

The effect of adaptive behaviour on the stability of population dynamics

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I consider how adaptive changes in behaviour with population size affect the stability of the population dynamics. In any given year the behavioural rule of a member of a single-species population is determined by the value of a certain trait. I allow for the possibility that this trait value can change from year to year. The number of descendants left in one year's time by an individual depends on its trait value, the values of other population members and the population size. The population dynamics is modelled as the change in population size from one year to the next. I focus on a population that is at a fixed point of the dynamics and in which members adopt the evolutionarily stable trait value for that equilibrium size. I compare the stability of the population dynamics under the following two assumptions about the dependence of trait values on population size: (i) trait values do not change from that at the equilibrium size, and (ii) trait values change so as to be evolutionarily stable for the current size. In a range of examples, I show that adaptive behaviour tends to destabilise population dynamics in the sense that stability under assumption (ii) implies stability under assumption (i). In other words, the region of parameter space for which there is instability under an adaptive response contains the region of instability under no response. Various equivalent general criteria for this to hold are given.

Introduction

As the size, and hence the density, of a population increases food and other resources become more scarce. As this occurs population members may modify their behaviour. For

example, they may exploit previously little used resources or become more aggressive in competitive interactions, leading to a change in how food is distributed amongst population members (e.g. Ens & Cayford 1996). The survival and reproductive success of population members

will depend on both population size and behaviour of population members. Thus the behavioural response to increased population size will affect population dynamics (*see* for example Sibly & Smith 1985, Sutherland 1996). For example, it has been suggested that the crash in population size seen in microtine rodent populations may due be in part to the increased frequency of aggressive encounters at high densities (Begon *et al.* 1986). In this paper, I am specifically interested in changes of behaviour that are adaptive. I model the effect of the behavioural responses on the stability of the population dynamics, contrasting adaptive behavioural changes with fixed behavioural strategies. The main focus of the analysis is to determine if and when adaptive changes tend to produce more unstable population dynamics than fixed behaviour.

Empirically, it is not always clear whether a change in behaviour with population density is adaptive, but there is evidence for such changes. For example, Moss and Watson (1985) suggest that the changes in the territorial spacing of red grouse with population density is adaptive and is also important for population dynamics. In theoretical studies a comparison of adaptive changes with other types of change has been made in specific cases (e.g. Ives & Dobson 1987, Houston & McNamara 1997). Here I develop principles and results that apply generally. I then use these results to analyse four specific examples. The first two examples deal with contests between population members over resources. In Example 1 a contestant chooses its level of aggression, in Example 2 a contestant chooses how long to persist before giving up. In both of these examples if behaviour changes adaptively with population size, contest intensify as population size increases. Example 3 looks at vigilance behaviour of members of a group. Example 4 analyses habitat selection under density dependence. In each of the four examples it turns out that adaptive behaviour tends to destabilise the population dynamics. I am not, however, claiming this to be generally

true: the main purpose of the paper is to highlight the general issue and to motivate others to study further cases.

Formulation of the problem

I consider a single-species population. Within this population the behaviour of an individual is determined by a single quantitative phenotypic trait. For example, the trait value might be the individual's level of aggression. I assume that the trait value of an individual does not change within a year, although it may change from year to year. In this population the number of descendants left by an individual in one year's time depends on that individual's current trait value, the current trait values of other population members, and the current population size. I adopt the following notation. Suppose that the focal individual has current trait value x , all other members of the population have the same current trait value y (which may be different from x), and the current population size is n . Then the expected number of descendants left in one year's time by the focal individual is denoted by $W(x,y,n)$ (cf. the fitness generating function of Vincent *et al.* 1993 and Cohen *et al.* 1999). I refer to W as the fitness of this individual.

In order to analyse population dynamics, assume that in any given year all population members have the same trait value. Let

$$K(x,n) = W(x,x,n) \quad (1)$$

Thus $K(x,n)$ is the fitness of each population member when all have trait value x and the population size is n . Suppose that the common trait value of population members varies from year to year, and in any given year is a function, $x(n)$, of the current population size, n . Then, when the population is size n , the fitness of a population member is $F(n) = K(x(n),n)$. The change in fitness with population size is thus given by

$$F'(n) = \frac{\partial K}{\partial x} \frac{dx}{dn} + \frac{\partial K}{\partial n}, \quad (2a)$$

which can be written heuristically as

$$\left\{ \begin{array}{c} \text{change in} \\ \text{fitness} \end{array} \right\} = \left\{ \begin{array}{c} \text{change due to change} \\ \text{in trait value} \end{array} \right\} + \left\{ \begin{array}{c} \text{change due to change} \\ \text{in population size} \end{array} \right\} \quad (2b)$$

For this population, if the population has size n in one year its size next year is \hat{n} where

$$\hat{n} = nF(n). \quad (3)$$

I refer to a n_0 as an equilibrium size of this population if it is a fixed point of the dynamics. Thus if the population is exactly size n_0 in a year it will be size n_0 in all subsequent years. I shall be concerned with cases for which the function $F(n)$ is a decreasing function of n that is greater than 1 for small n and less than 1 for large n . There will then be a unique equilibrium size n_0 satisfying $F(n_0) = 1$. In order to determine the stability of the equilibrium we consider how population size changes after a small perturbation away from size n_0 . The standard criterion is based on the magnitude of $d\hat{n}/dn$ at the equilibrium. Since $F(n)$ is a decreasing function of n $d\hat{n}/dn$ is less than 1, so stability depends on whether $d\hat{n}/dn$ is greater or less than -1 . It is easy to show that the criterion translates into the following. If

$$n_0 F'(n_0) > -2 \quad (4a)$$

then population size tends to n_0 as time t increases, and the equilibrium is stable. Conversely if

$$n_0 F'(n_0) < -2 \quad (4b)$$

then population size oscillates away from n_0 , and the equilibrium is unstable.

The above analysis applies to any function $x(n)$ relating trait value to population size. I now focus on a specific function; the common trait value of population members in a given year is the evolutionarily stable trait value appropriate to the current population size. This function is

defined as follows. Suppose that the population has size n in a given year. Let all but one member of this population have trait value y . I refer to y as the resident trait value. Let the remaining 'mutant' population member have trait value x . Thus this mutant has fitness $W(x, y, n)$. I assume that, for each given y , there is a unique value of x that maximises $W(x, y, n)$. I refer to this x as the mutant's best response to the resident trait value y . An evolutionarily stable trait value is such that, if this trait value is the resident value, then the best response of the mutant is also this trait value. I assume that, for every population size n , there is a unique evolutionarily stable trait value, which I denote by $x^*(n)$. Thus for population size n , if almost all population members have trait value $x^*(n)$, then the fitness of a mutant is maximised if the mutant also has this trait value. We have

$$W(x^*(n), x^*(n), n) = \max_x W(x, x^*(n), n) \quad (5)$$

(cf. Vincent *et al.* 1993, Cohen *et al.* 1999).

Consider a population that has size n_0 and trait value x_0 at this size where

$$K(x_0, n_0) = 1 \quad (6)$$

and

$$x^*(n) = x_0. \quad (7)$$

By Eq. 6 the population is of equilibrium size. By Eq. 7, given that the population is this size and members all have this trait value, no population member can increase its fitness by changing its trait value. The main focus of this paper is to compare the stability of this equilibrium under the following two assumptions about trait values away from the equilibrium size.

Case I: The trait is fixed and takes the value x_0 in all years regardless of the population size.

Case II: If population is size n in a year then the trait value of all population members is $x^*(n)$ in that year.

I refer to the second case as an adaptive change in trait value. In the examples that I later analyse I am not interested in an exact specifica-

tion of parameters for which the dynamics is stable and for which it is unstable. Rather I am concerned with whether stability under one assumption implies stability under the other. To this end I define the phrase ‘adaptive change in trait value tends to destabilise the population dynamics’ to mean that stability under an adaptive response implies stability under no response. This is equivalent to saying that the region of parameter space for which there is instability under an adaptive response contains the region of instability under no response.

In Case I, an individual has fitness $F_0(n) = K(x_0, n)$ when the population size is n . In Case II, an individual has fitness $F(n) = K(x^*(n), n)$ when the population size is n . By condition 4 the stability of the population dynamics in these cases is determined by the magnitudes of $F'_0(n_0)$ and $F'(n_0)$ respectively. In particular, if $F'(n_0) < F'_0(n_0)$ then stability in Case II implies stability in Case I, conversely if $F'(n_0) > F'_0(n_0)$ then stability in Case I implies stability in Case II. Thus adaptive change in trait value tends to destabilise population dynamics if $F'(n_0) < F'_0(n_0)$. Since

$$F'(n_0) - F'_0(n_0) = \frac{\partial K}{\partial x} \frac{dx^*}{dn}, \quad (8)$$

adaptive change in trait value tends to destabilise the population dynamics if the right-hand side of Eq. 8 is negative; that is if the first term on the right-hand side of Eq. 2a is negative. Thus by Eq. 2b

$$\left\{ \begin{array}{l} \text{adaptive change in trait value} \\ \text{tends to destabilise population} \\ \text{dynamics} \end{array} \right\} \Leftrightarrow \left\{ \begin{array}{l} \text{as the population size increases} \\ \text{the change in fitness due to change} \\ \text{in trait is negative} \end{array} \right\} \quad (9)$$

Best group trait value

Consider a population of equilibrium size n_0 . Suppose that all population members have trait value x . Then each population member has fitness $K(x, n_0)$. In this section, I assume that $K(x, n_0)$ is a unimodal function of x with a single

maximum at $x = x_{\text{group}}$. This can be regarded as the optimum trait value if population members have the same trait value as one another. I refer to x_{group} as the best group trait value. In general this trait value will not be evolutionarily stable since in a population with resident trait value x_{group} there will be some other trait value which will give a mutant that adopts this value higher fitness. In contrast if all population members have trait $x_0 = x^*(n_0)$ then each member is adopting its own selfish optimal trait value given the trait values of others, but overall fitness will not be maximised. This difference between what is best for all population members and what happens when they behave selfishly is epitomised in the ‘tragedy of the commons’. Here it is at the heart of why adaptive behaviour tends to stabilise population dynamics.

Suppose that $x_{\text{group}} < x_0$. Then since $K(x, n_0)$ is a unimodal function of x this function is decreasing for $x = x_0$. If $x^*(n)$ is an increasing function of n at $n = n_0$ then as population size increases the change in fitness due to change in trait is negative. Thus adaptive change in trait value tends to destabilise population dynamics. Other possible cases have similar logic and all can be summarised as follows.

$$\left\{ \begin{array}{l} \text{adaptive change in trait} \\ \text{value tends to destabilise} \\ \text{population dynamics} \end{array} \right\} \Leftrightarrow \left\{ \begin{array}{l} \text{as population size increases from its} \\ \text{equilibrium value } n_0 \text{ the trait value moves} \\ \text{away from the best group value at } n_0 \end{array} \right\} \quad (10)$$

This result will be illustrated in the examples given later.

Results from game theory

I now use the fact that $x^*(n)$ is the evolutionarily stable trait value to derive two useful subsidiary results. Recall that $W(x, y, n)$ is the fitness of a single ‘mutant’ individual in a population with resident trait value y and size n . Let $\partial W / \partial x$ denote the partial differential of $W(x, y, n)$ with respect to its first argument, $\partial W / \partial y$ the derivative with respect to the second argument, etc. In this notation the evolutionarily stable trait value $x^*(n)$ in a population of size n satisfies

$$\frac{\partial W}{\partial x}(x^*(n), x^*(n), n) = 0 \quad (11)$$

and

$$\frac{\partial^2 W}{\partial x^2}(x^*(n), x^*(n), n) < 0. \quad (12)$$

These conditions are sufficient to ensure that $x^*(n)$ is an evolutionarily stable strategy (ESS). I assume that $x^*(n)$ is not only an ESS but is also continuously stable (Eshel 1983, Taylor 1989). It is shown in Appendix 1 that under these assumptions

$$\frac{dx^*}{dn}(n) > 0 \Leftrightarrow \frac{\partial^2 W}{\partial x \partial n}(x^*(n), x^*(n), n) > 0. \quad (13)$$

In particular this relation can be used to infer whether increasing the population size from its dynamically stable value of n_0 increases or decreases the evolutionarily stable trait value. The relation shows that the trait value increases if and only if an increase in population size while holding the resident trait fixed means that a single mutant can increase its fitness by increasing its trait above $x^*(n_0) = x_0$.

Differentiating Eq. 1 with respect to x and making use of Eq. 11 gives

$$\frac{\partial K}{\partial x}(x_0, n_0) = \frac{\partial W}{\partial y}(x_0, x_0, n_0). \quad (14)$$

Then Eqs. 8 and 14 show that adaptive change in trait value tends to destabilise the dynamics if either $dx^*/dn > 0$ and $\partial W/\partial y < 0$ or $dx^*/dn < 0$ and $\partial W/\partial y > 0$. Here the derivatives are evaluated at $n = n_0$ and $x = y = x_0$. This result may be summarised as follows.

$$\left\{ \begin{array}{l} \text{adaptive change in trait} \\ \text{value tends to destabilise} \\ \text{population dynamics} \end{array} \right\} \Leftrightarrow \left\{ \begin{array}{l} \text{as population size increases from } n_0, \text{ the change in} \\ \text{the fitness of a mutant with fixed trait value } x_0 \text{ due} \\ \text{to the change in the resident trait value is negative} \end{array} \right\} \quad (15)$$

Example 1: level of aggression in a contest for a resource

At the beginning of a year each member of the population contests a resource with one other

population member. One contestant obtains the resource. This individual always survives the contest and leaves $V + R(n)$ expected descendants next year. If the loser survives the contest it leaves $R(n)$ descendants next year. If the loser dies it leaves 0 descendants next year. The trait value of an individual determines its level of aggression in the contest. Suppose an individual has trait value x and the opponent has trait value y . Then the individual obtains the resource with probability $P(x, y)$ and survives the contest with probability $S(x, y)$. Thus the expected number of descendant left is

$$W(x, y, n) = P(x, y)V + S(x, y)R(n). \quad (16)$$

$R(n)$ represents future success. Since this will be influenced by competition with other population members in the future I assume that it decreases with increasing n : i.e. $R'(n) < 0$. I assume that the probability that an individual obtains the resource increases with its level of aggression and decreases with the level of aggression of its opponent so that $\partial P/\partial x > 0$ and $\partial P/\partial y < 0$. I assume that an individual's survival decreases with both its level of aggression and that of its opponent so that $\partial S/\partial x < 0$ and $\partial S/\partial y < 0$. Finally, I assume that P and S are such that, for each population size n , there is a unique evolutionarily stable trait value $x^*(n)$ that satisfies Eqs. 11 and 12 and is continuously stable.

Note that by the assumptions on R and S we have $\partial^2 W/\partial x \partial n > 0$. Thus by condition 13 the evolutionarily stable level of aggression increases with population size.

Now consider dynamic stability. By the assumptions on P and S , $\partial W/\partial y < 0$, so that by Eq. 14, $\partial K/\partial x < 0$. Thus, since $dx^*/dn > 0$, condition 8 implies that adaptive change in trait value tends to destabilise the population dynamics. This result can also be seen by considering the best group trait value x_{group} . If all population member have the same trait value x then by symmetry each wins a contest with probability 0.5. Since mortality increases with x , fitness of population member is maximised by taking x to have its minimum value; i.e. $x_{\text{group}} = 0$ (Dawkins 1976). Thus $x_{\text{group}} < x^*(n_0)$ and criterion (10) implies that adaptive change in trait value tends to destabilise population dynamics. In this

example population members would do best if they settled contests without aggression, but such a strategy would not be evolutionarily stable. As population size increases, the benefits from the future, $R(n)$, decline, and it pays to become more aggressive in the current contest. This contributes to the decline in fitness of population members with increasing population size.

Example 2: persistence in a contest for a resource

Resources such as food or mates are scattered in the environment as discrete items. Members of the population search for these items. A proportion $\theta(n)$ of the items found by a searching individual are contested by another population member. If an item is not contested the individual obtains the item. If the item is contested the contestants play a war of attrition (*see e.g.* Maynard Smith 1982) in which each chooses how long to wait for the opponent to give up. The contestant that waits the longest obtains the item. Having obtained an item or given up in a contest an individual recommences searching for further items. The mean time to find the next item is τ . The number of descendants left next year by an individual is an increasing function of the mean rate at which item are obtained.

In this example, the trait of an individual specifies how long it is prepared to wait for a contested item. Motivated by the solution to the war of attrition, I assume that waiting times of an individual are exponentially distributed and take the individual's trait to be the mean of this distribution. On encountering a contested item an individual does not know the precise waiting time of its opponent. The longer that the individual waits the more likely it is to obtain the item, but the more time is lost which could have been spent in search for other items. The optimal waiting time for a given individual clearly depends on the waiting times of other individuals. Population members are thus involved in a game against one another. The optimal waiting time also depends on the proportion of items that are contested: if it is easy to find other uncontested items it is not worth wasting too much time on the present

item (*cf.* McNamara & Houston 1989). I suppose that the probability that an item is contested, $\theta(n)$, increases as population size increases.

Suppose that almost all population members contest an item for an exponential time with mean y ; that is the resident trait is y . Consider a contest between a mutant with trait x and a resident. Then it is easy to show that the mutant wins the contest with probability $x/(x + y)$ and the mean duration of this contest is $xy/(x + y)$. The mean rate at which the mutant obtains items is the probability that an item is obtained divided by the mean time between encountering successive items (*see e.g.* Houston & McNamara 1999). This rate is thus

$$W_{\text{rate}}(x, y, n) = \frac{1 - \theta(n) + \theta(n)x / (x + y)}{\tau + \theta(n) + \theta(n)xy / (x + y)}. \quad (17)$$

Since the number of descendants W increases with W_{rate} we can work with W_{rate} rather than W in determining evolutionarily stable trait values and the effect of behaviour on dynamics.

From the above form of W_{rate} it is straightforward to show that Eq. 11 has unique solution

$$x^*(n) = \frac{\tau}{(1 - \theta(n))}. \quad (18)$$

For this solution there is equality in Eq. 12 rather than an inequality. Nevertheless the evolutionary stability conditions appropriate to the war of attrition (Maynard Smith 1982) are satisfied. Furthermore, the solution is continuously stable. I, therefore, take it to be the evolutionarily stable trait value.

Since $\theta(n)$ increases with n , Eq. 18 shows that the trait $x^*(n)$ increases with increasing n . Thus under adaptive behaviour, population members become more persistent over contested resources as uncontested resources become scarcer. The increased persistence results in population members wasting more time and, as is easily verified from Eq. 17, lowers the rate at which items are obtained. Thus as population size increases, adaptive change in trait value contributes to the decline in the fitness of population members and tends to destabilise population dynamics. This result can also be

seen by looking at the best group trait. If all population members have the same trait value x each wins a contest with probability 0.5 but the least time is wasted by taking $x = 0$. Thus $x_{\text{group}} = 0 < x^*(n_0)$ and condition 10 applies.

Example 3: vigilance behaviour

Many bird species tend to feed in groups. There is evidence that the vigilance behaviour of a bird in a group decreases as the size of the group increases (e.g. Abramson 1979, Caraco 1979, Ekman 1987). A number of papers have sought to explain this phenomena in terms of the adaptive behaviour of group members. In particular the models proposed by Pulliam *et al.* (1982), Lima (1987), and McNamara and Houston (1992) share the following common features. It is assumed that predator attack rate and the food supply do not depend on group size; an assumption that is unlikely to hold precisely in practise. It is assumed that a bird can only increase its rate of feeding by decreasing its level of vigilance for predators. The predation risk to a feeding bird decreases as its own level of vigilance increases and as the vigilance level of other group members increases (the many eyes effect). Predation risk also decreases as group size increases because an attacking predator is less likely to select that individual (the dilution effect). Group members are involved in a game; each bird gains an advantage if others increase their level of vigilance allowing the given bird to decrease its own vigilance level and hence increase its feeding rate. These models all predict that the evolutionarily stable level of vigilance of a group member decreases with group size, in qualitative agreement with observations.

In general there may be no direct link between population size and group size. It is plausible, however, that in some circumstances group size will tend to increase with population size. Assuming this relationship to hold we can then ask whether the adaptive change in vigilance with group size tends to destabilise population dynamics. To formalise this, assume for simplicity that members of a population of size n feed in groups of size $g(n)$. Here $g(n)$

increases as n increases. Take the behavioural trait of an individual to be its feeding rate. Let $W(x, y, n)$ be the fitness of an individual that feeds at rate x when other group members feed at rate y and the group size is $g(n)$. The theoretical models mentioned above then predict that the evolutionarily stable trait value $x^*(n)$ (feeding rate) in a population of size n increases as n increases. In a group the predation risk to a given individual increases as the feeding rate of other group members increases. Thus $W(x, y, n)$ decreases as y increases, condition 15 holds and adaptive change in trait value tends to destabilise the dynamics.

In this example, individual population members gain an advantage from an increase in foraging group size *per se*, but the adaptive response to the increase acts to decrease fitness below what it would have been had vigilance levels been maintained.

Example 4: habitat selection

This model is based on one of the models of habitat selection of Brown (1997). Members of a population can forage in one of two habitats. While foraging in habitat 1 an animal is safe from predators. Habitat 2 has a better food supply than habitat 1 but has a predation risk of μ per unit time spent foraging there. The rate at which food can be found in a habitat is a decreasing function of the number of animals on that habitat. Population members forage for a time period of length T . During this time period each population member chooses the proportion of time spent in each habitat.

If an animal is killed during the period it leaves no descendants next year. If the animal is not killed and its total net energy intake is e it leaves $R(e)$ descendants next year.

Take the behavioural trait to be the proportion of time spent in habitat 2. Suppose that the population size is n and the resident trait value is y . I assume that at any time there are $n_1 = (1 - y)n$ animals in habitat 1 and $n_2 = yn$ animals in habitat 2. This results in net energy intake rates in the two habitats of $H_1(n_1)$ and $H_2(n_2)$ respectively where H_1 and H_2 are decreasing functions. Thus a mutant with trait value x has total net

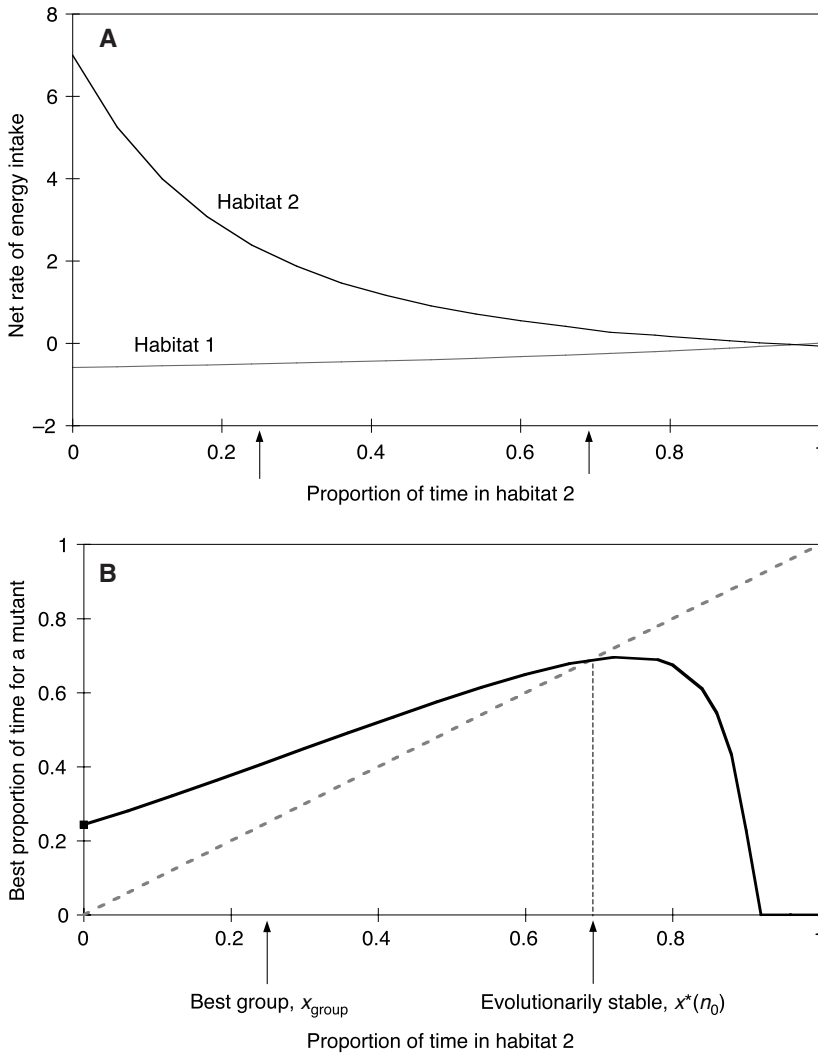


Fig. 1. Effect of the proportion of population members using habitat 2 on the food supply and optimal behaviour (Example 4). The population is at its equilibrium size $n_0 = 429.3$. — **A:** The net rate of energy intake in the two habitats. — **B:** The optimal proportion of time for a single mutant to spend in habitat 2 (solid line). The evolutionarily stable proportion of time on habitat 2, $x^*(n_0) = x_0$, is that proportion for the population as a whole that is also best for the mutant. The best group proportion x_{group} is also shown.

energy intake during the time period of

$$e(x, y, n) = [(1 - x)H_1(n_1) + xH_2(n_2)]T.$$

This mutant survives the period with probability

$$S(x) = \exp\{-x\mu T\}.$$

The fitness of the mutant is then

$$W(x, y, n) = S(x)R(e(x, y, n)).$$

I present results for the particular functions given in Appendix 2, making no claim about the generality of conclusions for other functions. Figure 1 illustrates the feeding rates and the best group and evolutionarily stable trait values in a population at the equilibrium size $n_0 = 429.3$. When resident population members spend all

their time in habitat 1 the net energy intake rate on habitat 2 is high (Fig. 1A). Consequently a mutant individual only needs to spend a relatively small proportion of its time on this risky habitat to achieve a high total net energy gain over the time interval, and its optimal proportion of time on habitat 2 is only 0.244 (Fig. 1B). A small increase in the proportion of time that resident population members spend on habitat 2 produces a strong decrease in the net energy intake rate on that habitat. Consequently a mutant must now spend a greater proportion of time on this risky habitat if it is to have a reasonable total net energy gain over the time interval, and its optimal proportion of time on habitat 2 is increased. Finally, when residents

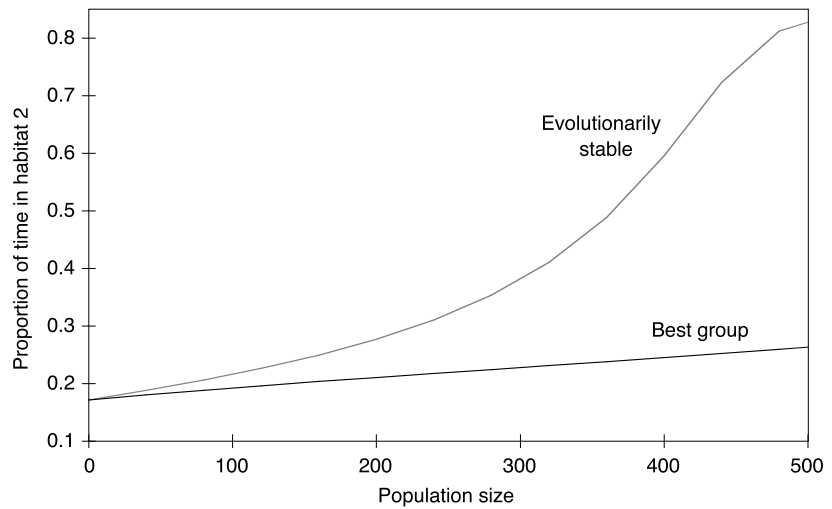


Fig. 2. Best group and evolutionarily stable trait values in Example 4.

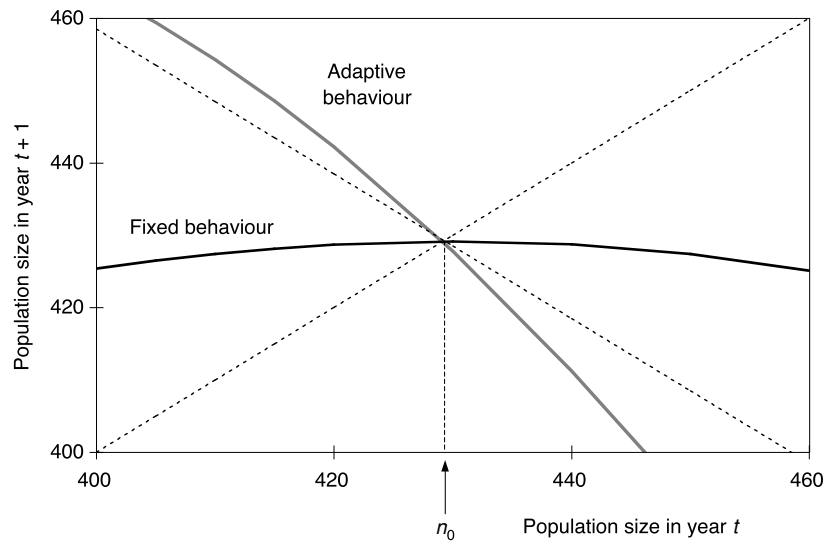


Fig. 3. Population dynamics in Example 4. The two solid lines show the dynamics when the proportion of time on habitat 2 is held fixed and when the proportion of time on habitat 2 changes adaptively with population size.

spend most of their time on habitat 2 the net rate of energy gain is so low there that the mutant does best to avoid this habitat altogether. The evolutionarily stable proportion of time on habitat 2 is that proportion for the resident population that is also best for the mutant. This proportion is illustrated in Fig. 1B and is $x_0 = x^*(n_0) = 0.689$.

Figure 1B also shows the best group proportion of time on habitat 2, x_{group} . As can be seen this proportion is very much less than x_0 . If all population members share the same trait value then their fitness is maximised if this value is x_{group} . However a mutant in a population with resident trait value of x_{group} maximises fitness by having a higher trait value (Fig. 1B). There

would then be selection pressure to increase the trait value in the population. As the resident trait value increased under this selection pressure the best mutant trait value would also increase (Fig. 1B). There would therefore be selection pressure for a further increase until the resident trait value equalled x_0 .

As can be seen from Fig. 2 the best group trait value is less than the evolutionarily stable value at all population sizes, not just at size n_0 . The figure also shows that the evolutionarily stable trait value is increasing with population size at size n_0 . It follows by criterion (10) that adaptive change in trait value tends to destabilise population dynamics. Figure 3 shows this directly. As can be seen from the figure a population with

fixed trait value of x_0 has highly stable dynamics. In contrast a population with flexible adaptive behaviour has unstable population dynamics. If the size of such a population were perturbed away from n_0 then population size would oscillate about n_0 with an amplitude that increased over time.

Discussion

I have contrasted the stability of the population dynamics for a given population under two assumptions about the behavioural response to change in population size. By the phrase 'adaptive change in trait value tends to destabilise the population dynamics' I have meant that stability under an adaptive response implies stability under no response. Of course this does not mean the dynamics under an adaptive response will always be unstable, only that the region of parameter space for which there is instability under an adaptive response contains the region of instability under no response.

In all the examples presented, adaptive change in trait value tends to destabilise population dynamics. When there are direct competitive interactions between population members, as in Examples 1 and 2, it is plausible that the intensity of competition will increase as population size increases and that the best group level of competition is low or zero. If these two properties hold, criterion (10) applies and behaviour tends to destabilise dynamics.

When competition for resources is indirect, as in Example 4, the selfish behaviour of individuals at high population density is likely to decrease the fitness of all population members. This 'tragedy of the commons' effect makes it plausible that destabilisation might be the norm here as well.

In this paper, I have taken as the baseline behaviour the evolutionarily stable trait value at the equilibrium population size. In contrast, Houston and McNamara (1997) compare adaptive behaviour with a fixed rule of thumb. Their results again suggest that adaptive behaviour

produces more unstable population dynamics.

Despite these examples, I am not claiming that adaptive behaviour always destabilises population dynamics. More work needs to be done analysing further specific cases. For instance, it would be instructive to examine the role of territorial behaviour on the stability of the population dynamics. In addition more work is needed to establish general results. My aim in this paper has been to draw attention to an issue rather than give a complete analysis of it.

When formulating a model care may be needed in defining what is meant by 'holding behaviour fixed as population numbers change'. The same behaviour can be produced by more than one underlying rule. It is the rule that is the trait that should be held fixed. To illustrate this, consider Example 4. In analysing this example I took the trait to be the proportion of time spent on habitat 2. Thus it was assumed that the underlying rule employed by an animal controlled this proportion directly. As an alternative I might have taken an animal's trait to be a specification of the total net energy gained over the time interval. Under given feeding conditions a target energy gain determines the proportion of time on habitat 2. However, as population size, and hence feeding conditions change holding the target fixed is not equivalent to holding the proportion fixed.

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Appendix 1

When does the evolutionarily stable trait value increase with population size?

I assume that the evolutionarily stable trait value in a population of size n satisfies Eqs. 11 and 12. I also assume continuous stability and hence that

$$\frac{\partial^2 W}{\partial x \partial y}(x^*(n), x^*(n), n) + \frac{\partial^2 W}{\partial x^2}(x^*(n), x^*(n), n) < 0 \quad (\text{A1.1})$$

(Eshel 1983, Taylor 1989). Using these equations, I investigate the dependence of $x^*(n)$ on n .

Differentiating Eq. 11 with respect to n gives

$$\left\{ \frac{\partial^2 W}{\partial x^2} + \frac{\partial^2 W}{\partial x \partial y} \right\} \frac{dx^*}{dn} + \frac{\partial^2 W}{\partial x \partial n} = 0, \quad (\text{A1.2})$$

where derivatives are evaluated at $x = y = x^*(n)$. Condition 13 then follows directly from Eqs. A1.1 and A1.2.

Appendix 2

Functions and parameters for the habitat choice model

I assume that if n_i animals are foraging in habitat i each has net energy intake rate

$$H_i(n_i) = \frac{a_i[1 - \exp(-b_i n_i)]}{n_i} - 1$$

(cf. Brown 1997). Here the first term on the right-hand side represents gross intake rate. The term -1 corresponds to energy expenditure. Results presented in Figs. 1–3 are based on the parameter values $a_1 = 200$, $b_1 = 0.005$, $a_2 = 400$ and $b_2 = 0.02$. I take an animal to start with energy reserves of 10 units. Thus its reserves at the end of the time interval are $e' = e + 10$ where e is the total net energy gain during the interval. If $e' \leq 0$ then the animal leaves 0 descendant next year, while if $e' > 0$

$$R(e) = \frac{2.4e'}{(10 + e')}$$

descendants are left. Other parameters are $\mu = 0.0125$ and $T = 50$.