

# **Can adaptive evolution or behaviour lead to diversification of traits determining a trade-off between foraging gain and predation risk?**

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## **ABSTRACT**

In this article, I examine the population-level consequences of adaptive change in a trait that determines both the ability of a species to capture food and its ability to avoid predation. I assume that the foraging trait of a focal species has an equilibrium that minimizes fitness, but which can be maintained by frequency-dependent selection (i.e. a ‘branching point’ equilibrium). Such a scenario has the potential for selection to favour diversification into a well-defended type with low food consumption ability and a poorly defended type with high food consumption. Population and trait dynamics are examined using models of a three-species food chain in which the middle species has a foraging/vulnerability trait that changes adaptively at a rate proportional to the rate of change in fitness with a unit change in the value of the trait. Conditions favouring evolutionary diversification at a fitness minimizing trait are: (1) weak density dependence in the food species and (2) a moderately decelerating relationship between the foraging trait and vulnerability to the predator. If these conditions are satisfied, diversification occurs when the rate of adaptive change is sufficiently low. However, rapid change, such as that which occurs when the trait is behaviourally determined, often generates population cycles that may prevent diversification. Fitness minimization at a branching point implies that, when the rate of adaptive change is sufficiently high, population and trait cycles will either be produced or altered. Thus, it is possible that there are many ecological scenarios under which adaptive behaviour frequently fails to produce polymorphism when analogous evolutionary models predict such diversification.

*Keywords:* adaptive foraging, anti-predator behaviour, behavioural dynamics, branching point, diversification, food chain, predation.

## **INTRODUCTION**

Many adaptive radiations are likely to have been driven by ecologically generated selection pressures (Schluter, 2000). Currently, most potential examples of adaptive radiations in animals are interpreted as being driven by selection on characters related to resource (usually food) acquisition (Schluter, 2000). However, diversification is at least theoretically

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possible for a number of different characters and different types of interactions (Geritz *et al.*, 1998; Doebeli and Dieckmann, 2000; Day *et al.*, 2002). The common feature of these situations is an evolutionary equilibrium where disruptive selection occurs, but the equilibrium is maintained by frequency-dependent selection.

For disruptive selection to persist over a long period, it is necessary for selection to push the trait back towards the equilibrium if the mean value of the trait deviates from that equilibrium. This occurs if the point has the property of 'convergence stability' (Eshel, 1983; see Taylor, 1989). Points that satisfy conditions for fitness minimization and convergence stability have been labelled 'branching points' (Metz *et al.*, 1996; Geritz *et al.*, 1998) because the sustained action of disruptive selection at such points may lead to evolutionary divergence (branching), if it is possible for the trait distribution in the population to become bimodal. This latter requirement may or may not be possible, depending on the details of the genetic system (Abrams *et al.*, 1993; Dieckmann and Doebeli, 1999; Abrams, 2001). The theoretical basis for most examples of ecologically driven diversification has been models in which a single characteristic of an otherwise constant population undergoes evolutionary change, and has a branching point equilibrium. However, in at least some of the most well-known cases of character displacement, empirical studies have shown that phenotypic plasticity or behaviour can bring about adaptive changes similar to those that might be produced by evolutionary divergence in trophic traits (e.g. Day *et al.*, 1994). This raises the question of whether adaptive behaviour is likely to result in diversification within species in ecological circumstances where the behavioural trait is subject to frequency-dependent disruptive selection at a behavioural equilibrium.

In this article, I examine two questions. First, when does a trade-off between resource exploitation and predator avoidance have the potential to result in evolutionary branching? Second, if the trade-off is behaviourally mediated, will diversification of behaviours occur in circumstances where evolutionary traits have the potential to exhibit branching? Such foraging–predation trade-offs have been demonstrated or implicated in scores of species (Lima, 1998). The fact that such trade-offs generally involve two independent limiting factors means that one of the necessary conditions to have evolutionary branching is satisfied (Day *et al.*, 2002). One previous analysis has demonstrated that branching could occur in a version of this scenario (Day *et al.*, 2002). However, Day *et al.* made the specific assumption that the potential dimorphism was the result of size structure, with larger individuals being predation-resistant. The trait under selection was the growth rate to the larger size class. Thus, their model assumed the existence of two phenotypes to begin with; past work does not tell us whether different defence phenotypes could arise in an initially homogeneous population. Like most previous studies of branching, Day *et al.* (2002) only examined the limiting case of evolutionary change that was very slow relative to population dynamics. However, analysis of behavioural dynamics is also needed because most known cases of trade-offs between foraging gain and predation risk are mediated by behaviours rather than genetically determined traits (Lima, 1998).

The ecological setting is a model of a three-species food chain, in which the middle (consumer) species has a trait that can increase its consumption of the bottom level (resource) species at the expense of a greater vulnerability to the top level (predator) species. I begin by deriving general conditions for a branching point equilibrium, using a model where functional forms of the population dynamical equations are not specified. I then use a specific model to examine the effect of different rates of adaptation. Numerical analysis of

a particular model is required to determine whether the more rapid speed of behavioural traits alters the conditions for diversification.

My initial expectation was that behavioural diversification would occur in most situations where evolutionary branching was possible. In a sexual species in which a quantitative trait determines the character involved in the trade-off, recombination acts to prevent diversification in cases where it might otherwise occur (Abrams *et al.*, 1993). Dieckmann and Doebeli (1999) have shown that it is at least theoretically possible for assortative mating to overcome the homogenizing effects of recombination. They also showed that the existence of a branching point equilibrium can itself select for assortative mating. However, the models considered by Dieckmann and Doebeli (1999) lacked any cost to the trait for assortative mating. It is therefore currently unclear how readily diversification will occur for traits determined by quantitative characters in sexually reproducing species. If the trait in question is under behavioural control, however, there are no constraints on the shape of the trait distribution within the population. One would then expect that frequency-dependent disruptive selection would always result in two classes of individuals, with trait values on either side of the equilibrium. This outcome is possible, but, as shown below, there are circumstances in which the population dynamical consequences of the behavioural change prevent such diversification. These circumstances are related to the fact that adaptive change in trophic characteristics can drive population cycles, with correlated cycles in the value of the trophic trait (Marrow *et al.*, 1996; Abrams and Matsuda, 1997a,b; Abrams, 2001).

## MODELS

### General considerations

The basic model of the three-species food chain consists of three ordinary differential equations describing the population dynamics of the three species. A single trait in the consumer species determines the two interaction coefficients with the resource and predator. The rate of change of the trait is proportional to the fitness gradient at the mean trait value – that is, the rate is proportional to the derivative of fitness with respect to the value of the trait in an average individual. Previous work has shown that this type of model can describe evolutionary change in a system where there is a relatively narrow trait distribution (Taper and Case, 1992; Abrams *et al.*, 1993; Gavrillets, 1997; Case and Taper, 2001). To examine the potential for branching, I split the consumer population into two or more independently adapting sets of individuals and allow the trait in each of these subpopulations to change independently of the other. Assuming independent populations eliminates the problem of producing a dimorphic population from one in which recombination of many loci maintains a unimodal trait distribution.

To be used as a model of behavioural change, it is only necessary to adopt much larger rate constants that translate a given fitness gradient into a rate of change in the character. However, the use of this framework to model behavioural change is more heuristic than is true of evolutionary change. To some extent, this is unavoidable because much less is known about behavioural dynamics than about evolutionary dynamics. There are several mechanisms that could result in behaviours changing at a rate proportional to the rate of increase of fitness with a given behavioural change (Harley, 1981; Boyd and Richerson, 1985; Taylor and Day, 1997). It is certainly difficult to conceive of a case where the fitness

rewards from a given change in behaviour would not be a major determinant of the rate of change. Simulating systems with two independent populations allows the behavioural trait distribution to become bimodal if selection favours divergence. The potential dependence of the results on the assumption of two subpopulations can be tested by increasing the number of subpopulations. In the models considered here, these modifications did not affect the qualitative results.

### Models of adaptation in a three-species food chain

The consumer species in the chain is assumed to have a trait that influences its ability to acquire resources and its vulnerability to the predator. The slope of the consumer's functional response to resource density is the sum of a trait-independent component,  $C_0$ , and a trait-dependent component,  $C$ . The slope of the predator's functional response to consumer density is the function  $s(C)$ , which increases with the foraging trait,  $C$ . This creates an evolutionary trade-off between resource consumption and predator avoidance. I also assume that  $C$  may affect the component of the per capita death rate of the consumer that is independent of predation, denoted  $m$ . The population dynamics of the resource (population  $R$ ), consumer ( $N$ ) and predator ( $P$ ) for a given trait value  $C$  are, then:

$$dR/dt = R[f(R) - (C_0 + C)N] \quad (1a)$$

$$dN/dt = N[b([C_0 + C]R) - m(C) - s(C)P] \quad (1b)$$

$$dP/dt = P[B_p s(C)N - D] \quad (1c)$$

where  $f(R)$  is the per capita growth rate of the resource as a function of its own population size. The function  $b([C_0 + C]R)$  describes the consumer's per capita birth rate as determined by its food intake rate. The parameter  $B_p$  is the (constant) conversion efficiency of consumers eaten into new predators (restricting the predator's per capita birth rate function to this linear form does not qualitatively change any of the results presented below). The parameter  $D$  is the predator's per capita death rate. The mean trait  $C$  is assumed to change at a rate that is proportional to the rate of change of individual fitness with a unit change in  $C$  (Abrams *et al.*, 1993), evaluated at the mean. This assumes a narrow distribution of traits within the population at any given time, so that the dynamics can be described simply by following the mean value. The quantity in brackets in the following equation for the dynamics of the mean  $C$  represents the derivative of individual fitness with the trait value,  $C$ , evaluated at the current mean  $C$ :

$$dC/dt = \nu g(C) \{Rb' - m' - s'P\} \quad (1d)$$

Here,  $\nu$  is a rate constant and  $g(C)$  is a function that adjusts the rate of change of the trait based on its current value. Primes are used to denote derivatives with respect to the entire argument of the function – for example,  $b' = db/d(CR)$  and  $m' = dm/dC$ . The function  $g$  reduces the rate of change of  $C$  as it approaches its maximum or minimum possible value (the minimum  $C$  must be at least zero, and there may be a maximum as well). As the mean  $C$  approaches an extreme value, the rate of change in the direction of that extreme must decrease, both because some individuals are likely to already have the extreme value, and those that do not are close enough that their maximum change towards the extreme is relatively small. If  $C$  is genetically determined, genetic variance is depleted as the mean approaches an extreme value, requiring that change of the trait in either direction is

reduced. The  $g(C)$  function has this effect. If  $C$  is behaviourally determined, change in the direction away from an extreme trait value may be quite large, even when the rate of change towards that extreme must be small because the mean trait value is already close to that extreme. The dynamics of such behavioural traits are more appropriately modelled by an equation of the form:

$$dC/dt = v\{Rb' - m' - s'P + \sigma(C - C_{\min}) - \sigma(C_{\max} - C)\} \quad (1e)$$

where  $\sigma$  is a function that is close to zero unless its argument is close to zero, in which case it can become very large. The two functions  $\sigma$  in equation (1e) push the trait away from extreme values, but have very little effect on the trait dynamics when  $C$  is significantly different from its minimum or maximum value. In most of the following analysis, I assume trait dynamics described by equation (1d), but use equation (1e) for some cases involving very rapid trait dynamics. Because the function  $\sigma$  is very small at intermediate values of  $C$ , the condition for local stability of the system using equation (1e) is usually well-approximated by the stability conditions for the system with trait dynamics described by equation (1d) provided  $g$  is close to unity, or  $v$  in equation (1e) is adjusted appropriately if  $g \neq 1$ .

Equations (1a–d) can be augmented to explore the dynamics of two independently adapting classes within the consumer population. This is done by splitting equations (1b) and (1d) into two equivalent equations. Consumers of type  $i$  are characterized by a mean trait value  $C_i$ , yielding,

$$dR/dt = R(f(R) - (C_0 + C_1)N_1 - (C_0 + C_2)N_2) \quad (2a)$$

$$dN_1/dt = N_1[b((C_0 + C_1)R) - m(C_1) - s(C_1)P] \quad (2b)$$

$$dN_2/dt = N_2[b((C_0 + C_2)R) - m(C_2) - s(C_2)P] \quad (2c)$$

$$dP/dt = P[B_p(s(C_1)N_1 + s(C_2)N_2) - D] \quad (2d)$$

$$dC_1/dt = vg(C_1)\{Rb' - m' - s'P\} \quad (2e)$$

$$dC_2/dt = vg(C_2)\{Rb' - m' - s'P\} \quad (2f)$$

Here, we are interested in equilibrium points of system (1a–d) where individual fitness is minimized and which are convergence stable – that is, branching point equilibria. Such points can result in evolutionary branching if the phenotypic distribution can become bimodal in form (Brown and Vincent, 1987; Metz *et al.*, 1996; Geritz *et al.*, 1998). It is clear that equations (2) will also have a line of equilibria corresponding to the point equilibrium of equations (1). This line is characterized by the same values of  $R$  and  $P$  as the equilibrium of equations (1); in addition,  $C_1 = C_2 = C$  and  $N_1 + N_2 = N$ . The sufficient condition for individual fitness of the consumer species to be minimized at this equilibrium in either equations (1) or (2) is

$$R^2b'' - m'' - s''P > 0 \quad (3)$$

This condition means that a sufficiently large positive second derivative of  $b$ , or sufficiently large negative second derivative of  $m$  or  $s$ , can produce an evolutionary equilibrium where fitness is minimized. Equations (2) may have additional equilibria where the two consumer species have different trait values.

An equilibrium value of  $C$  that satisfies condition (3) is said to be ‘convergence stable’ (Eshel, 1983) if the trait value is pushed back towards this equilibrium when it is displaced. In the context of a multi-variable dynamic system, system stability depends on many aspects of the interaction of populations and the trait. However, convergence stability of the trait may be determined by assuming that population dynamics are much faster than are trait dynamics, and that the population dynamic system comes to a stable equilibrium. This allows the equilibrium values of  $R$  and  $P$  to be expressed in terms of  $C$ . The convergence stability criterion then follows by taking the derivative of the right-hand side of equation (1d) with respect to  $C$ . A negative value of this derivative indicates that, if a trait is displaced from equilibrium, it will return, at least when evolutionary change is much slower than population dynamical change. The condition for convergence stability of the equilibrium point of equations (1) (see Appendix) is:

$$-s^2 f'(R^2 b'' - m'' - s''P) - \frac{b'f}{(C_0 + C)} \left( \frac{s - (C_0 + C)s'}{s} \right)^2 - R s f b'' (s - (C_0 + C)s') < 0 \quad (4)$$

where all variables are evaluated at the equilibrium point. The Appendix shows that, when the rate of adaptive change in the trait is sufficiently slow ( $v_g$  small) at the equilibrium, condition (4) guarantees local stability of the equilibrium point of the entire dynamic system. Condition (4) is complicated, but it is clear that, for it to be satisfied, the sum of the last two terms must be negative and large enough in magnitude to outweigh the first term,  $-s^2 f'(b''R^2 - s''P - m'')$ , which must be positive based on inequality (3) and the fact that the resource has density-dependent growth ( $f' < 0$ ). The sum of the last two terms must be negative if  $b$  is a linear function, provided that the factor  $(s - (C_0 + C)s')$  is non-zero. The convergence stability of this point is a consequence of the delayed frequency dependence operating via changes in predator and resource populations that follow a change in the mean trait value. Increases in  $C$  decrease  $R$  and usually decrease  $P$ , favouring a return to the equilibrium point; decreases in  $C$  have the opposite effects on  $R$  and  $P$ , also favouring a return to the equilibrium  $C$ .

Several results follow from the convergence stability condition. First, convergence stability cannot occur if the predator vulnerability,  $s$ , is directly proportional to the foraging trait,  $C$ , and the resource capture rate at the minimum trait value is zero (i.e.  $C_0 = 0$ ). This follows because in this case  $s = (C_0 + C)s'$ , making the sum of the second and third terms in inequality (4) equal to zero. More generally, convergence stability is strongly affected by the magnitudes of the minimum resource capture rate,  $C_0$ , and the minimum vulnerability,  $s(0)$ , because these both affect the magnitude of the factor  $s - (C_0 + C)s'$ ; increasing  $s(0)$  increases this factor, while increasing  $C_0$  decreases it; either change may shift the system from convergence stability to instability, depending on the rest of expression (4). Another general result is that a large curvature of the consumer’s fitness function ( $R^2 b'' - m'' - s''P \gg 0$ ) or strong resource density dependence ( $f' \ll 0$ ) will prevent convergence stability, by increasing the magnitude of the first term in inequality (4). Thus, a branching point equilibrium is more likely to occur if the fitness minimum is relatively shallow and resource density dependence is weak.

Conditions (3) and (4) define a branching point, but there are additional constraints on the functions  $b$ ,  $m$  and  $s$  that must be met for the equilibrium densities of all of the species and the value of the trait to be positive. The condition that the trait be at equilibrium implies that  $P = (Rb' - m')/s'$ . When this predator density is substituted into the expression

for the per capita growth rate of the consumer, the result must be positive for some resource densities if consumers are to exist. This means that there must exist resource densities for which the following condition is satisfied:

$$b - m - (s/s')(Rb' - m') > 0 \quad (5)$$

This condition is most easily understood when the trait does not affect mortality other than that caused by the predator. In this case, expression (5) simplifies to  $b - m - (s/s')Rb' > 0$ . If, in addition,  $b$  is linear – that is,  $b = B_N(C_0 + C)R$  – a sufficiently large value of  $R$  will satisfy condition (5) if

$$C_0 + C > s/s' \quad (6)$$

If this inequality is reversed, then no value of  $R$  will satisfy condition (5). If  $s$  is a monotonic function that increases at a decelerating rate [necessary for condition (3) to be satisfied if  $b$  is linear and  $m$  is small], condition (6) specifies the minimum value of  $C_0$  that is required for an evolutionary equilibrium with positive fitness. For example, if  $s = \sqrt{C}$ , then condition (6) becomes  $C_0 > C$ . Alternatively, if  $s$  has the form  $s = S_{\max}C/(\varepsilon + C)$ , then a positive equilibrium requires that  $C_0 > C^2/\varepsilon$ . Thus, in the numerical examples considered below, I assume that  $C_0 > 0$ . The branching point equilibria that are of interest here are most likely to exist if the resource capture rate has a relatively large minimum value.

The conditions for local asymptotic stability of an equilibrium point of the full system (equations 1a–d) are given in the Appendix and are considerably more restrictive than inequality (4) alone. As is shown in the Appendix, the fitness minimization condition (inequality 3), combined with a sufficiently rapid rate of adaptive change,  $v$ , results in local instability of the equilibrium of the entire dynamic system. Thus, rapid rates of change may be associated with cycles or other non-equilibrium dynamics in trait values around a value that minimizes fitness (Abrams and Matsuda, 1997a). In this case, examining selection at the equilibrium point can no longer reliably identify those cases when divergence of two initially similar lineages will occur; it is necessary to determine conditions for divergence numerically.

To investigate the implications of dynamic instability further, it is necessary to specify the component functions of equations (1). A branching point can be produced if  $b'' > 0$ ,  $m'' < 0$  or if  $s'' < 0$ . If  $b'' > 0$ , the conversion efficiency of resources into offspring increases faster than linearly. This is reasonable if resource intake is quite low; the need to invest in reproductive functions means that the efficiency of producing offspring should increase with intake until that necessary preliminary investment in reproductive physiology becomes a small part of the total investment. However, it is virtually inevitable that a sufficiently large intake rate results in a deceleration in  $b$ , simply due to constraints on the maximum production rate of offspring, and it is also more likely that the equilibrium would occur when the birth rate was high enough to be above the accelerating phase of the relationship. Similarly, the effects of a larger trait on the non-predatory mortality are more likely to increase at an accelerating ( $m'' > 0$ ) rather than a decelerating rate. More importantly, if  $b'' > 0$  or  $m'' < 0$ , the trait will increase indefinitely in the absence of predators, as can be shown by an analysis analogous to that in the Appendix. Thus, it is most likely that a branching point in this system might arise if  $s'' < 0$ , (i.e. if predation rate increases at a decreasing rate with the trait).

There are several mechanisms that might lead to a decelerating vulnerability function (i.e.  $s'' < 0$ ). If the trait,  $C$ , is body size, larger size might make the consumer species more

attractive to predators, but also make the prey better able to resist or escape if a predator attacks. The combination of these two factors could lead to a decelerating increase in vulnerability. A similar result could occur when a trait makes a prey more vulnerable to capture, once it is detected, but does not affect the probability of detection. Large values of such a trait may make the probability of capture approach 100%, but  $s$  will become more limited by the probability of detection, resulting in a decelerating increase of  $s$  with  $C$ .

One would not expect a trait that increased resource capture to increase indefinitely in the absence of predators. Thus, in the absence of a simple constraint setting the maximum  $C$ , runaway evolution in the absence of predators can be avoided if non-predatory costs,  $m$ , increase at an accelerating rate when  $C$  becomes large, or if birth efficiency,  $b$ , increases at a decreasing rate. In the example below, I make the first assumption. It is also likely that trait values much smaller than the norm will have some fitness disadvantage even in the absence of predators. These biological considerations can be incorporated into the model by assuming that non-predatory mortality,  $m$ , is a U-shaped function of  $C$  that increases at both very low and very high values of  $C$ .

The accelerating increase in non-predatory mortality,  $m$ , at large values of  $C$  prevents runaway evolution of ever-larger trait values in the presence, as well as the absence, of the predator. If I again assume a linear consumer birth rate,  $b = B_N(C_0 + C)R$ , and assume that all populations quickly reach demographic equilibrium with the resource, then the trait dynamics equation becomes  $dC/dt = \nu g(B_N(s - s'(C_0 + C))(R/s) + s'm/s)$ , where  $R$  is a function of  $C$ . If  $s$  increases at a less-than-linear rate with  $C$ , then a sufficiently large initial value of  $C$  will make  $s > s'(C_0 + C)$ , and will therefore result in continual increase in  $C$ . As  $C$  becomes very large, both the consumer population and the predator population become small, and selection for higher resource exploitation drives the increase in the trait. Such a runaway process is eventually stopped if a high enough trait value increases non-predatory mortality, resulting in an equilibrium at a high  $C$ . Because  $m'' > 0$ , this equilibrium would maximize fitness locally and would, therefore, not be a branching point.

### A numerical example

Numerical examples are the only way to investigate how dynamic instability of the entire system affects the possibility of diversification. The ideas discussed above also require some numerical exploration of particular examples simply to determine the long-term evolutionary outcome of branching. The following example represents a mathematically simple realization of equations (1), incorporating the considerations regarding the shapes of  $b$ ,  $m$  and  $s$ , discussed above. The goal of the numerical analysis is to illustrate some possible results of branching and of instability, rather than providing a complete analysis of the potential dynamics of this particular model (which has too many parameters for a complete analysis to be practical).

The component functions of equations (1) in this example are:

$$\begin{aligned} f(R) &= (1 - (R/K)^\theta) \\ b((C_0 + C)R) &= B_N(C_0 + C)R \\ m(C) &= M_0 + M_1 C^\epsilon + M_2 \exp[-\gamma C] \\ s(C) &= S_0 + S_1 C / (1 + \lambda \sqrt{C}) \\ g(C) &= (C - C_{\min})^2 / (\beta + (C - C_{\min})^2) \end{aligned}$$

The resource growth function is the generalized logistic model introduced by Gilpin and Ayala (1973). The birth rate function for the consumer is a linear function of resource intake, with a conversion efficiency,  $B$ , and a minimum resource capture rate constant of  $C_0$ . The non-predatory mortality function contains three terms that together produce the U-shape described above. The first term,  $M_0$ , is a constant, density- and trait-independent per capita mortality rate. The trait increases non-predatory mortality at both low and high values of  $C$ ; the latter occurs due to the exponential term with the coefficient  $M_2$ , while the former occurs due to the power function of  $C$  with coefficient  $M_1$ . The parameters in both of these components of  $m(C)$  are chosen so that the effect of  $C$  on  $m$  is small unless it is much higher or lower than the equilibrium in the presence of the predator. When the equilibrium is at an intermediate  $C$ , this can be achieved by making  $\gamma$  and  $e$  large and  $M_i$  small, for  $i = 1, 2$ . The vulnerability function  $s(C)$  does not approach an asymptote, but does have a negative second derivative; the latter property is necessary to produce a fitness minimizing equilibrium. The form chosen for  $s$  implies that predation risk increases approximately linearly with trait value when  $C$  is close to its minimum of zero. At larger values of  $C$ ,  $s$  increases approximately as the square root of  $C$ . The rate function  $g$  slows the rate of change in the trait when  $C$  approaches its minimum value of  $C_{\min}$ , which is chosen to be zero or a small positive number. The coefficient  $\beta$  determines how rapidly the maximum rate coefficient,  $\nu$ , is approached as  $C$  increases above its minimum. Here,  $\beta$  is chosen to be a small positive constant. These assumptions result in the following dynamic system for traits and population densities:

$$\frac{dR}{dt} = rR \left( 1 - \left( \frac{R}{K} \right)^\theta \right) - (C_0 + C) RN \quad (7a)$$

$$\frac{dN}{dt} = N \left( B_N(C_0 + C) R - M_0 - M_1 C^e - M_2 \exp[-\gamma C] - S_0 P - \frac{S_1 CP}{1 + \lambda \sqrt{C}} \right) \quad (7b)$$

$$\frac{dP}{dt} = P \left( B_P \left( S_0 + \frac{S_1 CP}{1 + \lambda \sqrt{C}} \right) N - D \right) \quad (7c)$$

$$\frac{dC}{dt} = \frac{\nu(C - C_{\min})^2}{\beta + (C - C_{\min})^2} \left( B_N R - \frac{(2 + \lambda \sqrt{C}) S_1 P}{2(1 + \lambda \sqrt{C})^2} - e M_1 C^{e-1} + \gamma M_2 \exp[-\gamma C] \right) \quad (7d)$$

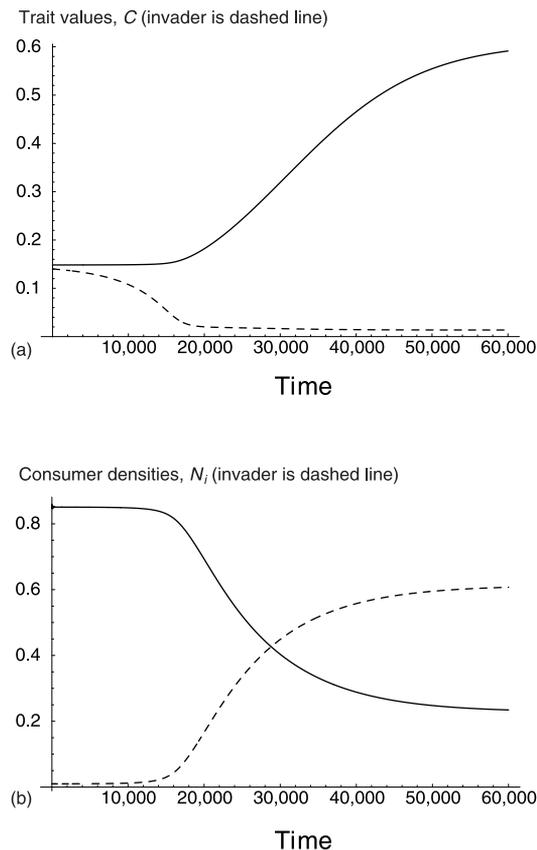
This can be extended to a system with two or more independent consumer subpopulations in the same way that equations (2) were produced from equations (1)

In general, it is necessary to determine the equilibrium point of the entire dynamical system numerically. Even if the  $M(C)$  function is reduced to a constant to simplify the analysis, the resulting equilibrium conditions involve a 6th degree polynomial equation. Determining the stability of an equilibrium point numerically is straightforward, and the expected destabilization with increasing evolutionary rate,  $\nu$ , occurs when there is a branching point equilibrium. If  $C$  is constant, the linear functional responses of consumer and predator guarantee that an equilibrium with positive densities of the three species satisfies qualitative conditions for local stability (Jeffries, 1974; Pimm, 1982).

If there is a dynamically stable branching point equilibrium, then augmenting the model with a second consumer following identical dynamics [changing from system (1) to system (2)] resulted in divergence of each subpopulation's trait value from the equilibrium of equations (7) in all of our simulations. In all of the cases examined, the ultimate outcome

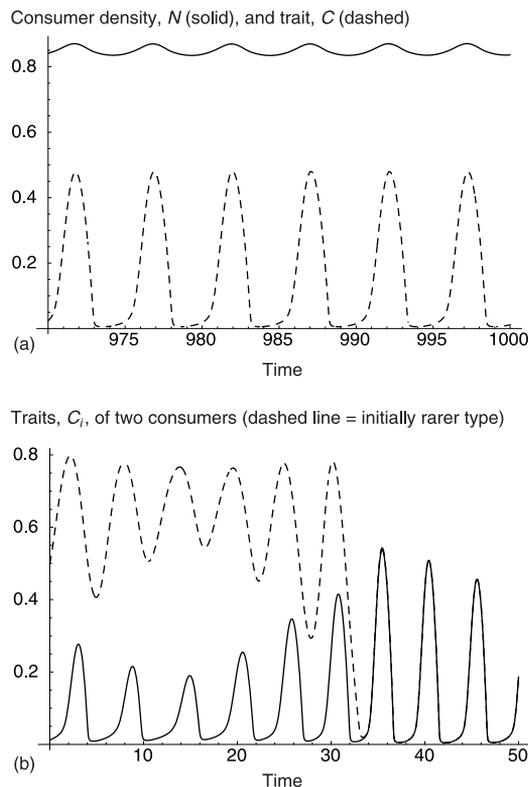
consists of one consumer having a trait,  $C$ , close to zero, and the second having a much larger value of  $C$ ; that is, there is one well-defended consumer type and one poorly defended phenotype. Models with three independent consumer populations produced the same outcome, with two of the three being identical to one of the phenotypes in the two-population model. Figure 1 is an example of divergence in a two-consumer model. Both species have locally fitness-maximizing trait values and the resulting system can be shown to be stable whenever the two consumers are able to persist (Armstrong, 1979).

A necessary condition for stability of a branching point equilibrium of equations (7) is that the rate of adaptive change be less than a threshold value. Because the derivative of the right-hand side of equation (7d) with respect to  $C$  is positive at a branching point, a large enough  $v$  will result in a large positive diagonal element of the Jacobian matrix, which will violate conditions for local stability of the equilibrium. If a branching point equilibrium in



**Fig. 1.** Evolutionary branching in a model in which there is a dynamically stable branching point equilibrium. The parameter values in the augmented (two-consumer) version of equations (7) are:  $v = 0.002$ ;  $B = 1$ ;  $r = 1$ ;  $K = 1$ ;  $M_0 = 0.1$ ;  $M_1 = 0.02$ ;  $e = 4$ ;  $s_0 = 0.05$ ;  $s_1 = 1$ ;  $D = 0.15$ ;  $\beta = 0.001$ ;  $C_0 = 1$ ;  $\lambda = 0.5$ ;  $\gamma = 100$ ;  $M_2 = 0.001$ ;  $\theta = 2$ . The solid line in each of the two panels represents the resident, which is present initially at its equilibrium density and trait value. The dashed line is the invader, which is introduced at a density approximately 1% of that of the resident, and a trait value approximately 5% less than that of the resident.

a single-consumer system is destabilized by increasing the rate constant,  $\nu$ , the outcome may be cyclic or chaotic dynamics. Figure 2 represents a system identical to the single-consumer version of the system shown in Fig. 1, except that the adaptive rate,  $\nu$ , has been increased to a value that might be appropriate for representing behavioural change ( $\nu = 0.002$  in Fig. 1 and  $\nu = 15$  in Fig. 2). When  $\nu = 15$ , the result is small amplitude cycles in population densities of all three species and large amplitude cycles in the trait. Figure 2b shows the convergence in trait values that occurs when two independent populations initially have very different traits. The minimum  $\nu$  required to destabilize the equilibrium of the single-consumer system is quite small, and convergence occurs for most of the range of  $\nu$  that produces population cycles. Values of  $\nu$  close to the stability threshold (e.g.  $\nu = 0.05$ ) can exhibit convergence or divergence depending on the initial values of  $C_1$  and  $C_2$ ; more similar initial values are more likely to converge.



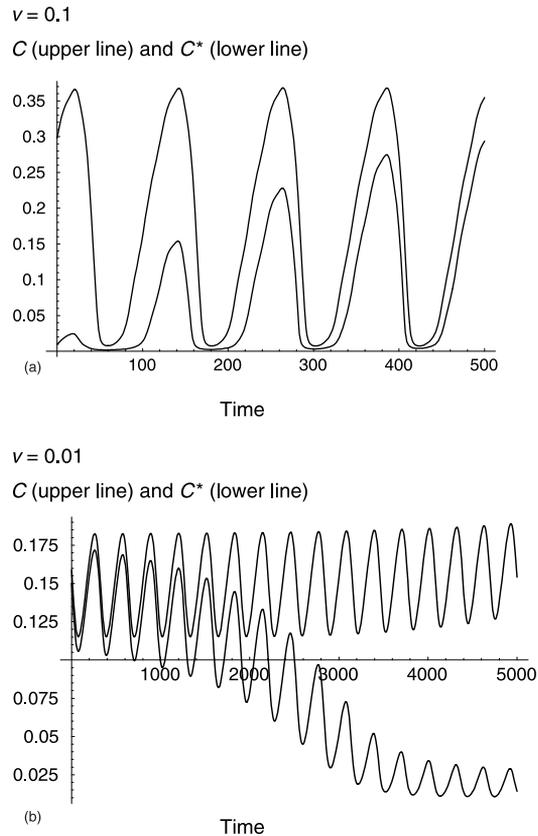
**Fig. 2.** Cycling in the system described in Fig. 1 when the evolutionary rate constant is larger ( $\nu = 15$ ). Panel (a) shows the cycles in consumer density and in the foraging trait. Panel (b) shows the convergence in trait values that occurs when two consumer populations with identical parameters but different initial trait values interact. The initially rarer consumer population was assigned a trait of 0.5 [close to the maximum that occurs during the cycle shown in panel (a)] and the more common consumer had an initial trait value of 0.012 [close to the minimum that occurs in panel (a)]. Once trait values have converged, the two-consumer system eventually has dynamics identical to the one-consumer system.

Cycling does not guarantee convergence. However, convergence can occur with sustained non-equilibrium dynamics, because the average selective pressure experienced over the course of a cycle in a non-linear system like equations (7) differs from that at the equilibrium point. The out-of-phase oscillations in predator and resource densities subject different consumer subpopulations to periods of very similar directional selection, and this is often sufficient to change the expected pattern of divergence to convergence. However, without determining the mean selection pressure over the course of a cycle numerically, it is difficult to predict what sets of parameters and initial conditions lead to convergence rather than divergence. In the system modelled here, the equilibrium after convergence is neutrally stable, because both consumers are identical. As a result, ecological drift, ending in exclusion of one subpopulation, would occur in a stochastic environment. However, if each consumer subpopulation has a small negative effect of its own density on per capita growth rate, persistence of the convergent types will occur. Such intraspecific density dependence could arise from conflict related to mating, species-specific diseases or any of a number of other factors (Stern *et al.*, 1997).

Figure 3 shows some additional numerical results obtained using equations (7), which illustrate that the rate of adaptive change can affect the selective pressure for divergence. Figure 3a is a case in which the rate constant is relatively large ( $\nu = 0.1$ ) and convergence occurs for many initial conditions, including some in which the invader initially has a trait value close to zero (i.e. its equilibrium if divergence had occurred). Figure 3b shows the same model with a reduced rate of adaptive change ( $\nu = 0.01$ ). This results in a reduced amplitude of the cycle in the single-consumer case and, as shown in the figure, even when the invader has a trait value similar to that of the resident, it diverges, in this case towards a minimum value of  $C$  approaching zero. The final state is a stable equilibrium in which  $N_2^* = 0.613$ ,  $N_2 = 0.228$ ,  $C^* = 0.01366$ ,  $C = 0.6095$ . The convergence observed at the more rapid rate of adaptation shown in Fig. 3a occurs over a wide range of initial densities of the invader, but does not occur if initial densities and traits are close enough to the stable divergent two-consumer equilibrium. In the latter case, the outcome is divergence and, eventually, a stable equilibrium, as in Fig. 3b. Convergence can occur even when there is no stabilizing selection on other mortality rates ( $M_2 = M_1 = 0$ ). Much higher rates of adaptation in this example produce convergence for most initial conditions.

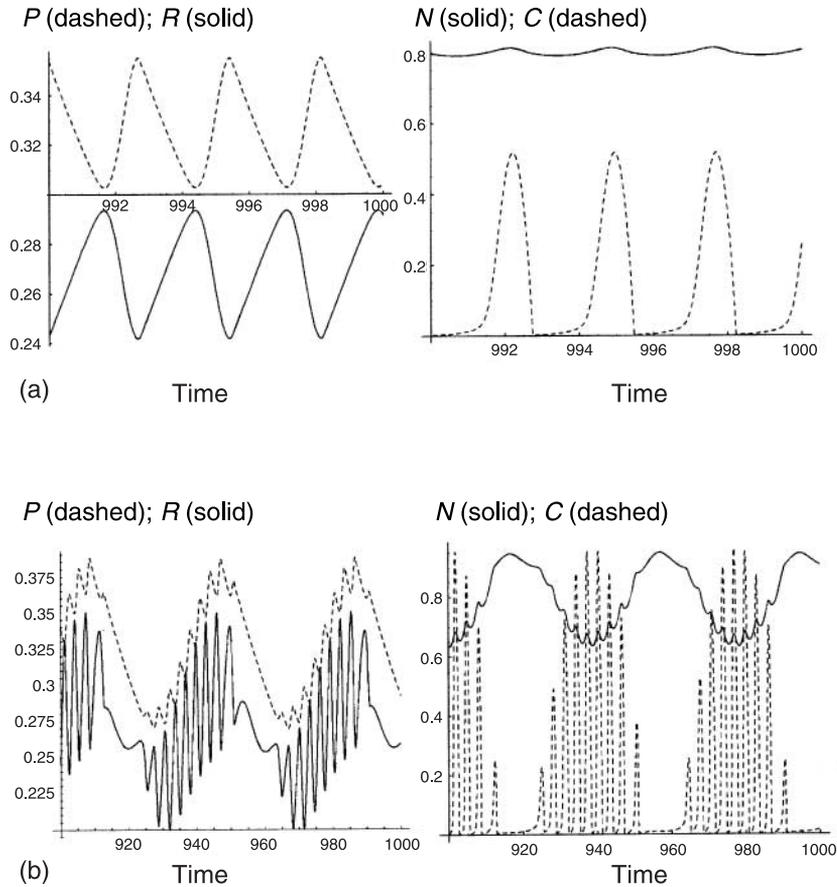
The system described by equations (7), and the corresponding augmented system with a second consumer, are both capable of a wide range of dynamics. There are examples of systems with very large amplitude cycles in single-consumer models where convergence never occurs in two-consumer models. When divergence occurs, the species with the larger trait value may continue to undergo large-amplitude oscillations in its trait, while the trait value of the other species continues to approach zero. Another possibility is that both consumer types continue to undergo large amplitude cycles in their trait values following a moderate amount of divergence. Chaotic dynamics are common in both one- and two-consumer systems with rapid adaptation, and the fact that the two consumers are very similar means that transient dynamics often last for many thousands of generations. Delineating the full range of dynamics, and the parameter ranges where different types occur, is beyond the scope of this article.

There are several ways that the underlying population dynamical model considered here could be changed. Changes that are likely to be required to reflect many natural situations include the addition of intraspecific density dependence in the consumer and predator species (Stern *et al.*, 1997) and the change from a type-1 to a type-2 functional response



**Fig. 3.** The effect of the rate of adaptive change,  $v$ , on divergence in the model given by equations (7), augmented with a second consumer. The two panels show the evolutionary trajectory in the two consumers for cases with different rate constants,  $v$ . Parameter values are:  $r = 1$ ;  $K = 1$ ;  $B_N = 1$ ;  $B_p = 1$ ;  $C_0 = 1$ ;  $D = 0.15$ ;  $S_0 = 0.05$ ;  $S_1 = 1$ ;  $M_0 = 0.1$ ;  $M_1 = 0.02$ ;  $e = 4$ ;  $\theta = 2$ ;  $M_2 = 0.001$ ;  $\beta = 0.001$ ;  $\lambda = 0.5$ ;  $\gamma = 100$ . The figure shows the resident's trait,  $C$ , and the invader's trait,  $C^*$ . In each panel, the invader is the lower line. The initial trait values are shown in the figure. The initial population density of the invader was 0.02 times that of the resident.

in both of those species. More limited sets of simulations with these features suggest that the results above are often not changed by these elaborations, provided the system is still capable of exhibiting cycling due to the dynamics of the trait. It is also of interest to examine the alternative form for the trait-dynamics equation provided by equation (1e). Because our model only has a minimum trait ( $C = 0$ ), this can be accomplished by adding a function  $\sigma$  to the fitness gradient having the form  $\varphi/C^2$ , where  $\varphi$  is a very small positive constant. Reanalysing the example in Fig. 3 with this modification often changed the pattern of fluctuations in the trait and the populations for a given value of  $v$ , but did not greatly change conditions for divergence and convergence. Relatively rapid behavioural change appears to produce two different types of dynamics in systems with a monomorphic consumer population. The first is very small-amplitude population oscillations around their equilibrium values at the branching point. This is illustrated in Fig. 4a. Another pattern,



**Fig. 4.** Dynamics of equations (7) for the case of behavioural change, using equation (1e) for trait dynamics. The two panels show the effects of different demographic rates of the predator. Parameters for panel (a) are:  $r = 1$ ;  $K = 1$ ;  $B_N = 1$ ;  $B_P = 1$ ;  $C_0 = 1$ ;  $D = 0.15$ ;  $S_0 = 0.05$ ;  $S_1 = 1$ ;  $M_0 = 0.25$ ;  $M_1 = 0.02$ ;  $e = 4$ ;  $\theta = 2$ ;  $M_2 = 0.001$ ;  $\varphi = 0.0000001$ ;  $\lambda = 0.25$ ;  $\gamma = 100$ ;  $\nu = 25$ . The parameters for 4(b) are identical except  $B_P = 0.25$  and  $D = 0.0375$ ; these proportional decreases do not affect the equilibrium point.

which occurs in the same system if the top predator has slower demographic rates, involves relatively large-amplitude oscillations of all three populations, which are overlain by the smaller-amplitude oscillations caused by the trait fluctuating back and forth across the branching point. This pattern is shown in Fig. 4b. This was observed in models with rapid trait dynamics when the demographic rates of the predator are significantly slower than those of the resource.

## DISCUSSION

The above analysis establishes that evolutionary branching is possible when the middle species in a three-species food chain experiences disruptive selection on a trait that influences both its resource capture rate and its predator vulnerability. The only previous model to suggest that evolutionary branching could occur in a food chain assumed that

the consumer population began with two size classes, with large individuals being more resistant to the predator, and where the trait was growth rate to the large form (Day *et al.*, 2002). The present analysis shows that, although a number of conditions are required for branching, it is possible in non-structured populations of consumers in a food chain. This raises the possibility that the trade-off between food intake and predation risk may lead to speciation. This appears to be an extremely common trade-off in ecological communities (Werner and Anholt, 1993; Lima, 1998). Recent work (Bohannon and Lenski, 1999) has begun to study evolution in microbial communities where species share both resources and predators. Other studies of microorganisms in simple food webs should provide opportunities for observing some of the phenomena predicted here.

I also examined whether a branching point that arises in a model with a behavioural trait is likely to result in behavioural diversification that is similar in form to the evolutionary diversification that might occur if the trait were genetically determined. With behavioural adaptation, joint population and trait cycles that arise as the result of the behavioural dynamics can eliminate the bimodal trait distribution that would be expected to arise in a comparable system with a slowly evolving trait. The conditions that make diversification in the food chain scenario possible also make possible population and trait cycles when the rate of adaptive change is sufficiently rapid. Such cycles are often capable of reducing or eliminating the disruptive selection that could lead to divergence. This occurs because the cycles cause both consumer types to experience population densities and selective pressures that may be quite different from those at the equilibrium point. When convergence is possible, its occurrence often depends on the initial similarity of the species, with greater similarity making convergence (and possibly competitive exclusion) more likely. The fact that a branching point requires fitness minimization means that it will always produce the potential for dynamic instability by introducing a positive diagonal element,  $(\partial/\partial C)/(dC/dt)$ , in the stability-determining Jacobian matrix. This appears to be true of any ecological scenario that can have branching points, including models of the evolution of traits determining capture rates of two foods (P. Abrams, unpublished). Such cycles can eliminate diversification in other systems for the same reason it is prevented in the food chain.

The fact that rapid adaptive change produces cycles in the current models suggests that behavioural trade-offs between food intake and predation risk, which appear to be very common (Lima, 1998), could be responsible for some of the many observed and unexplained cases of population cycles (Kendall *et al.*, 1998). The plausibility of this mechanism for generating cycles depends on how often predation risk increases at a decreasing rate as the per capita capture rate of resource (food) increases. This is presently unknown.

The origin of diversity is distinct from the question of how divergent types adapt when they interact. Recent work by Abrams and Chen (2002a,b) suggests that interspecific differences in traits determining resource use and predator defence may either be magnified or diminished as the result of the indirect interactions of two consumer species via their shared predator and resources.

The assumption that each consumer subpopulation has limited variation is consistent with scenarios of slow evolutionary change or behavioural change in traits that can quickly converge on the current optimum. However, the assumption is less defensible under rapid evolution, which can only occur with a significant amount of genetic variation. In this case, the fitness gradient at the mean trait may or may not be a good approximation to the gradient averaged over the trait distribution (Abrams *et al.*, 1993; Gavrillets, 1997). Cases

with rapid evolution have not been discussed here, but it is clearly possible for evolution to drive cycles, which may prevent branching in the same manner as behaviour. Such cycles can occur with values of  $v$  that require relatively limited genetic variation, given the appropriate parameters.

All of the conclusions reached here must be qualified by noting that both the range of models considered here, and the range of empirical evidence that could be used to assess their realism, are quite limited. Even in the more frequently studied case of divergence due to competition for resources (Taper and Case, 1985; Doebeli and Dieckmann, 2000), empirical evidence for branching is largely circumstantial. Nevertheless, understanding the conditions that are needed for branching is clearly a prerequisite for determining whether it has occurred.

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## APPENDIX

### Conditions for convergence stability of $C$ and local stability of the internal equilibrium of equations (1a–d)

Convergence stability occurs when the total derivative of the right-hand side of the trait dynamic equation, (1d), expressing  $R$  and  $P$  as functions of  $C$ , is negative. The equilibrium conditions for equations (1a) and (1c) together can be used to derive an expression for  $\partial\hat{R}/\partial C$ , and the equilibrium condition for equation (1b) provides a relationship between  $\partial\hat{R}/\partial C$  and  $\partial\hat{P}/\partial C$ . Expressing the equilibrium  $N$  as  $f/(C_0 + C)$ , the convergence criterion becomes inequality (4) in the text.

The conditions for the local stability of an equilibrium of equations (1a–d) follow from the characteristic equation of the Jacobian matrix:  $\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$ , where

$$a_1 = vg(m'' + s''P - R^2b'') - f'R \quad (\text{A1})$$

$$a_2 = vgN[(C_0 + C)R^2b'' + b'R + BPs'^2] - vgRf'(m'' + s''P - R^2b'') + N(Bs^2P + b'(C_0 + C)^2R) \quad (\text{A2})$$

$$a_3 = vgN(m'' + s''P - R^2b'')(b'(C_0 + C)^2R + BPs^2) - Bf'NPR(s^2 + s'^2vg) \quad (\text{A3})$$

$$a_4 = vgBNPR[N(s - (C_0 + C)s')(b''(C_0 + C)Rs + b'(s - (C_0 + C)s')) - s^2f'(m'' + s''P - R^2b'')] \quad (\text{A4})$$

To satisfy the Routh-Hurwitz criteria for local stability, all of these coefficients must be positive. The fact that  $f' < 0$  guarantees that the first three coefficients must be positive if  $vg$  is sufficiently small. Stability also requires that the quantity  $a_1a_2a_3 - a_1^2a_4 - a_3^2$  be positive; this expression is lengthy, but when  $v$  approaches zero, it approaches the positive quantity,  $f'^2R^3N^2BPs^2b'(C_0 + C)^2$ . Confining attention to branching point equilibria, condition (A4) must be satisfied, because the quantity in square brackets must have the opposite sign of the left-hand side of inequality (4) in the text, given that  $N = f/(C_0 + C)$  at equilibrium. Coefficients  $a_1$  and  $a_3$  are both positive in the limit when  $v$  approaches zero. However, both these terms become negative at sufficiently large  $vg$ , given a branching point equilibrium. Instability at faster adaptive rates can occur because  $a_1 < 0$  if  $f'$  is close to zero (little resource density dependence at the equilibrium). Instability at faster adaptive rates can also occur because  $a_3 < 0$  if the predator dynamics are relatively slow ( $B$  and  $D$  both small), or when  $f'$  is close to 0.