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Journal of Theoretical Biology 236 (2005) 208–215

Journal of Theoretical Biology

www.elsevier.com/locate/yjtbi

The evolution of stability in a competitive system

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Received 27 October 2004; received in revised form 2 March 2005; accepted 2 March 2005
Available online 18 April 2005
Communicated by Yoh Iwasa

Abstract

The characteristics governing the dynamics of populations can evolve and this evolution can either be towards stability or chaos. Yet it is not obvious how or why such population characteristics can evolve through selection on individuals. In this paper we construct a mathematical model, inspired by experimental results, illustrating the dynamics of a population of competing *Drosophila*. We demonstrate how selection of life history characteristics and stability influence one another as a population interacts with its environment. We generalize this result and show that population stability can evolve as a consequence of selection on individuals.

Keywords: *Drosophila*; Competition; Fitness; Life history; Selection

1. Introduction

The evolution of stability in populations has received much attention in population biology (for reviews see Ferriere and Fox, 1995 and Mueller et al., 2000). If unstable populations are less likely to persist one could even speculate that evolution would lead to population stability (Stokes et al., 1988; Thomas et al., 1980; Berryman and Millstein, 1989). This is essentially a group selection argument that has been challenged (Allen et al., 1993; Rosko et al., 1994) as such a mechanism can only work under very restrictive conditions (Mueller et al., 2000). Evolution generally works on the traits of individuals and not on the characteristic of populations. Therefore, one cannot expect that stability will necessarily evolve. However, as empirical evidence by Prasad et al. (2003) shows, selection on individual traits can alter population characteristics. Here we investigate how evolution affects stability properties, in a simple population model for intra-specific competition, and clarify why stability evolves.

As well as stability, limit cycles and chaotic population dynamics can evolve depending upon the exact form of the trade-off between the reproductive capacity and the ability to cope with unfavourable circumstance (Metz et al., 1992). Using a similar mathematical model Doebeli and Koella (1995) found that, without constraints, parameters under selection evolved to reduce fluctuations in population size by moving to regions of parameter space associated with stable equilibrium dynamics. However, lack of density dependence unrealistically allowed selection for ever increasing equilibrium densities. What caused these tendencies was not obvious; which makes it hard to generalize Doebeli and Koella's findings beyond their model. Mueller (1988), and Jansen and Sevenster (1997) formulated models of population dynamics of *Drosophila* spp. in food-limited environments. In both these models high female fecundity and strong larval competition lead to unstable population dynamics. Female fecundity and competitive ability are important components of fitness and,

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doi:10.1016/j.jtbi.2005.03.004

therefore, it can be hypothesized that selection upon these two traits will have consequences on the dynamics of a population. This was investigated experimentally by Mueller et al. (2000) who found that feeding rates, which are an important component of the competitive ability in this system (Jansen and Sevenster, 1997), altered in response to larval density over time. Although identifying the importance of female fecundity on population stability no direct evidence of selection affecting the dynamics was found.

Often a change in the genetic make-up that changes one characteristic will also change the other. Here we will assume that an increase in competitive ability will generally decrease fecundity. Although there is no equivocal evidence of the quantitative details of this trade-off, this is motivated by two observations: Firstly, one can expect energetic constraints will dictate such a trade-off (Joshi and Mueller, 1996), and secondly, if more competitive individuals would also be more fecund, this would lead to the evolution of a Darwinian demon: a type that is both maximally competitive and maximally fecund. As fecundity and competitive ability are, in reality, constrained we shall assume that more competitive larvae are less fecund. To describe the evolution of population characteristics, and to interpret previous experimental results, we construct a mathematical model based on the biology of competing laboratory *Drosophila*. We will show that there exists a simple connection between the dynamics of a population and traits under individual selection and also how life history characteristics evolve in the presence of a trade-off amongst traits.

2. The model

The life cycle of *Drosophila* can be simplified into three stages: larval, pupal, and adult. In laboratory populations of *Drosophila* competition among larvae for food is the main force regulating the population (Bakker, 1961). Crowding during one stage of a life cycle has consequences on the population at another. Adult fertility is influenced by pre-adult density. The fecundity of adult females is greatly dependent on their size (Prout and McChesney, 1985; Mueller, 1988) which, in turn, is dependent upon the population density during the larval stage owing to competition for food. Competitive ability does not only influence fertility levels but also the likelihood of larvae to survive (Bakker, 1961; Mueller, 1988). When resources are limited individuals in a population will be forced into competition as the population grows in size. If the selective values of the individuals' phenotypes respond differently to population size then density-regulated selection will occur.

3. Model for a single strain

The model we use is loosely based on the model by Mueller (1988, 2000):

$$n_{t+1} = \tfrac{1}{2} F(n_t) W(n_t) V n_t. \qquad (1)$$

The model is based on discrete generations where t is the generation number and n_t represents the number of eggs laid in that generation. F is the mean fecundity of females, W describes the viability of larvae (the probability of larvae surviving to adulthood) and both F and W are density-dependent functions. V is the probability of an egg reaching the first instar larval stage and $\frac{1}{2}$ signifies the sex ratio. For simplicity the effect of adult density on fecundity is omitted.

Next we specify the functions for viability, W, and fecundity, F. The type of competition between larvae is predominantly of the scramble form. Organisms vying for food in this manner will consume varying amounts depending upon their competitive abilities if food is in short supply (Bakker, 1961; Parker, 2000; Nicholson, 1954). We introduce, φ, as the amount of food per larva:

$$\varphi = \frac{b}{V n_t}, \qquad (2)$$

where b is the total amount of food available. A minimum amount of food, m, is required for a larva to survive. If the amount of food per larva is below m then none survive. Above this limit larval survival increases, the further away from m the larvae reach, up to a plateau at which larvae reach a maximum viability (Fig. 1). This can be described by

$$W(\varphi) = \frac{(\varphi - m) W_{max}}{c + \varphi - m}, \qquad (3)$$

where W_{max} is the maximum survival of larvae and c is the half saturation constant. If the excess amount of food per larva, $\varphi - m, = c$ then survival is half the maximum survival. If the amount of food per larva is

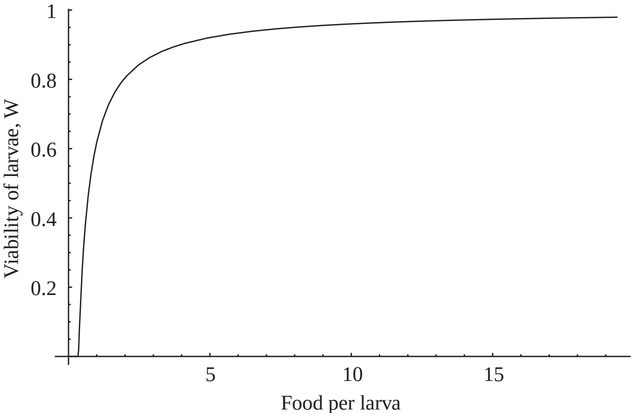

Fig. 1. Graph showing how larval survival, W, changes with the amount of food per larva, φ for $f_{max} = 100$ $Q = 1.4$ $m = 0.35$; $b = 400$; $V = 0.21$ and $W_{max} = 1$.

less than m then

$$W(\varphi) = 0. \tag{4}$$

By replacing φ with Eq. (2) and multiplying the numerator and denominator by n_t we find

$$W(\varphi(n_t)) = \frac{W_{max}(b/V - mn_t)}{b/V + (c-m)n_t}. \tag{5}$$

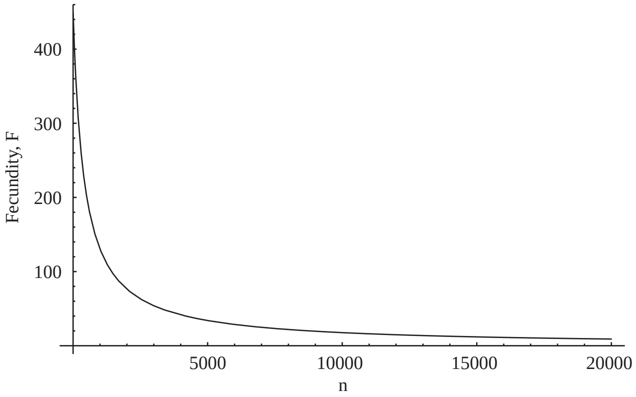

Fig. 2. Shape of the fecundity, F, curve as it changes with egg number, n For $b = 400$; $V = 0.21$.

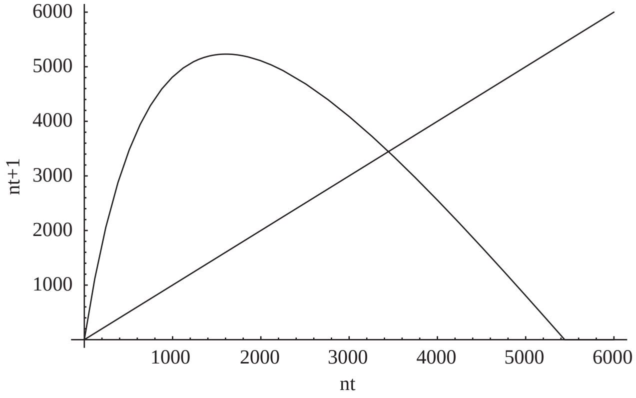

Fig. 3. A Ricker graph for the model showing the dependence of n_{t+1} on n_t at $f_{max} = 100$, $Q = 1.4$, $b = 400$, $V = 0.21$, $W_{max} = 1$ and $c = 0.4$.

Fecundity is dependent upon the size of the emergent adult females which, in turn, is dependent upon the amount of food each larva consumes.

Introducing φ into the fecundity function highlights this relationship. The saturating response of female fecundity to the amount of food per larva is described by

$$F(n_t) = \frac{f_{max}\varphi(n_t)}{Q + \varphi(n_t)}, \tag{6}$$

where f_{max} is the maximum fecundity and Q the half-saturation constant. Fig. 2 shows how the fecundity, F, depends on egg number.

The population size of the next generation, and its dynamics, is determined by the population size of the previous generation (Fig. 3). The population will grow in size up to a point. After this point, however, larvae continue to consume the food available until competition becomes so great that larvae become unable to pupate to adulthood, causing the population to crash. Increasing f_{max} leads from population stability to cycles, chaos and, eventually, extinction (Fig. 4). To quantify the dynamical behaviour we analyse the stability of the model. The equilibrium density, $\bar{n}$, can be found by solving $1 = \frac{1}{2}F(\bar{n})W(\bar{n})V$ (see appendix).

The stability of the equilibrium can be determined in a standard way by linearizing the dynamics around the equilibrium point. To do so we introduce the population growth rate, A;

$$A(n) = \tfrac{1}{2}F(\varphi(n))W(\varphi(n))Vn. \tag{7}$$

A small deviation from the equilibrium changes according to $n_{t+1} - \bar{n} = (n_t - \bar{n})S$. The resilience, S, can be found by differentiating Eq. (7)

$$\begin{aligned} S = \left.\frac{\delta A}{\delta n}\right|_{n=\bar{n}} &= \left.\frac{\partial A}{\partial \varphi}\frac{\delta \varphi}{\delta n}\right|_{n=\bar{n}} + \left.\frac{\partial A}{\partial n}\right|_{n=\bar{n}} \\ &= \frac{1}{2}\left[\left.\frac{\partial F}{\partial \varphi}\right|_{n=\bar{n}} W(\varphi(\bar{n})) \right. \\ &\quad \left. + F(\varphi(\bar{n}))\left.\frac{\partial W}{\partial \varphi}\right|_{n=\bar{n}}\right] V\bar{n}\left.\frac{\partial \varphi}{\partial n}\right|_{n=\bar{n}} + 1. \end{aligned} \tag{8}$$

The equilibrium is stable if the multiplier, S, has a value between -1 and 1. Note that $\bar{n} = 0$ implies that $S = 1$,

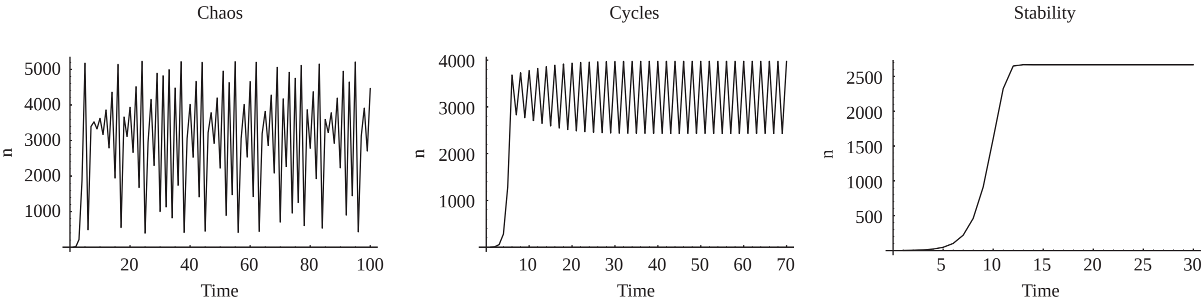

Fig. 4. Various dynamic behaviour observed in model for $f_{max} = 100$, 50 and 21, respectively.

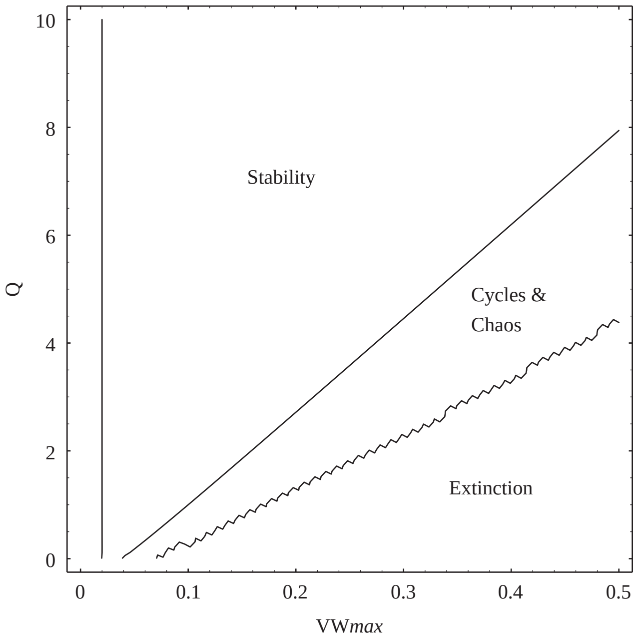

Fig. 5. Where S must reside in order for stability to be maintained. The boundary between extinction and the domain with cycles and chaos was found by evaluating at which parameter combination the maximum population size would lead to extinction ($A(\max(A))=0$) and therefore, represent a necessary condition for extinction. Here $b=400$, $V=0.21$ and $f_{max}=100$.

hence if at the point where a non-trivial equilibrium comes into existence the multiplier S is 1. Further evaluation of terms did not lead to transparent results, hence stability is investigated numerically. Fig. 5 displays the stability and extinction boundaries of S.

4. Model for two competing strains

To study the evolution of stability we next extend the model to describe competition between strains. The strains differ in their fecundity and competitive ability. To quantify competitive ability we introduce larval feeding rate, r. We will study how a newly appearing mutant strain, which differs in some aspect from the other resident strain, fares.

Competitive ability will be determined by how fast the larvae feed; the faster the feeding rate the more competitive the larvae (Bakker, 1961; Jansen and Sevenster, 1997). Differences in competitive ability cause differences in the amount of food per larva, φ, and is modified to describe both the resident (denoted by $\varphi(n,n^*)$) and the mutant (denoted by $\varphi^*(n^*,n)$) for time food available (dependent upon feeding rates (r, r^*) and population sizes (n, n^*)), t. If we assume that larvae have constant rates of ingesting food, r and r^*, then the total food supply will be finished after $\frac{b}{V(rn+r^*n^*)}$ units of time. The amount of food the resident and mutant larvae get is therefore

$$\varphi(n,n^*)=\frac{rb}{V(rn+r^*n^*)} \tag{9}$$

and

$$\varphi^*(n^*,n)=\frac{r^*b}{V(rn+r^*n^*)}, \tag{10}$$

respectively.

Note that if either resident or mutant is absent the model reduces to the model for one strain. The model for two competing strains is now given by

$$n_{t+1}=\tfrac{1}{2}F(\varphi)W(\varphi)Vn_t, \tag{11}$$

$$n^*_{t+1}=\tfrac{1}{2}F^*(\varphi^*)W(\varphi^*)Vn^*_t, \tag{12}$$

where

$$F^*(\varphi^*)=\frac{f^*_{max}\varphi^*}{Q+\varphi^*}=\frac{f^*_{max}}{f_{max}}F(\varphi^*). \tag{13}$$

To study the effects of fecundity a mutant was introduced into the model boasting a higher f_{max} while keeping the feeding rates equal for both strains. As expected the mutant out-competes, and eventually replaces, the resident fly when introduced to vie for the same food supply. Selection always favours more fecund adults and will drive evolution towards instability, chaos and, eventually, extinction.

Investigating the effects of selection on r can be observed by introducing a mutant amongst a resident population. A mutation giving a greater competitive ability out-competes a resident population and, thus, would be selected for. However, unlike f_{max}, parameter r does not affect the population dynamics directly, and an evolutionary change that only affects parameter r will not change the population dynamics.

Next we study the evolution of the feeding rate, r. We assume a trade-off exists between fecundity and competitive ability in *Drosophila*. This trade-off can be justified on the basis of energetic constraints (Joshi and Mueller, 1996) and in order to prevent the emergence of simultaneously maximally fecund and maximally competitive types. The trade-off between fecundity and competitive ability is given by

$$f_{max}(r)=\frac{\gamma}{r^\alpha}, \tag{14}$$

where γ and α parameterise the trade-off; for positive values of α the maximal fecundity decreases with competitive ability. The population dynamics of this trade-off through evolution in r are demonstrated in Fig. 6.

5. Fitness

The fitness of a mutant type with feeding rate r^*, which exists in a population dominated by a resident with a feeding rate of r, can be calculated as the linearized per capita growth rate of a rare mutant (Metz et al., 1992). Assuming that the resident is at equilibrium this is

$$Z(r^*, r) = \tfrac{1}{2} F^*(\varphi^*(0, \bar{n}))\, W(\varphi^*(0, \bar{n}))\, V \tag{15}$$

$$= \frac{1}{2} \frac{f^*_{max}}{f_{max}} F(\varphi^*(0, \bar{n}))\, W(\varphi^*(0, \bar{n}))\, V \tag{16}$$

and the marginal fitness, i.e the change in fitness due to a small change in r^*, can be expressed as

$$\left.\frac{\partial Z(r^*, r)}{\partial r^*}\right|_{r=r^*} = \frac{1}{f_{max}} \frac{\partial f^*_{max}}{\partial r^*} + \frac{1}{2} \left[\frac{\partial F}{\partial \varphi^*} W(\varphi^*(0, \bar{n})) + F(\varphi^*(0, \bar{n})) \frac{\partial W}{\partial \varphi^*} \right] V \left.\frac{\partial \varphi^*}{\partial r^*}\right|_{r=r^*}. \tag{17}$$

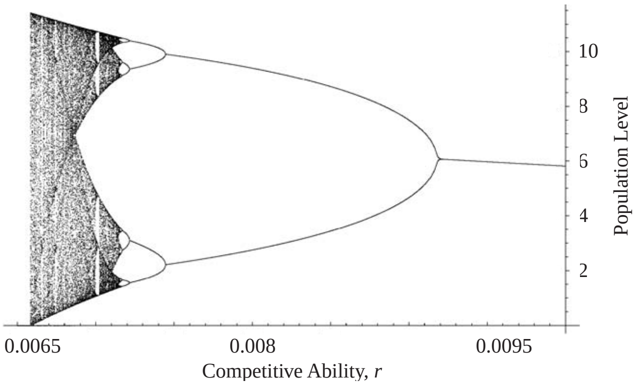

Fig. 6. The influence of r on the population dynamics. This bifurcation diagram shows the influences that competitive ability has on the dynamics through its trade off with f_{max}. Increasing r leads away from extinction, chaos and cycles to stable dynamics and, eventually, an exponential decrease in the equilibrium population level. $Q = 2.45$; $m = 0.350$; $b = 0.8$ and $V = 0.2$; $W_{max} = 1$; $\gamma = 1$; $\alpha = 1$; $c = 0.4$.

The first term describes the effect of a change in f_{max} through the trade-off. The second term describes the direct effect on the fitness due to a change in the growth rate. This expression can be simplified by realising that

$$\left.\frac{\partial \varphi^*}{\partial r^*}\right|_{r=r^*} = -\bar{n} \left.\frac{\partial \varphi}{\partial n}\right|_{n=\bar{n}} \tag{18}$$

and hence the second term can be rewritten using the resilience, S, which we have calculated to establish the stability of the equilibrium. Combining Eqs. (8) and (17) gives

$$\left.\frac{\partial Z(r^*, r)}{\partial r^*}\right|_{r=r^*} = \frac{1 - S - \alpha}{r}. \tag{19}$$

This shows how the marginal fitness is linked to the stability of the equilibrium through selection at the level of the individual. Through this relationship it can be seen that, not only does the stability measure evolve but, the strength of selection itself actually depends directly upon the stability of the equilibrium. The stability of the equilibrium at the ESS is given by

$$S = 1 - \alpha. \tag{20}$$

If the trade-off is weak evolution will favour stability. In the case of the trade-off being a dominant factor instability will evolve. In Fig. 7 we confirm this numerically: we found that the marginal fitness as calculated exactly matches the theoretically predicted values if the equilibrium is stable. For periodic solutions our results hold approximately true but the result for marginal fitness deviates the further from the stability boundary it is measured. Our theoretical results in all cases predict correctly whether or not stability will evolve, but only if evolution leads to stability can we correctly predict the value of the ESS. Furthermore, the presence of resilience as part of an individual's marginal fitness is not particular to this model. In Appendix B we generalize this finding to a large class of competitive scenarios.

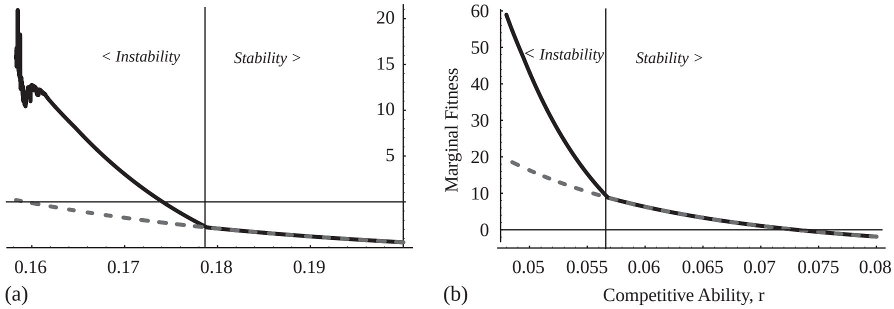

Fig. 7. Two diagrams showing simulated (solid line) and predicted (dashed line) marginal fitness as it changes with respect to competitive ability, r. Divergence of these two lines occurs towards instability. (a) Scenario where the direction evolution (i.e. towards the marginal fitness = 0) would lead to unstable dynamics; (b) to stable dynamics. $Q = 1.4$; $m = 0.350$; $b = 400$ and $V = 0.21$; $W_{max} = 1$; $\gamma = 1$; α in (a) = 2.5, in (b) = 1.5; $c = 0.4$.

6. Discussion

The replacement of an original population through the selection of traits will change the dynamic characteristics of a population. Stability is a characteristic of a population while evolution is driven by selection of individuals. It is, therefore, not a priori obvious that evolution can favour a population characteristic. Our model describes density-dependent selection on the traits of competitive ability and female fecundity, and the subsequent population dynamics. In isolation these traits would continue to evolve to ever increasing values. Our model assumes a trade-off between fecundity and competitive ability. The resulting dynamics make evident that a population can, but need not, evolve towards stability: the deciding factor being the trade-off between competitiveness and fecundity. In the absence of such a trade-off evolution will drive the dynamics towards the stable regime. In fact, without a trade-off, the population will evolve towards the shortest feeding time possible; this is an example of the pessimization principle (Mylius and Diekmann, 1995).

Our findings highlight a clear connection between traits under the influence of selection and the stability of a population. In addition, we show that the stability measure of a population is an element of the individual fitness function. We arrived at this conclusion by considering individual selection only and without invoking group or kin selection arguments. The reason for this connection is that both stability and selection coefficients are governed by competition. This observation explains why certain populations evolve towards stability.

A similar line of reasoning, in which population characteristics have been explained as resulting from individual selection, has been applied to the evolution of chaos, evolution towards the edge of chaos and evolution towards criticality (Bak and Sneppen, 1993; Kaufman et al., 1998; Rai and Schaffer, 2001). All these characteristics are properties of the population. As with the evolution of stability there is no a priori reason why they should result from selection on the individual. However, within the model presented here, special choices of the trade-off function can lead to evolution towards the edge of chaos. But our results suggest that such behaviour, in general, will not be robust. For a robust example of evolution towards criticality in a biologically plausible scenario see (Stollenwerk and Jansen, 2003). We have shown that stability can, but need not, evolve in a large class of scenarios. In all these cases the evolution of such population characteristics is a direct consequence of the details of the density-dependent selection, in particular the strength of frequency-dependent selection in relation to the strength of frequency-independent selection and, ultimately, of the particulars of the interactions rather than representing a law or governing principle.

Acknowledgements

We thank the National Environment Research Council (NERC) for the studentship and their support.

Appendix A

From the equilibrium density this gives

$$\frac{\bar{n}}{B}=\frac{-(c-m+Q+\frac{f_{max}mU}{2})+R}{2(c-m)Q}.$$

The parameters B, U and R are defined as

$$B=\frac{b}{V},$$

$$U=VW_{max},$$

$$R=\sqrt{-4(cQ-mQ)\left(-\frac{1}{2}f_{max}U\right)+\left(c-m+Q+\frac{f_{max}mU}{2}\right)^2}.$$

Note that parameter B serves only as a scaling factor. The equilibrium density depends on all other parameters in a nonlinear way.

Appendix B

To demonstrate that the appearance of the resilience of a population in an individual's marginal fitness is a general feature, and not restricted to the particular model in this paper, we will here generalize this finding. To do so, consider the general growth model

$$n_{t+1}=n_tf(r,\phi(r,E)), \tag{B.1}$$

where n_t is the population density at time t, r is a trait that we will allow to change under evolution. The *per capita* growth rate f depends directly on the trait, and through a feedback on the environment, which is represented by $\phi(r,E)$. Here E represents the state of the environment, which we will assume depends both on the trait and on the population density, and can be represented by a scalar, hence $E(r,n_t)$. The environment is not affected by the trait if there are no individuals present: $\partial E(r,n)/\partial r|_{n=0}=0$. In what follows we will also assume that the environment depends on individuals that differ in their value for r, however if such individuals are absent they will not influence the state of the environment. Note that the environment is the same for all individuals, irrespective of the trait value they possess, but that the way an individual feels' this environment is mediated by the trait value through $\phi(r,E)$.

The equilibrium value, $\bar{n}$ is defined by

$$f(r,\phi(r,\bar{E}))=1,$$

where $\bar{E}=E(r,\bar{n})$. The stability of this equilibrium is determined by the linearized growth rate in the neighbourhood of this equilibrium:

$$(n_{t+1}-\bar{n})\approx(n_t-\bar{n})S,$$

where the resilience, S, is given by

$$S=\frac{\partial f}{\partial\phi}\frac{d\phi}{dn}\bigg|_{n=\bar{n}}+1.$$

Next, we will study how a mutant with a different trait value, r^*, will fare in this environment. The change in the population size of this mutant at time t, n_t^*, is given by

$$n_{t+1}^*=n_t^*f(r^*,\phi(r^*,E)).$$

The environment now depends on the population sizes of the mutant and the resident and their respective traits: $E(r,r^*,n,n^*)$, and, as before, we will assume that if a population is absent, it leaves no mark on the environment

$$\frac{\partial E(r,r^*,n,n^*)}{\partial r^*}\bigg|_{n^*=0}=0$$

and $E(r,r^*,n,0)=E(r,n)$. The fitness of this mutant, if it is rare, in a population dominated by the resident at equilibrium is given by $W_{r^*,r}=f(r^*,\phi(r^*,E(r,\bar{n})))$. The marginal fitness is

$$\frac{\partial W_{r^*,r}}{\partial r^*}\bigg|_{r^*=r}=\frac{\partial f}{\partial r^*}\bigg|_{n^*=0,r^*=r,n=\bar{n}}+\frac{\partial f}{\partial\phi}\frac{\partial\phi}{\partial r^*}\bigg|_{n^*=0,r^*=r,n=\bar{n}}.$$

Note that because we assumed that the environment is not affected by the mutant population if it is absent, there is no need to include the effect of a change in the mutant's trait on the environment. By substituting S we can rewrite this as

$$\frac{\partial W_{r^*,r}}{\partial r^*}\bigg|_{r^*=r}=\frac{\partial f(r,\phi(r,\bar{E}))}{\partial r}+(S-1)\,\frac{\partial\phi/\partial r}{d\phi/dn}\bigg|_{n^*=0,r^*=r,n=\bar{n}}.$$

which demonstrates the generality of our finding. The interpretation of this result is that a trait can affect the fitness in a frequency-independent way, given by the first term, and indirectly in a frequency-dependent way, through a one-dimensional feedback environment, represented by the second term. The relative importance of these two factors is gaged by the resilience.

For this result to hold the density dependence needs to work through a single dimensional feedback environment. Using the same line of reasoning it is straightforward to explore evolution in a k-dimensional feedback environment. Let the population dynamics be given by

$$n_{t+1}=n_tf(r,\phi_1(r,E_1),\ldots,\phi_k(r,E_k)),\qquad\text{(B.2)}$$

where $E_i=E_i(r,n_t)$ represents the state of the ith feedback variable, which depends both on the trait and on the population density. As before we assume that the variable is independent of the trait if there are no individuals present. At equilibrium we have $f(r,\phi_1(r,\bar{E}_1),\ldots,\phi_k(r,\bar{E}_k))=1$ where the $\bar{E}_i=E_i(r,\bar{n})$. The resilience is given by

$$S=\sum_{i=1}^{k}\frac{\partial f}{\partial\phi_i}\frac{d\phi_i}{dn}\bigg|_{n=\bar{n}}+1.$$

The marginal fitness of a rare mutant with trait value r^* is given by

$$\frac{\partial W_{r^*,r}}{\partial r^*}\bigg|_{r=r^*}=\frac{\partial f}{\partial r^*}\bigg|_{n^*=0,r^*=r,n=\bar{n}}+\sum_{i=1}^{k}\frac{\partial f}{\partial\phi_i}\frac{\partial\phi_i}{\partial r^*}\bigg|_{n^*=0,r^*=r,n=\bar{n}}$$

which can be rewritten as

$$\frac{\partial W_{r^*,r}}{\partial r^*}\bigg|_{r=r^*}=\frac{\partial f(r,\phi_1,\ldots,\phi_k)}{\partial r}+\sum_{i=1}^{k}m_i\frac{\partial f}{\partial\phi_i}\frac{d\phi_i}{dn}\bigg|_{n=\bar{n}}$$

where the multipliers m_i are defined as: $m_i=\frac{\partial\phi_i}{\partial r^*}/\frac{d\phi_i}{dn}|_{n^*=0,r^*=r,n=\bar{n}}$. Only if all m_i are equal will the resilience explicitly form part of the expression for marginal fitness. This will not generally be the case if $k>1$.

This result relates to evolution in populations which exhibit limit cycles or chaotic dynamics. Let the densities over a limit cycle be given by the sequence n_t, where the n_t satisfy recursion (B.1). Because the densities in such cases change from time step to step, the value of the environment will potentially also take different values. Let E_t denote the value of the environment at time t, i.e. $E_t=E(r,n_t)$. Because the value of n_t is a function of n_0 through (B.1), the value of the environment at time t is a function of the density at time 0: $E_t=k(r,n_0)$. The dynamics from time point 0 to T are given by

$$n_T=n_0\Pi_{t=0}^{t=T}f(r,\phi(r,k(r,n_0))).$$

This recursion is a special case of (B.2), hence we can conclude that over a limit cycle or chaotic orbit it is, in general, not possible to describe the marginal fitness in terms of the resilience.

In sum, we have found that the resilience will generally appear in the marginal fitness equation if the density dependence works through a single dimensional feedback environment, which can be represented by a scalar. Although this does make clear that in a large class of models stability will evolve through individual selection and that this evolution will seek a balance between frequency-dependent and frequency-independent selective processes, it is not possible to draw general conclusions on whether or not stability will evolve.

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