers face a trade-off in either of three different foraging related traits. Although Vincent et al. do consider flexible prey choice in the consumer, the evolutionary consequences of choice behavior are not studied. More recently, Svanbäck and Bolnick (2005) analyzed a model where a consumer’s handling times for different resources are determined by one locus with two alleles. These authors find that individuals with different handling times show different diet compositions resulting in disruptive selection for a wide range of conditions. However, Svanbäck and Bolnick do not model consumer dynamics but keep the population size constant. Therefore they cannot explore the consequences of the feedback between population dynamics, diet choice, and trait evolution. An alternative approach is taken by Abrams and coworkers (Abrams, 1999; Abrams and Matsuda, 2003; Ma et al., 2003; Abrams and Matsuda, 2004). These authors focus on population dynamical systems with one consumer feeding on two prey without a stable equilibrium. They show that non-instantaneous diet choice or relatively fast evolutionary changes can cause complex population dynamics and thereby lead to unexpected mean trait values.

The structure of the present paper is as follows. First a model of one opportunistic consumer feeding on two discrete resources is introduced, based on chapter 3, which is subsequently extended towards flexible consumer behavior. The resulting evolutionary dynamics of the model with flexible diet choice are compared to those obtained in chapter 3. 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 chapter 3, 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 both the dynamics of 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 time scale argument (cf. Schaffer, 1981; Geritz and Kisdi, 2004). The consumer is an annual organism and the population is censused once a year after juvenile mortality. It is assumed that consumer densities are constant within years. The dynamics of the resources occur on a much faster time scale and these dynamics are followed in continuous time within a year. Since the consumer density does not change on this time scale, resource densities reach a within-year equilibrium. First the dynamics of the consumer is introduced as a function of the equilibrium densities of the resources. In a second step the resource dynamics and their equilibrium are derived.

The recurrence equation for the consumer is given by

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

where \( C_i \) is the functional response of the consumer for resource \( i \). The constant \( \alpha_i \) 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):

\[ C_i = \frac{e_i \hat{R}_i t p_i f_i}{1 + e_1 \hat{R}_i t p_1 (t_{p1} + f_1 t_{m1}) + e_2 \hat{R}_2 t p_2 (t_{p2} + f_2 t_{m2})} \quad \text{for} \quad i \in \{1, 2\}. \]

The number of encountered prey per time step is the product of search efficiency \( e_i \) and resource density \( \hat{R}_i t \) in year \( t \). Upon encounter the consumer decides to attack the prey with probability \( p_i \). In chapter 3 it was assumed that any prey is attacked upon encounter, i.e., \( p_1 = 1 = p_2 \). In this paper the optimal \( p \)-values are derived according to optimal diet choice theory and the detailed procedure is described below. The capture probability describes the probability that an attacked prey is actually subdued and is denoted by \( f_i \). The handling time consists of two
components: the pursuit time $t_{pi}$ and the manipulation time $t_{mi}$. 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, 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, named search probability,

$$s = 1 / \left( 1 + e_1 R_{11} t_{p1} + f_1 t_{m1} + e_2 R_{21} t_{p2} + f_2 t_{m2} \right)$$

(3)
is the fraction per time step spent searching for prey. Equation (1) can now be
written as

$$N_{t+1} = s \left( \alpha_1 e_1 R_{11} t_{p1} + \alpha_2 e_2 R_{21} t_{p2} \right) N_t.$$ 

(4)

If both the pursuit and the handling time are negligible, attacking a prey is cost-
free resulting in opportunistic consumers.

The resource dynamics within the foraging season in year $t$ is followed on a within-
year time scale $\tau$:

$$\frac{dR_{it}}{d\tau} = b_i - d_i R_{it}(\tau) - C_i N_t \quad \text{for} \quad i \in \{1, 2\}.$$ 

(5)

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 of the resource equilibria $\hat{R}_{it}$ using equation (2) and (3) can be given:

$$\hat{R}_{it} = \frac{b_i}{d_i + e_i p_i f_i s N_t} \quad \text{for} \quad i \in \{1, 2\}. \quad (6)$$

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

**Evolutionary Dynamics**

As in chapter 3, the evolutionary dynamics of five different foraging-related traits are studied separately (see table 2). Each trait consists of two resource-specific components, e.g., $f_1$ and $f_2$, subject to a trade-off: an increase in one resource-specific component of the trait is accompanied by a decrease in the other component. Each pair of traits can be written as a vector, e.g., $f = (f_1, f_2)$. We assume that evolution proceeds along the boundary of a set of feasible trait combinations (fig. 1). This boundary is called trade-off curve. The trait combinations $x = (x_1, x_2)$, where $x \in \{e, f, t_p, t_m, \alpha\}$, on this curve in the $(x_1, x_2)$-space are parameterized by a specialization coefficient $\theta$ that varies continuously between 0 and 1. We chose parameterizations such that $\theta = 0$ corresponds to a specialist for resource one while $\theta = 1$ corresponds to a specialist for resource two. Specialization for resource $i$ corresponds to an increase in $\alpha_i C_i$ (see eq. [1]), that is, to an increase in either $\alpha_i$, $e_i$ or $f_i$, or to a decrease in $t_{pi}$ or $t_{mi}$. Consequently we have to parameterize the trade-off curve in opposite directions for $\alpha$, $e$, and $f$ when compared to $t_m$ and $t_p$ (fig. 1). The curvature of the trade-off curve is determined by a parameter $z$ in such a way that $z > 1$ gives rise to a convex phenotype set (bounded by a weak trade-off) while $z < 1$ gives rise to a concave phenotype set (bounded by a strong trade-off). For numerical calculations one of the following parameterizations is used: if $x \in \{\alpha, e, f\}$, then $x = (x_{1\max}(1 - \theta)\frac{1}{2}, x_{2\max}\theta\frac{1}{2})$ and if $x \in \{t_p, t_m\}$, then $x(\theta) = (x_{1\max} - x_{1\min}(1 - \theta)\frac{1}{2}, x_{2\max} - x_{2\min}\theta\frac{1}{2})$, where $x_{1\min}, x_{1\max}, x_{1\min}, x_{2\min}$ are positive constants. Throughout this article both the vector $x = (x_1, x_2)$ and the specialization coefficient $\theta$ are used to characterize a pair of resource specific traits on the trade-off curve.

The possibility that a rare mutant invades a resident community depends on its invasion fitness $w$, i.e., its long term per capita growth rate in an environment where equilibrium resource densities $\hat{R}_i$ are determined by the traits and behavior of the resident community (e.g. Metz et al., 1992). We assume that mutations are rare and of small effect. Because of the first assumption the ecological
Table 2: Overview of traits considered evolvable. Each parameter stands for a vector of two traits coupled by trade-off.

<table>
<thead>
<tr>
<th>Trait</th>
<th>( \text{dim}(I)^* ) in the absence of flexible diet choice</th>
<th>Behavioral switch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conversion efficiency, ( \alpha )</td>
<td>one</td>
<td>yes</td>
</tr>
<tr>
<td>Search efficiency, ( e )</td>
<td>two</td>
<td>no</td>
</tr>
<tr>
<td>Capture probability, ( f )</td>
<td>two</td>
<td>yes (if ( t_m ) not negligible)</td>
</tr>
<tr>
<td>Manipulation time, ( t_m )</td>
<td>one</td>
<td>yes</td>
</tr>
<tr>
<td>Pursuit time, ( t_p )</td>
<td>one</td>
<td>yes</td>
</tr>
</tbody>
</table>

\* Dimension of feedback environment \( I \).

and evolutionary time scales are separated: a population has reached its ecological equilibrium before a new mutant arises. This approximation is an essential prerequisite to use the toolbox of adaptive dynamics (Metz et al., 1996a; Geritz et al., 1998; Waxman and Gavrilets, 2005). Both assumptions together assure that the evolutionary dynamics of clonal populations consisting of a single phenotype, is equivalent to those of a diploid sexual model with additive genetics (Van Dooren, in press; Metz, in press).

The growth rate of a rare mutant is influenced by both its foraging morphology \( \theta' \), or equivalently \( x' = (x'_1, x'_2) \), and its diet choice \( p' = (p'_1, p'_2) \). To account for this, both morphology and behavior are incorporated as arguments in the fitness function. For \( x \in \{e, f, t_p, t_m\} \) invasion fitness is given by

\[
w(\theta', p', \theta, p) = \alpha_1 C_1(\theta', p', \hat{R}_1(\theta, p), \hat{R}_2(\theta, p)) + \alpha_2 C_2(\theta', p', \hat{R}_1(\theta, p), \hat{R}_2(\theta, p)),
\]

where \( C_i \) is given by equation (2) and \( \hat{R}_i(\theta, p) \) denotes resource equilibria across years set by a consumer with trait value \( \theta \) and diet choice behavior \( p \). For \( x = \alpha \) the \( \alpha_i \)'s are functions of \( \theta' \) instead of the \( C_i \)'s. It is important to notice that the probability of attacking a certain prey, \( p_i \), is not a free parameter but assumed to be conditional on the morphology of the consumer individual under consideration and the availability of the two resources (see the next section and appendix A).

Mutants with \( w(\theta', p', \theta, p) > 1 \) can invade while mutants with \( w(\theta', p', \theta, p) < 1 \) certainly go extinct. The direction of evolutionary change can be derived from the fitness gradient, i.e., the first derivative of the fitness function (eq. 7) with respect to the mutant’s trait evaluated at the resident’s trait. Trait values \( \theta^* \) where the fitness gradient equals zero, that is,

\[
0 = \left. \frac{\partial w(\theta', p', \theta^*, p)}{\partial \theta'} \right|_{\theta' = \theta^* \text{, } p' = p} \tag{8}
\]
Figure 1: Trade-off in capture probability $f$ (a) and manipulation time $t_m$ (b). The number next to each curve is the parameter $z$ determining the strength of the trade-off. Note that for capture probability the phenotype set (i.e., the set of possible phenotypes) lies below the trade-off curve and that the opposite holds true for manipulation time. The trade-off curve is parameterized in such a way that $\theta = 0$ corresponds to a specialist for resource one, and $\theta = 1$ corresponds to a specialist for resource two. Therefore the two trade-off curves are parameterized in opposite direction. All filled circles half way on the trade-off curve correspond to the generalist with $\theta = 0.5$. Other parameter values: (a) $f_{max} = (1, 1)$, (b) $t_{mmax} = (1, 1)$, $t_{mmmin} = (0.5, 0.5)$.

are of special interest. These are called evolutionarily singular points by Metz et al. (1996a) and Geritz et al. (1998) and they can be classified according to two independent properties: convergence stability and invadability (Geritz et al. 1998, chapter 1). The first property determines whether a singular trait value is reachable from nearby (Eshel, 1983; Christiansen, 1991; Abrams et al., 1993b; 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 $\theta^*$ (Maynard Smith, 1982). Singular trait values that are both convergence stable and invadable are final stops of evolution and were named continuously stable strategies or CSSs by Eshel and Motro (Eshel and Motro, 1981; Eshel, 1983) while singular points that lack both properties are evolutionary repellors. A convergence stable and invadable trait value is called an evolutionary branching point (Metz et al., 1996a; Geritz et al., 1998). At these points selection becomes disruptive and favors increased genetic variation.

**Diet Choice**

The 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), and Wilson and Turelli (1986). These authors assume that consumers behave opportunistically. In chapter 3 both $p$-values are explicitly set equal to one. In this paper 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”, i.e., an individual either always or never attacks a certain resource (Stephens and Krebs, 1986). In order to make population level predictions, an ESS argument has to be invoked: can a population that behaves monomorphically as either an opportunist or as a selector be invaded by individuals with identical morphology but different behavior? And if so, will the new behavior go to fixation or can it coexist with the old one in a behavioral dimorphism where the fitness of opportunists and selectors equilibrate at a certain frequency?

In appendix A it is shown that behavioral polymorphisms cannot occur in a morphologically monomorphic population. For the present model, either all individuals are selectors or all individuals are opportunists. In order to decide between these different cases, resources are assigned a profitability (Stephens and Krebs, 1986). This is defined as the fitness gain a certain resource item entails for the consumer per investment of time:

$$\rho_i = \frac{\alpha_i f_i}{t_{pi} + f_i t_{mi}}.$$  \hspace{1cm} (9)

If pursuit time $t_{pi}$ is negligible, profitability simplifies to $\rho_i = \alpha_i / t_{mi}$. For each individual consumer it is always beneficial to attack the resource with the higher profitability. The question is whether it also pays to attack the lower ranked resource. 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 could sustain a consumer population on its own (see also Vincent et al. (1996)) and that this condition is met when

$$\rho_i > 1.$$  \hspace{1cm} (10)

How do consumers behave in a morphologically polymorphic 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 eq. [7]) and its scope to coexist with the resident. Here it is assumed that individuals are immediately able to adjust their behavior and that it takes no learning period to get familiar with the environmental condition. Whether a mutant only attacks the resource with the higher profitability or also feeds on the lower ranked resource, crucially depends on the resource abundance it encounters and therefore on the morphological traits and the behavior of the
resident (appendix A). Once a polymorphic population dynamical equilibrium is established, the behavior of each type is again determined by condition (10).

**Feedback Environment**

In our notation in equation (7) we made explicit that the fitness of a mutant depends on the trait and the behavior of the mutant and of the resident. In the model, interactions between mutants and residents are not direct but mediated through components of the environment, or, more precisely, through the abundance of the resources. These environmental components are determined by the resident community and simultaneously set the condition a mutant has to cope with. We therefore refer to them as feedback environment $I$ (Heino et al., 1997, 1998; Diekmann et al., 2003; Meszéna et al., 2006). With a slight abuse of notation we can now write invasion fitness as $w(\theta', p', I(\theta, p))$. An important feature of the feedback environment with far-reaching evolutionary consequences is its dimensionality, that is, the minimum number of scalars needed to describe the interaction between residents and mutants. If $I$ is one-dimensional, no rarity advantage and no robust coexistence are possible (Heino et al., 1998; Meszéna et al., 2006). A single scalar can only account for density-dependence through the resident population but not for frequency-dependence through the effect of any structure within that population. A minimum requirement for robust coexistence of different types in a protected polymorphism is that $I$ is two- or higher-dimensional. While one interaction variable can account for the density of the resident population, any further dimension can account for the frequencies of different types and their specific impact on the environment. We define selection in one-dimensional feedback environments as frequency-independent and in two- and higher-dimensional feedback environments as frequency-dependent. Note, that this definition differs from the classical one of population genetics where frequency-dependence is defined as a dependence of selection coefficients on allele frequencies.

Since interactions between mutants and residents are mediated via the resource densities, it seems intuitive to equate $I$ with the two-dimensional vector $(\hat{R}_1, \hat{R}_2)$. However, a main result of chapter 3 is that the dimension of $I$ depends on the trait that is considered evolvable (see table 2). If the population shows genetic variation in manipulation time $t_m$, pursuit time $t_p$ or conversion efficiency $\alpha$ while variation is absent in search efficiency $e$ and capture success $f$, then one scalar is sufficient to describe the feedback environment. This can be seen easily for the case of symmetric parameter values $b_1 = b_2$, $d_1 = d_2$, $e_1 = e_2$ and $f_1 = f_2$. Under this condition we see from equation (6) that $\hat{R}_1 = \hat{R}_2$, regardless of the amount of genetic variation and the degree of specialization in terms of $t_m$, $t_p$ and $\alpha$. The reason for this is that these traits influence the resource equilibria only.
via the search probability $s$ and the consumer density $N$. These are parameters that influence both resource equilibria in the same way. Hence, one scalar is sufficient to describe the feedback environment. In chapter 3 this result is proven for the general case without the above symmetry assumption. If the population is variable in $e$ or $f$, then $I = (R_1, R_2)$ does not collapse to a single scalar. These traits influence the relative values of the resource equilibria (cf. eq. [6]) and two variables are needed to track changes in the resource densities while the consumer population evolves.

In appendix B of this paper we prove that $I$ is two-dimensional for any population that is behaviorally polymorphic, regardless of the genetic composition of the population. An immediate result is that flexible diet choice can promote coexistence of different types that could not coexist with fixed diet choice. However, in those parts of the trait space where mutants do not deviate in their diet choice from the resident, that is, when foraging behavior in a model with flexible diet choice and a model version with fixed behavior are identical, the dimension of the feedback environment collapses to one when genetic variation occurs in $t_m$, $t_p$ or $\alpha$. It is therefore helpful to present the results according to two groups of traits. The evolutionary dynamics in each group of traits has different dimensions of the feedback environment in the absence of flexible diet choice (cf. chapter 3).

## Results

### Search Efficiency $e$ and Capture Success $f$

In the absence of diet choice the generalist is a globally attracting CSS, given weak trade-offs. When the trade-off becomes strong, the generalist remains convergence stable but loses its uninvadability, hence, it turns into an evolutionary branching point and polymorphisms can emerge from a monomorphic population (for more details see chapter 3). How does flexible diet choice alter this pattern?

**Search Efficiency $e$:** From equation (9) we can see that the profitabilities of the resources are independent of search efficiency. This is because of the assumption made in optimal foraging theory that encounter without attack takes no time and entails no extra costs (Stephens and Krebs, 1986). Therefore the frequency of encounter has no influence on the decision to attack. Depending on other parameters, either both resources or only one of them is attacked, independent of the values of $e$. If both resources are attacked, results are identical to those without diet choice. If only one resource is attacked, selection towards specialization for the chosen prey occurs independent of the initial condition and the curvature of
the trade-off.

**Capture Probability f:** Once a prey is captured successfully, manipulation time has to be invested. Hence, the probability that a prey item is captured influences profitability of an attacked prey. Invasion fitness is given by equation (7) with $x = f$ and

$$C_i = \frac{e_i \hat{R}_i(f, p) p'_i f'_i}{1 + e_i \hat{R}_i(f, p) p'_i (t_{p1} + f'_i t_{m1}) + e_2 \hat{R}_2(f, p) p'_2 (t_{p2} + f'_2 t_{m2})}.$$  \hfill (11)

The consequences of flexible diet choice for the evolutionary dynamics is discussed first for monomorphic populations and further below for dimorphic populations.

In the region of the trait space where the resident consumer behaves opportunistically, that is, where $p = (1, 1)$, the model is identical to the version without diet choice. This is the case within an interval around the generalist’s trait $\theta = 0.5$ (fig. 2a, 3a,b), where the profitability $\rho_i$ (eq. 9) of both resources is relatively high. Whenever the ancestral type lies within this interval it experiences directional selection towards the generalist. At the generalist trait value, the population experiences either stabilizing (weak trade-off) or disruptive selection (strong trade-off) (fig. 2a, 3a,b). The region of the trait space corresponding to opportunistic residents grows with decreasing strength of the trade-off (with increasing values of $z$). This is because weak trade-offs correspond to a high profitability $\rho_i$ ($e_i, f_i$ and $\alpha_i$ are increasing functions of $z$, while $t_{pi}$ and $t_{mi}$ are decreasing functions of $z$, see figure 1), which makes it more likely that the condition for opportunistic behavior (eq. 10) is met. With increasing distance from $\theta = 0.5$, consumers become more specialized for one resource and less specialized for the other. At a certain value $\theta$ the inequality (10) turns into an equality. Here the two behavioral alternatives yield exactly the same fitness for the resident population and the probability to attack the less suitable resource can take any value between zero and one without affecting fitness. Any deviation towards the boundary of the trait space reverses the inequality sign of condition (10) and the consumer turns into a selector. At these switch points, not only the behavior of residents changes discontinuously but also that of mutants and therefore the fitness gradient (eq. 8) is not defined. These trait values are named “degenerate singular points” here, because they are critical points of the fitness function but lack differentiability. Though the model behavior is special at the degenerate singular points, they are not considered here any further because such traits are never attractors of the evolutionary dynamics and therefore will generically not be adopted by a population for a long time. Whenever the ancestral type is close enough to the boundary such that it behaves selectively, i.e., when $p = (1, 0)$ or $p = (0, 1)$, it does not feel the trade-off and selection favors further specialization independent of the curvature of the trade-off. Therefore, for both weak and strong trade-offs, the generalist is not globally attracting anymore but only attracts within
Figure 2: Bifurcation diagram of singular strategies with bifurcation parameter \( z \), the strength of the trade-off curve. Strategies are represented by the specialization coefficient \( \theta \). Arrows give the direction of evolutionary change. The hatched area indicates parameter combinations corresponding to non-viable populations. The white area corresponds to parameters where consumers behave opportunistically while the gray area corresponds to selectors. Results for capture probability \( f \) (a) and manipulation time \( t_m \) (b). Other parameter values: (a) \( t_m = (0.5, 0.5), f_{\text{max}} = (1, 1), (b) t_{m\text{min}} = (0.5, 0.5), t_{m\text{max}} = (1, 1), f = (1, 1), (a, b) \alpha = (1, 1), e = (0.05, 0.05), t_p = (0.1, 0.1), b = (5000, 5000), d = (0.1, 0.1). \)
the interval where the resident consumer behaves opportunistically (fig. 2a, 3a). Hence, the possibility that a polymorphism emerges at an evolutionary branching point depends on initial conditions (fig. 2a, 3b).

Once a population is dimorphic in capture probability, the further co-evolutionary dynamics of the two types can be read from figure (4a, b). These figures depict the sets of pairwise coexisting phenotypes which are given by the overlapping parts of the ‘+’ region of a pairwise invadability plot (PIP) and its mirror image taken along the main diagonal (for further details see Metz et al. (1996a); Geritz et al. (1998, 1999)). Note that the plots in figure 4 are symmetric with respect to the main diagonal. The two symmetric parts show the same dynamics but with a reversed numbering of the two types.

When a dimorphism emerges at an evolutionary branching point, both types remain opportunists in the initial phase after the branching event. In the course of further divergence both types become genetically more specialized and approach the parameter region where prey selection pays off. Usually divergence will be more or less asymmetric such that one type 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 towards ever increasing specialization (fig. 4a) and after further divergence, the remaining opportunistic type will also turn into a selector. Finally the population will reach a continuously stable coalition with two extreme specialists that are selectors for different resources.

The second route to polymorphism is the emergence of a mutant that differs sufficiently from the resident and starts to behave differently as a side-effect. This can result in the coexistence of types that would not be able to do so in the absence of flexible diet choice. The behavior of mutants is indicated in the PIPs by mutant choice boundaries (fig. 3). These lines are defined by an equality in the switching conditions (eq. [A1] in appendix A). The behavior of a mutant deviates from the behavior of the resident when a line drawn vertically from the mutant-resident combination to the main diagonal crosses a mutant choice boundary. If such a mutant is successful, it can show different transient dynamics in its behavior. It either sticks to its behavior until the new population dynamical attractor is reached or it changes behavior while it increases in frequency. The first happens when the mutant’s trait lies sufficiently close to the boundary of the trait space where traits correspond to selectors in case they are the resident. The latter happens when the mutant trait lies in the region of the trait space where traits correspond to selectors when they are rare and to opportunists when they are the resident (fig. 3). In this case a horizontal line drawn from the mutant’s trait to the main diagonal crosses a mutant choice boundary again.

In case of strong trade-offs this route to polymorphism leads also to a coalition of
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, $p = (p_1, p_2)$, is indicated at the underbraces at the x-axes while diet choice of mutants, $p' = (p'_1, p'_2)$, is indicated next to the mutant choice boundaries. Other parameter values as for figure 2.
two selectors that are completely specialized on a single resource. With weak trade-offs the situation is more interesting since an evolutionarily attracting isocline exists for the opportunist (Geritz et al., 1998, 1999). Along this isocline only the selector experiences directional selection while the opportunist cannot be invaded by any other type (fig. 4b). Whenever the selectors become invaded by a more specialized type the population no longer resides on the isocline and opportunists become susceptible to invasion of mutants that improve on the resource that is neglected by the selector. The isocline is given by the dimorphic fitness gradient evaluated for the opportunistic type $i$:

$$
\frac{\partial w(\theta', p', \theta^1, p^1, \theta^2, p^2)}{\partial \theta'} \bigg|_{\theta' = \theta^i, p' = p^i} = 0.
$$

Superscripts correspond to the two coexisting types of the resident community. The isoclines are attached to the boundary of the set of coexistence vertically above and below the branching point and horizontally to the left and to the right of the branching point. This can be calculated numerically but also follows from geometrical considerations presented in Geritz et al. (1999). If the trade-off is sufficiently weak, the isoclines connect the point just described with the boundary of the trait space ($z = 1.4$, fig. 4d). This boundary point constitutes an alternative continuously stable coalition where one type is a specialized selector and the other type behaves opportunistically and is morphologically a generalist with a bias towards the resource not taken by the selector. However, with decreasing values of $z$ the bias in the opportunist towards specialization on the resource not taken by the selector increases until it finally pays to become a selector as well ($z = 1.2$, fig. 4b). In this case the coevolutionary dynamics have entered the region of the trait space where both types behave selectively resulting in complete morphological specialization.

**Manipulation Time $t_m$, Pursuit Time $t_p$, and Conversion Efficiency $\alpha$**

In the absence of flexible diet choice the classical results of Levins (1962) apply for these traits. Strong trade-offs result in either of the two specialists. Both these specialists are CSSs while the generalist is an evolutionary repellor. Which of the two specialists is approached, depends on initial conditions. Weak trade-offs change the specialist’s traits into repellors while the generalist turns into a globally attracting CSS (see fig. 2b in chapter 3).

From equation (9), it follows that all three traits influence the profitability of resources and therefore potentially also diet choice. The effect of flexible diet choice on the evolutionary dynamics is presented here in detail for manipulation
time $t_m$. Results are qualitatively identical for pursuit time $t_p$ and conversion efficiency $\alpha$. Invasion fitness is given by equation (7) with $x = t_m$ and

$$C_i = \frac{e_i p'_i \bar{R}_i(t_m \cdot p) f_i}{1 + e_1 p'_1 \bar{R}_1(t_m \cdot p)(t_{p1} + f_1 t_{m1}) + e_2 p'_2 \bar{R}_2(t_m \cdot p)(t_{p2} + f_2 t_{m2})}. \quad (13)$$

Both monomorphic and dimorphic evolution are affected by diet choice in a similar way to the previous section (fig. 2b, 3c,d, 4c,d) and here only differences between the traits of the two categories are highlighted. For strong trade-offs the generalist’s trait is repelling both for opportunistically and selectively behaving consumers (fig. 2b & 3c). In the first case the model behaves as the version without diet choice. When consumers turn into selectors for one resource, they further specialize because they do not feel the trade-off any longer. Although no branching point in the sense of the adaptive dynamics literature (Metz et al., 1996a; Geritz et al., 1998) exists, a polymorphism might nevertheless emerge through small mutational steps in the neighborhood of degenerate singular points. To see this, consider a scenario with an ancestral type with $\theta < 0.5$ that behaves opportunistically. Selection then favors mutants with smaller trait values $\theta$, i.e., types with a shorter manipulation time for resource one (see fig. 2b & 3c). At some point evolution has driven the population just across the point where resource two is dropped from the diet and therefore the consumer selects resource one only. Mutants that have slightly larger trait values $\theta$ than the resident, cross the mutant choice boundary for resource two (fig. 3c). Although such mutants differ only slightly from the resident in morphological terms, they forage on both resources and therefore can coexist with the former resident (fig. 4c). Further trait substitutions lead to an increase in morphological difference. The scope for the emergence of polymorphisms through small mutational steps at such a degenerate singular point is limited compared to proper branching points for two reasons. Firstly, since degenerate singular points are always repelling towards the boundary of the trait space, these points are only approached from one side. Secondly, degenerate singular points can be crossed by a series of mutations that code for an ever increasing degree of specialization. However, since the fitness landscape is extremely flat in the vicinity of (degenerate) singular points, the evolutionary dynamics will be very slow. In reality, when evolution is not fully mutation limited, this increases the chance that mutants appear with trait values in the coexistence region.

**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
Figure 4: Evolution in dimorphic populations for capture probability $f$ (a, b) and manipulation time $t_m$ (c, d). Each axis gives the value of the specialization coefficient $\theta$ of one consumer type. White areas correspond to combinations that can coexist in a protected dimorphism. Diet choice corresponding to each resident type is given next to the underbraces. Arrows indicate the direction of selection. Thick lines correspond to stable isoclines while dashed lines correspond to a change in the diet of one of the two types. Plots show scenarios for strong trade-offs with $z = 0.8$ (a, c) and weak trade-offs with $z = 1, 2$ (b) and $z = 1.4$ (d). Other parameter values: (a, c) $\alpha = (1, 1)$, (b) $\alpha = (0.85, 0.85)$, (d) $\alpha = (0.93, 0.93)$. All other parameters as in figure 2.
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 the profitabilities, i.e., 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 non-optimal behavior. Such costs are determined by the fitness difference between opportunistic and selective behavior which can be expressed as the difference between the two sides of the switching condition given by inequality (A1). We implement this semi-mechanistic argument by using the following equation to describe the probability of attack $p_i$:

$$p_i = \left[1 + \exp\left(a\frac{\alpha_j e_j \hat{R}_j(\theta, \mathbf{p}) f_j}{1 + e_j \hat{R}_j(\theta, \mathbf{p})(t_{pj} + f_j t_{mj})} - \rho_i\right)\right]^{-1}.$$ (14)

When $p_i$ is plotted as function of the specialization coefficient $\theta$ 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 switch curves 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 becomes more and more similar to that found in the absence of diet choice (chapter 3). 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 genetic variation in either manipulation time $t_{m}$, pursuit time $t_{p}$ or convergence efficiency $\alpha$, the situation is more complicated. Two qualitatively different ways exist in which a degenerate singular point can unfold. Figure 6b shows the first scenario in which the degenerate singular points disappear. The generalist strategy becomes immediately globally repelling, as in the case without prey choice. Figure 6c shows the second scenario in which a slight inaccuracy leads to a bifurcation of the degenerate singular points into an CSS and a repellor. In both cases the fitness landscape stays relatively flat in the vicinity of the former degenerate singular point for moderate inaccuracies, and without strict mutation limitation genetic variation can build up. This increases the chance that individuals can appear that deviate enough to enter the region of coexistence.
Overall the co-evolutionary dynamics of two coexisting types does 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 possible emergence of polymorphisms by small mutational steps at degenerate singular points as described in the previous section is hampered. The scenario relied on the fact that a mutant that only slightly differs in its morphology from the resident can behave as an opportunist whereas the resident behaves as a selector. When foraging inaccuracy causes the degenerate singular point to disappear altogether (fig. 6b), mutants have to differ more from the resident in order to enter the area of coexistence when compared to
Figure 6: Effect of foraging inaccuracy on the evolution of manipulation time $t_m$ in monomorphic (a,b,d) and dimorphic populations (c,e,f). Singular points lose their degeneracy when foraging inaccuracy is introduced but this unfolding is not robust with respect to other parameter values. The PIP in (a) shows the case where $a \rightarrow \infty$ and can be generated from two different parameter combinations: (1) $z = 0.56$, $t_p = (0.05, 0.05)$ and (2) $z = 0.8$, $t_p = (0.1, 0.1)$. Figure (b) and (d) illustrate the the effect of foraging inaccuracy ($a = 50$) for each of these parameter combinations. Figure (c) and (e) show the corresponding figures for dimorphic evolution. For the first set of parameters the degenerate singular points disappear altogether while for the second set of parameters the degenerate singular points unfold into an evolutionary repellor and a CSS. In this case new evolutionary isoclines appear (fig. f). Other parameter values as in figure 2.

the case without foraging inaccuracy (fig. 6c). On the other hand, when foraging inaccuracy causes the degenerate singular point to give rise to a CSS and a repellor (fig. 6d), a small mutational step can still lead into the area of coexistence (fig. 6e). However, in this case two new evolutionary isoclines appear that prevent further divergence of the newly established type but impose convergent selection such that the dimorphic population eventually collapses to become monomorphic again (fig. 6f). Only mutations that lie beyond these isoclines can give rise to dimorphisms that undergo disruptive selection.
Discussion

This paper 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 (chapter 3). In the original model consumers were assumed to be opportunists: every resource item is attacked upon encounter regardless of the consumer’s morphological adaptations. In this study each individual is allowed to choose whether it wants to attack or reject a certain resource item upon encounter.

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 generalist’s trait that is convergence stable (CSS or branching point), will only be approached when the initial trait value corresponds to an opportunistically behaving consumer. Whenever the initial trait value corresponds to a selectively behaving consumer, directional selection will lead towards specialized morphologies. Therefore diet choice results in a reduced basin of attraction and whether a population can diversify at a branching point depends on the initial conditions of the system. (iii) Whenever a rare mutant differs in terms of its behavior from the resident, this mutant will not replace the resident but will coexist with it in a protected polymorphism. The behavior of such a mutant can change during the process of invasion when its increase in frequency starts to affect the abundance of resources. Then it may become beneficial for a mutant to switch behavior again. The emergence of polymorphisms mediated by differential diet choice can occur for a wide range of parameters through the immigration of phenotypes that deviate strongly from the resident or through mutations of large effect. However, this mechanism can also create polymorphism in the absence of immigration and when mutational steps are constrained to be small. In the neighborhood of degenerated singular points, i.e., at traits where a switch in resident behavior takes place, mutants need only to deviate little from the resident in order to adopt a different behavior. (iv) The incorporation of flexible diet choice enlarges the set of conditions producing coexistence. Whenever two types have mutually exclusive diets, coexistence is guaranteed. Furthermore, coexistence is possible when the two types have nested diets, i.e., when one type feeds on both resources while the other selects only one of them. For some traits (conversion efficiency $\alpha$, pursuit time $t_p$ and manipulation time $t_m$) diet choice is the sole mechanism to mediate coexistence of different types while for other traits (search efficiency $e$ and capture probability $f$) coexistence is also possible in the absence of diet choice and then mediated
by negative frequency-dependent interactions. (v) In models lacking diet choice the only continuously stable coalition (i.e., attracting and co-evolutionarily stable community) consists of two extreme specialists (Lawlor and Maynard Smith 1976; Abrams 1986; chapter 3). In the present model two additional continuously stable coalitions exist in combination with sufficiently weak trade-offs. These consist of one selecting extreme specialist and one opportunistic generalist which is biased in its morphology towards the resource that is neglected by the specialist. The boundary between the basins of attraction for these alternative communities is given by the trait values where the unspecialized opportunistic type switches its behavior to become a selector.

Vincent et al. (1996) analyzed coexistence of competitors in a model that yields a fitness function equivalent to the one analyzed here. Though they allow for behavioral diet choice, they dismiss the possibility that this mechanism mediates coexistence. They argue that resources that are not included in the diet of a consumer cannot be considered a resources because they cannot sustain a consumer population on their own. This view seems valid when one limits the scope to the ecological time scale where morphological traits are fixed but is not appropriate in an evolving population where resources can be excluded from or included in the diet as a consequence of evolutionary change in morphology.

When consumers affect resources such that the density of the former is coupled to the densities of the latter, diet choice becomes a frequency-dependent decision. In this case the diet choice of individual consumers depends on the diet choice of its conspecifics. It is therefore in principle possible that a morphologically monomorphic population shows a behavioral dimorphism. For the model analyzed here, it is proven that such a polymorphism cannot occur; all individuals in a morphologically monomorphic population behave either selectively or opportunistically. This property also applies to the model of Vincent et al. (1996) who did not consider the possibility of behavioral polymorphism explicitly. The model of Brown (1990; 1996) describes a different ecological system in which a morphological monomorphic population can consist of a mixture of opportunists and selectors. At these trait values the population is prone to become morphologically polymorphic as well because selectors and opportunists experience very different selection pressures.

An important result of optimal foraging theory is that resources with a low profitability are neglected by consumers when resources with a higher profitability are sufficiently abundant (Stephens and Krebs, 1986). The predictions of optimal foraging theory are valid for the ecological time scale where resource densities can vary in time. In the model presented here, the process of invasion occurs on the ecological time scale. Initially the mutant type is rare and does not affect the resource densities. In this phase it can be beneficial to feed selectively on the more profitable resource. With increasing frequency of the mutant type, it
depletes the preferred resource to such an extent that opportunistic behavior yields the higher fitness. By contrast, the argument of optimal foraging theory does not apply to the evolutionary time scale where consumers are assumed to reach a stable population dynamical equilibrium. The equilibrium is reached when consumers have depleted resources such that each consumer individual on average replaces itself over its lifetime. 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 $\rho_i$ is greater than unity (eq. 10), a condition that purely depends on consumer traits and not on the population dynamics of the resource (eq. 9). In this sense the statement of Stenseth (1984) and Brown (1990) that abundant resources favor selective consumers that subsequently undergo morphological specialization is not relevant.

Our model is based on the assumption of clonal genetics. In the limit of rare mutations with small phenotypic effect and random mating, the results do apply to monomorphic diploid sexual populations and polygenic traits. In case of polymorphic sexual populations the course of evolution cannot be predicted straightforwardly from a clonal model. However, some predictions can still be made. Intermediate heterozygotes will also behave as either opportunists or selectors. Whenever such heterozygotes are inferior, mechanisms like assortative mating or dominance modification are selected for, two processes leading to two discrete phenotypes. 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 given in a model by Svanbäck and Bolnick (2005). This imposes disruptive selection on handling times for different resources, a trait determined by one locus with two alleles in the model by Svanbäck and Bolnick. The problem of heterozygotes is circumvented altogether when disruptive selection leads to a diversification of the sexes. In this scenario a polymorphism emerges from a population with undifferentiated sexes when a mutation alters the genetic system such that the phenotypic correlation between the sexes is broken. If the two sexes differ sufficiently from each other in terms of their morphology they will also start to express a different diet choice and subsequently undergo further morphological differentiation. Given that the phenotypic correlation is not constrained to be perfect, the above scenario is on theoretical grounds more likely than the emergence of a genetic polymorphism (Bolnick and Doebeli, 2003; Van Dooren et al., 2004).

The presented model is based on three different limits. (i) Mutation rate is slow. This allows for the separation of ecological and evolutionary time scale. (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 any real situation. They are primarily considered because they make the model mathematical tractable.
Investigating such limits is generally informative as a guideline for understanding the phenomena we observe in nature. Of course it is important to explore how violation of the limiting situation alters the model behavior. The first limit has been backed up by simulations on the one hand (e.g. Metz et al., 1996a; Geritz et al., 1998, 1999; Kisdi and Geritz, 1999) and on the other hand it has been shown that the approximation employed here gives identical results when compared to models that are derived from quantitative genetic models with standing genetic variation (Iwasa et al., 1991; Taper and Case, 1992; Abrams et al., 1993b). We explore deviations from the second limit by introducing inaccurately foraging consumers. In this case the step-like 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 within an organism’s life span. When individuals need a learning period in order to behave optimally, then the extinction probability of rare mutants will increase. This will slow down the evolutionary dynamics.

In all scenarios considered here, traits evolved one by one and not simultaneously as in natural systems. The simultaneous evolution of several traits can lead to very different predictions. Imagine a scenario where a trait that allows for evolutionary branching, e.g. search efficiency $e$, jointly evolves with a trait that does not allow for evolutionary branching, e.g. manipulation time $t_m$. Assum further that trade-offs for both traits are strong and that therefore selection in $e$ acts in the direction of the generalist’s trait where a population would subsequently experience disruptive selection while selection in $t_m$ acts towards ever increasing specialization. Under these assumptions the combination of $e$ and $t_m$ that corresponds to a generalist has turned into a saddle point of the two-dimensional evolutionary dynamics. With diet choice the final outcome will depend on the relative speed of evolutionary change in the two traits. If evolution in manipulation time proceeds faster than in search efficiency, then the population will reach a degree of asymmetry in manipulation time where it pays to become a selector. Once the consumer solely feeds on one resource, the fitness landscape changes abruptly such that increased specialization is favored for both traits, and selection on $e$ leads away from the branching point. The scope for branching is even more limited since in the neighborhood of a branching point the fitness landscape is relatively flat in the direction of $e$. Consequently, evolutionary dynamics towards a generalist with respect to search efficiency will be very slow, shifting the odds towards the emergence of selective behavior.

To summarize, this paper 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 upon 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 polymorphisms 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. The dynamics of a co-evolving consumer population can lead not only to a community of two selectively behaving specialists but also to a community of one selective specialist and one opportunistic generalist.

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Appendix A: Diet Choice

Each consumer individual always attacks the resource with the higher profitability $\rho_i$ (see eq. [9]). Consider the case $\rho_1 > \rho_2$. A population that behaves monomorphically as a selector for resource one can be invaded by opportunistically behaving individuals with the same morphology if

$$\rho_2 > \frac{\alpha_1 e_1 \hat{R}_1(\theta, (1, 0)) f_1}{1 + e_1 \hat{R}_1(\theta, (1, 0))(t_{p1} + f_1 t_{m1})},$$

(A1)

where $\hat{R}_i(\theta, (1, 0))$ indicates the equilibrium density of the $i$th resource as it results from consumption by a monomorphic consumer population with trait-value $\theta$ and emergent behavior $p = (1, 0)$. The right-hand side of inequality (A1) per definition equals one because it describes the per capita growth rate of a consumer at ecological equilibrium. Hence, condition (A1) simplifies to $\rho_2 > 1$.

The profitability $\rho_2$ is the limit of the per capita growth rate of a selector for resource two when the resource abundance is increasing:

$$\lim_{R_2 \to \infty} \frac{\alpha_2 e_2 R_2 f_2}{1 + e_2 \hat{R}_2(t_{p2} + f_2 t_{m2})} = \frac{\alpha_2 f_2}{t_{p2} + f_2 t_{m2}}.$$  

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

$$\rho_2 < \frac{\alpha_1 e_1 \hat{R}_1(\theta, (1, 1)) f_1}{1 + e_1 \hat{R}_1(\theta, (1, 1))(t_{p1} + f_1 t_{m1})}.$$  

(A2)

For this model it is possible to prove that in a morphologically monomorphic population all individuals behave either as selectors or as opportunists, that is the conditions (A1) and (A2) cannot be fulfilled simultaneously. This follows from $\rho_2 = 1 \Leftrightarrow \hat{R}_1(\theta, (1, 0)) = \hat{R}_1(\theta, (1, 1))$ and $\rho_2 > 1 \Leftrightarrow \hat{R}_1(\theta, (1, 0)) > \hat{R}_1(\theta, (1, 1))$ (mathematica notebook available on request), which implies that condition (A2) is never met for $\rho_1 > \rho_2 > 1$.

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 one because the traits governing the mutant’s functional response do not equal the traits that determine the abundance of the resources.
Appendix B: Dimension of Feedback Environment

We refer to appendix B in chapter 3 for a more formal introduction to the notion of feedback environment $I$. There we have shown that the dimension of $I$ depends on the trait for which genetic variation exists. $I$ is one-dimensional when the population is considered evolvable in $t_m$, $t_p$ or $\alpha$ while being monomorphic for $e$ and $f$. $I$ is two-dimensional when the population is considered evolvable in $e$ or $f$. In this appendix we show that the feedback environment is two-dimensional for any consumer population that is behaviorally polymorphic, regardless of its genetic composition.

Assume for the moment, that two different genotypes, $\theta^1$ and $\theta^2$, are present in the resident population with corresponding manipulation times $t^1_m = (t^1_{m1}, t^1_{m2})$ and $t^2_m = (t^2_{m1}, t^2_{m2})$, respectively. These morphological traits result in the genotype specific behavior $p^1 = (p^1_1, p^1_2)$ and $p^2 = (p^2_1, p^2_2)$, 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

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

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

In order to track changes in the resource equilibria while the consumer population is evolving the following two-dimensional $I$-vector has to be followed: $I = (\sum_{j=1}^2 p^j_1 s^j \hat{N}^j, \sum_{j=1}^2 p^j_2 s^j \hat{N}^j)$. The identical result holds when the population is polymorphic in $t_p$ or $\alpha$. In case the population is polymorphic in $f$, the following two-dimensional vector describes the environmental condition: $I = (\sum_{j=1}^2 f^j_1 p^j s^j \hat{N}^j, \sum_{j=1}^2 f^j_2 p^j s^j \hat{N}^j)$. The result for a population polymorphic in $e$ is analogous.