

Group selection and the ‘shifting balance’

S. ROUHANI¹ AND N. H. BARTON^{2,*}

¹ Physics Department, Sharif University of Technology, and Institute for Studies in Theoretical Physics and Mathematics, Tehran, PO Box 11365-9161, Iran

² Division of Biology, University of Edinburgh, King's Buildings, Edinburgh EH9 3JT, U.K.

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Summary

We investigate the establishment and spread of new adaptive peaks within Wright's ‘shifting balance’. The third phase of the ‘shifting balance’ involves a kind of group selection, since demes in which a superior peak has been established contain more individuals, and so send out more migrants. We assume that population size, N , increases with mean fitness, \bar{W} , according to the exponential relation, $N \propto \bar{W}^k$. Here, k is a measure of the weakness of density-dependent regulation, and equals the inverse of the regression of $\log(\text{fitness})$ on $\log(N)$. In the island model, we find that just as with soft selection ($k = 0$), two distinct types of behaviour exist: group selection makes no qualitative difference. With low numbers of migrants, demes fluctuate almost independently, and only one equilibrium exists. With large numbers of migrants, all the demes evolve towards the same adaptive peak, and so the whole population can move towards one or other of the peaks. Group selection can be understood in terms of an effective mean fitness function. Its main consequence is to increase the effect of selection relative to drift (Ns), and so increase the bias towards the fitter peak. However, this increased bias depends on the ratio between k and the deme size (k/N), and so is very small when density-dependence is reasonably strong.

1. Introduction

The evolution of a population can under certain conditions (Akin, 1979) be represented by an adaptive landscape. We take this to be a graph of mean fitness against allele frequencies, or any other set of characteristics which describe the state of the population (see Provine, 1986, Wright, 1988). Natural selection causes movement up gradients of mean fitness, towards ‘adaptive peaks’. This movement may trap a population at a local maximum, so that higher adaptive peaks remain out of reach. Wright proposed that random fluctuations such as sampling drift allow escape from local maxima (Wright, 1931, 1932, 1940). He argued that there is a shifting balance between random drift, which can take a deme into the domain of attraction of a new peak; selection within demes, which completes the movement to the new peak; and selection between demes, which aids the spread of a new adaptive peak through the whole population. Wright's (1931) theory of the ‘shifting balance’ has

received considerable and continued attention, as a mechanism for both adaptation and speciation (e.g. Lande, 1985, Provine, 1986, Kauffman & Levin, 1987, Crow *et al.* 1989, Wade & Goodnight, 1991).

When sampling drift is the source of stochastic fluctuations, the rate of shifts between peaks for a single deme takes the form $A \exp(-BNs)$, where N is the population size, s is the selection coefficient, and A, B are constants of order 1. For large NS , shifts will be rare. Thus, the ‘shifting balance’ requires that there be a large number of demes, which are small enough ($Ns \approx 1$) and loosely coupled enough ($Nm \approx 0.1 - 1$) that each can readily explore the ‘adaptive landscape’. However, such a population may still be unlikely to shift as a whole to a higher peak: the third phase of the shifting balance, in which a new adaptive peak spreads through the whole population, is crucial to the process. Spread may occur in three ways. First, whole demes might go extinct, and be replaced by colonists from demes in a different state. Second, gene flow between demes can overcome selection, and cause the certain spread of the new peak. Third, the influx of migrants from demes carrying a different

* Corresponding author.

peak makes it more likely that the deme will shift to that peak as a result of random fluctuations.

If higher mean fitness results in a larger number of emigrants, the fitter peak will be more likely to spread than the lower peak, under all three mechanisms. This differential emission of migrants has been thought significantly to accelerate the spread of the higher peak (Wright, 1940, 1965, 1977, Crow *et al.* 1989). The question which concerns us in this paper is whether the bias towards 'superior' peaks is caused by group, as opposed to individual, selection during the third phase of the 'shifting balance'. We concentrate on spread by stochastic infection, the third of the mechanisms listed above.

We examine an idealized island model. In each of an infinite number of demes, a polygenic character under disruptive selection can shift between two alternative mean values. The evolution of the whole population can be described by movement up a landscape, though this includes the effects of migration as well as of mean fitness. In a previous paper (Barton & Rouhani, 1993) we analysed a general method for deriving the distribution of a quantitative character in such a model, and found approximations which hold when selection is either very weak, or very strong. Here, we extend these methods to allow for group selection, in which demes at the higher adaptive peak make a greater contribution to the migrant pool. We assume that the size of a deme, and hence the number of emigrants, is a definite function of its mean fitness: thus, selection is 'hard', in that deme size depends on mean fitness (Christiansen, 1975).

There are various definitions of 'group selection'. On the strictest, only differential extinction and recolonization of whole groups would be included (Maynard Smith, 1964). At the other extreme, Wade (1978) defined group selection as 'that process of genetic change which is caused by the differential extinction or proliferation of groups of organisms'. Our model of hard selection counts as group selection under the latter definition, but not the former. Nunney (1985) criticizes the broad definition, on the grounds that 'group selection' would occur even if groups were randomly defined: arbitrary groups that by chance contain fitter individuals will produce more offspring. Nunney therefore defines group selection as 'a process by which a trait spreads... because of the differential reproduction of genotypes that arises from the positive associations of individuals exhibiting that trait'. Whether our model should be classed as group selection under Nunney's definition then depends on whether demes with high mean fitness have more members because of positive interactions between fit individuals, or simply because a balance between the genotypic and density dependent components of individual fitness is reached at higher numbers. We will use the term group selection throughout this paper in the broadest sense, to refer to the consequences of differences in deme size which are caused

by differences in genotype. Note that in our scheme, if deme size *decreased* with mean fitness, group and individual selection would be opposed, giving a model for the evolution of altruism.

We show that as in the original analysis, where deme size was fixed (i.e. where selection was 'soft'), there is a critical migration rate below which the whole population can move towards the higher peak. Just below this critical value, adaptation is most effective, in that there is a strong bias towards the higher peak. We will show that group selection does increase this bias, but only very slightly.

2. Summary of results for soft selection

We first outline the analysis of Barton & Rouhani (1992), and then explain how it can be extended to allow for group selection. Suppose that each of an infinite number of demes exchanges a fraction m of its members with a common migrant pool. Selection is soft, so that the number of individuals is fixed at N per deme, regardless of their genetic state. Each deme is characterized by z , which in this case represents the mean of a polygenic trait. (We will assume throughout that the additive genetic variance of the trait, v , is constant. This is a good approximation when the number of loci involved is very large; see Barton & Rouhani, 1993.) The whole population is described by the distribution of z across demes, $\psi(z)$. With no migration, this would follow Wright's formula, $\psi(z) \propto \bar{W}^{2N}$, and would be clustered around the adaptive peaks. Migration pulls the distribution towards the mean of the migrant pool, \bar{z} , so that the distribution is now a function of the state of the migrant pool: $\psi(z|\bar{z}) \propto \bar{W}^{2N} \exp(-(Nm/v)(z-\bar{z})^2)$ [eqn (4) of Barton & Rouhani, 1993]. If all demes contributed equally to the migrant pool, \bar{z} would equal the unweighted mean across the whole ensemble of demes, which we denote by $\langle z \rangle = \int z \psi(z|\bar{z}) dz$. The equation $\langle z \rangle = \bar{z}$ can then be solved to find the joint mean at equilibrium, and hence the whole distribution.

Although the mean fitness has two peaks, this equation may or may not admit two equilibria. When there are few migrants ($Nm \ll 1$), demes fluctuate independently, and most demes will be at or near the fitter peak. The population then admits only one equilibrium state, with the mean across demes being somewhere between the fitness peaks. As number of migrants increases, the bias of the migrant pool towards the fitter peak pulls the whole population further towards that peak; this feedback can greatly accentuate the bias to the fitter peak, regardless of the value of Ns . However, as the number of migrants increases further, demes start to fluctuate together, and the whole population can become trapped at either of two stable equilibria, corresponding to the two peaks. These two regimes are separated by a sharp transition at a critical Nm , which is at

approximately (v/Ω^2) , where 2Ω is the distance between the peaks.

Our analysis showed that the 'shifting balance' can ensure that the population becomes concentrated around the highest peak, even when that peak is only slightly above the alternatives. This process is most effective just below the critical number of migrants. If the number of migrants is higher, then migration from other demes prevents the spread of the new adaptive peak, whilst if it is lower, there is less bias towards the fitter peak. When selection is very weak, or very strong, convergence to equilibrium will be slow. However, there is a wide range of selection strengths over which the process can operate within a reasonable time ($0.01 \ll Ns \ll 30$, say). The similarity between results for quantitative traits and for selection against heterozygotes, and general results for strong selection when demes are clustered around the two peaks, suggest that these patterns extend to any form of selection that sustains alternative equilibria. We argue that within an extended and inhomogeneous spatial distribution, the fitter peak may be established in regions where Nm is near its critical value, and (provided that Nm varies sufficiently slowly with distance) can then spread through the rest of the range.

3. Incorporating hard selection

For a given state of the migrant pool, one can use the diffusion approximation to follow the evolution of the distribution across demes of some population characteristic, such as the mean of a polygenic character. At any instant, the mean of the characteristic in the migrant pool equals its average calculated using this distribution. In general, this average is weighted by the contribution of each deme, which may in turn be a function of its genetic composition. Thus, one must solve a pair of equations: a diffusion equation for the distribution of the characteristic, and an equation relating the state of the migrant pool to this distribution. Although the state of each deme fluctuates randomly, the distribution as a whole changes deterministically. Barton & Rouhani (1993, Appendix 2) showed how this deterministic model can be derived in the limit where the number of demes tends to infinity.

The equilibrium can be found from Wright's (1935) distribution. This requires the assumption that frequency-dependency and linkage disequilibria are negligible, so that the effects of migration, mutation, selection and drift can be described by a potential function, proportional to the mean fitness. The same method gives the distribution of the mean of a quantitative character, provided that the genetic variance is constant (Lande, 1976). In a single population, this is a good approximation if large numbers of loci are involved, and if selection is weak enough relative to recombination that linkage dis-

equilibrium can be neglected (see Discussion in Barton & Rouhani, 1993).

We assume that a constant fraction m is exchanged with the migrant pool in every generation; variation in m with mean fitness should have similar effects to variation in N . We assume that the population size of a deme is determined by its genetic composition, so that population size is a function $N(z)$ of the mean of the polygenic character. This will be a good approximation if density dependent regulation acts much faster than selection, so that the deme quickly moves towards an equilibrium size that depends on its current genetic state. In a future paper, we intend to investigate models with explicit population dynamics, in which both genetic state and population size vary stochastically.

Any particular deme will receive $\bar{N}m$ migrants from the common pool, where \bar{N} is the mean size of the demes contributing to the migrant pool. This must equal the mean across demes, which we denote by $\langle N \rangle$. (It is convenient to distinguish between the mean number coming in from the migrant pool, \bar{N} , and the average across the distribution ψ , which determines the contribution to the migrant pool, and which we denote by $\langle N \rangle$).

$$\bar{N} = \langle N \rangle = \int N(z) \psi(z, \bar{z}, \bar{N}) dz. \tag{1 a}$$

The mean of the character in the migrant pool, \bar{z} , is equal to the weighted average across demes, $\langle z \rangle$:

$$\bar{z} = \langle z \rangle = \int z \frac{N(z)}{\langle N \rangle} \psi(z, \bar{z}, \bar{N}) dz. \tag{1 b}$$

Since we assume that selection is weak, the expected change of the mean under selection and gene flow is approximately continuous:

$$\frac{\partial z}{\partial t} = v \frac{\partial \ln(\bar{W})}{\partial z} + m(\bar{z} - z) \frac{\bar{N}}{N(z)}. \tag{2}$$

The effect of migration is inversely proportional to the deme size, $N(z)$. Sampling drift causes uncorrelated random fluctuations in z , with variance $v/N(z)$. This stochastic differential equation has the equilibrium distribution (Gardiner, 1983):

$$\psi(z) = CN(z) \exp(2U) \tag{3}$$

where $U(z) = \frac{1}{v} \int N(z) \frac{\partial z}{\partial t} dz$.

C is a normalization constant, chosen such that the distribution integrates to 1. Equation (3) may be partially integrated to give:

$$\psi(z | \bar{z}, \bar{N}) = CN(z) \exp\left(-\frac{\bar{N}m}{v}(z - \bar{z})^2 \times \int N(z) \frac{\partial \log \bar{W}}{\partial z} dz\right). \tag{4}$$

This is a recursive relation for ψ , since \bar{N} and \bar{z} are themselves determined by ψ through eqn (1). By

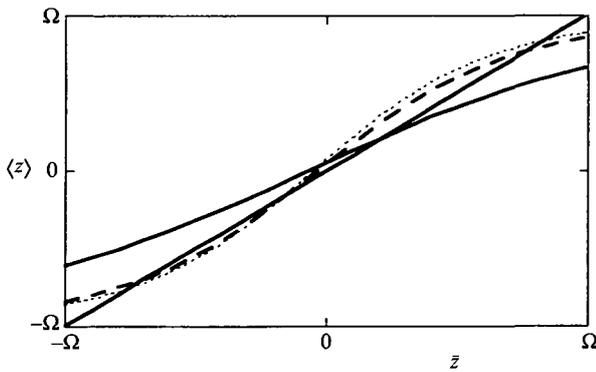


Fig. 1. The mean of emigrants, $\langle z \rangle$, as function of the mean of immigrants, \bar{z} . The equilibrium corresponds to $\langle z \rangle = \bar{z}$, and is represented by the diagonal line. The solid line shows the relation for soft selection ($k = 0$, so that $\langle N \rangle = N_0 = N$), with low gene flow ($Nm\Omega^2/v = 0.5$, $\alpha = 0.01$, $Ns = 10$). There is only one equilibrium, in which demes shift freely between the two peaks. Increasing gene flow to $Nm\Omega^2/v = 1$ (broken line) gives three equilibria, the middle one being unstable. The whole population can now be trapped near one or other of the peaks. Adding hard selection ($k/N_0 = 0.5$; dotted line), with the same high level of gene flow ($\bar{N}m\Omega^2/v = 1$) slightly increases the effectiveness of selection, thus steepening the graph of $\langle z \rangle$ against \bar{z} .

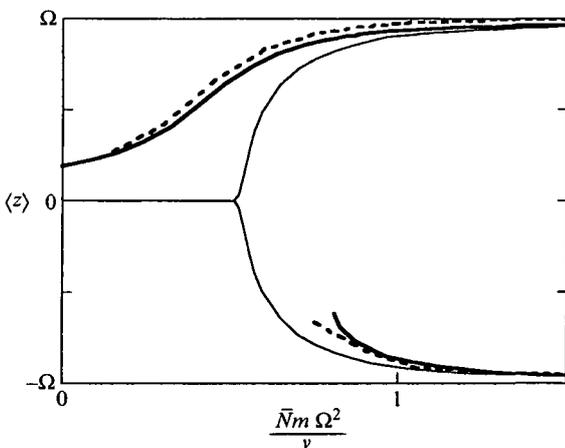


Fig. 2. The position of equilibria $\langle z \rangle$ as function of $\bar{N}m\Omega^2/v$. The thin line shows the soft selection limit with no asymmetry ($\alpha = 0$), and $Ns = 30$. With low migration (left of figure) the number of demes at either peak is the same, so that $\langle z \rangle$ is zero. As migration increases beyond $\bar{N}m\Omega^2/v = 0.5$, a bifurcation occurs, and two equilibria appear. With slight asymmetry ($\alpha = 0.01$, thick line), the critical number of migrants above which two equilibria appear increases. Adding hard selection ($k/N_0 = 0.1$; broken line) increases the bias towards the commoner peak, and slightly reduces the critical number of migrants. However, the change is small.

assuming a particular form of hard selection, $N(z)$, we may proceed further with eqn (4). Barton (1986) suggested the exponential relation:

$$N(z) = N_0 \bar{W}^k. \tag{5}$$

Here, k is a measure of the weakness of density-dependent regulation: if mean fitness increases by a small factor, $x\%$, then population size increases by

$kx\%$. If fitness is the product of a genetic component (\bar{W}), and a component that depends on density (i.e. if selection is density independent), and selection is weak, then k is the inverse of the regression of log fitness against log (N) (Barton, 1986). Other relations between N and \bar{W} would give the same results, provided that selection is weak enough for fluctuations in \bar{W} to be small. Interactions between individuals can alter the value of k : for example, an altruistic trait could give a negative k . (Though note that the relation must then break down for very unfit populations, since \bar{W}^k tends to infinity as \bar{W} becomes small, if k is negative.) Group selection would be most effective for large k , corresponding to weak density-dependence; however, population size would then fluctuate greatly, leading to frequent extinction of demes. We expect k to be around 1 for most populations.

Using eqn (5), we integrate eqn (4) to get:

$$\psi(z) = C \bar{W}^k \exp\left(-\frac{\bar{N}m}{v}(z-\bar{z})^2 + 2\frac{N_0}{k}(\bar{W}^k - 1)\right). \tag{6a}$$

Here, $\bar{N}m = N_0 \langle \bar{W}^k \rangle m$ is the average number of migrants across demes. Since $(\bar{W}^k - 1) \approx k \log(\bar{W})$ for small k , we recover the distribution for soft selection in the limit $k = 0$:

$$\psi(z) = C \bar{W}^{2N_0} \exp\left(-\frac{N_0 m}{v}(z-\bar{z})^2\right). \tag{6b}$$

Equation (6b) is identical to eqn (4) of Barton & Rouhani (1993).

Examination of eqn (6a) shows that it depends only on $\bar{N}m/v$, k/N_0 , and $N_0 \log(\bar{W})$. This is our most important conclusion, since it implies that hard selection will only have significant effects when k is comparable with the deme size, which seems implausible (see Discussion).

Now consider a definite model of disruptive selection, which acts such that the log mean fitness is:

$$\ln(\bar{W}) = -\frac{s}{8\Omega^4} \left((\Omega^2 - z^2)^2 + \frac{4\alpha\Omega}{3}(z-2\Omega)(z+\Omega)^2 \right). \tag{7}$$

This quartic polynomial has peaks at $z = -\Omega$ and $+\Omega$, separated by a valley at $-\alpha$. The left-hand peak has log mean fitness $(2s\alpha/3)$ lower than the right-hand peak. The consequent asymmetry in population sizes between demes at different peaks is $(\bar{W}_2/\bar{W}_1)^k = \exp(2\alpha ks/3)$. For example, when $\alpha = 0.1$, $s = 0.3$, the mean fitness of the two peaks differ by only 2%. However, if density-dependence is very weak ($k = 10$) the sizes of demes at different peaks differ by 22%. The drop from the inferior peak down to the valley is $s(1-\alpha)^3(1+\alpha/3)/8$; this is the barrier that must be overcome by random drift if the population is to shift from the lower to the higher peak. Barton & Rouhani (1993) give the individual fitness function which leads to eqn (7).

We can now solve eqns (1) and (6) to find the equilibria. First, consider soft selection [$k = 0$; eqn

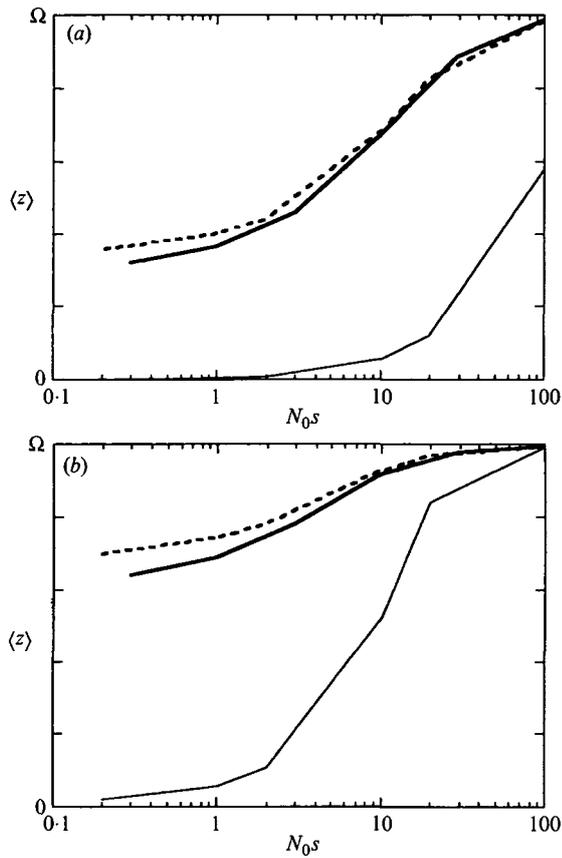


Fig. 3. The critical bias towards the higher peak, as a function of N_0s . (a) Even with a small asymmetry ($\alpha = 0.01$) the bias towards the higher peak at the critical number of migrants is considerable. When there is no migration (thin line) this bias increases only at large values of Ns . With migration at the critical rate (solid line), the bias is much larger. Hard selection ($k/N_0 = 0.1$) only slightly increases the critical bias (dashed line). (b) With larger asymmetry ($\alpha = 0.1$), the bias is more visible, but the effect of interdemic selection (dashed line) is still small.

(6b)]. There are two distinct possibilities. For large values of $Nm\Omega^2/v$, we observe two stable equilibria (dashed line in Fig. 1), whereas smaller values of $Nm\Omega^2/v$ allow only one equilibrium (solid line in Fig. 1). As the asymmetry increases, the domain of attraction of the fitter peak expands, and so a larger number of migrants is needed to ensure the existence of two equilibria.

With hard selection, we again solve eqn (1), but this time use the distribution of the mean as given by eqn (6a). This gives a solution in terms of the average number of migrants, $\bar{N}m$. This could itself be calculated from the parameters, by finding the average of $N_0 \bar{W}^k$. However, for the range of parameters we consider, \bar{N} is close to N_0 ; it must lie between the values given by substituting \bar{W} for the valley, and for the higher peak. We will therefore not generally carry through this step, and will treat the results simply as a function of $\bar{N}m$.

Using the distribution with hard selection [$k/N_0 = 0.1$; eqn (6a)] we can again solve eqn (1) and find the

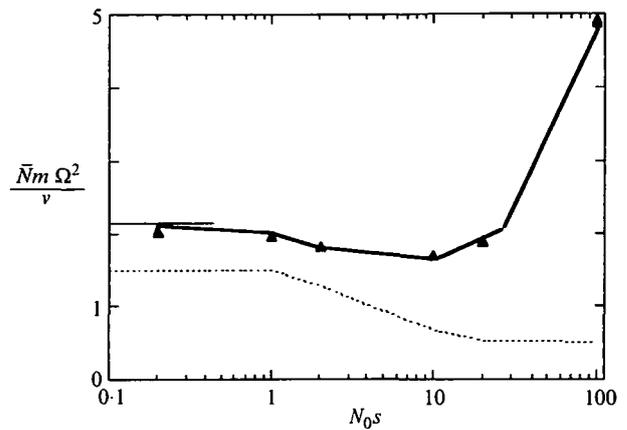


Fig. 4. The critical numbers of migrants, $\bar{N}m\Omega^2/v$, as function of N_0s . The dotted and solid lines show the critical values for soft selection, with asymmetry, for asymmetry $\alpha = 0$ (dotted line) and $\alpha = 0.1$ (solid line). The triangles show the effect of hard selection ($k/N_0 = 0.1$), with asymmetry $\alpha = 0.1$; the critical numbers are hardly affected, and in any case, are similar for all but very strong selection. The thin line on the left shows the prediction from the small Ns approximation [from eqn (13)].

equilibria (e.g. Fig. 1, dotted line). As with soft selection, there is a critical migration rate above which two equilibria exist. Figure 2 shows a graph of the position of the equilibria as $\bar{N}m\Omega^2/v$ increases. The effect of hard selection is to increase the bias towards the higher peak, and slightly to reduce the critical migration rate (dotted line in Fig. 2). The maximum bias to the higher peak is achieved at the critical migration rate. Figure 3 shows this maximum bias as a function of N_0s , for asymmetry $\alpha = 0.01$ (Fig. 3a) and $\alpha = 0.1$ (Fig. 3b). The 'shifting balance' does greatly increase the bias to the higher peak, as can be seen by comparing the solid curve, which gives the maximum bias for soft selection, with the lower light curve, which gives the bias with no migration. However, hard selection ($k/N_0 = 0.1$) has little effect, as can be seen by comparing the solid and dotted curves.

Figure 4 shows the critical number of migrants ($\bar{N}m\Omega^2/v$) as a function of the strength of selection. The curves show results for soft selection, with asymmetry $\alpha = 0$ and $\alpha = 0.1$. Hard selection (triangles; $k/N_0 = 0.1$, $\alpha = 0.1$) causes a slight reduction in the critical number. Nevertheless, the critical migration rate is of the same order over the whole range of selection and asymmetry; it becomes large only for moderate asymmetry and very strong selection, in which case peak shifts are extremely rare, so that the 'shifting balance' will be ineffective.

4. The effective mean fitness

The effects of group (or 'hard') selection can be understood by thinking of the soft selection model that is equivalent to that with hard selection. The distribution of z in the migrant pool, which is what

matters for the calculation of the weighted averages $\langle z \rangle$ and $\langle N \rangle$ is $(N(z)/\langle N \rangle) \psi(z|\bar{z}, \bar{N})$ [eqn (1)]. The effect of migration does not depend on whether selection is hard or soft: it consists of multiplication by a Gaussian with variance $(v/2\bar{N}m)$. We can therefore concentrate on the factor which represents the distribution across demes in the absence of migration. The distribution with hard selection [eqn (6a)] is equivalent to one with soft selection [eqn (6b)], provided that we define 'effective parameters' such that

$$CN^*W^{*2N^*} = N(z)\psi(z) = N(z)^2 \exp(2(N_0/k)(\bar{W}^k - 1)),$$

where C is a normalization constant.

Taking logs, and writing the mean fitness as $\bar{W} = \exp(\log(\bar{W}))$, we see that only the dimensionless combinations $N \log(\bar{W})$ and $N^* \log(\bar{W}^*)$ matter:

$$N^* \log(\bar{W}^*) = \left(\frac{k}{N_0}\right) (N_0 \log(\bar{W})) + \left(\frac{N_0}{k}\right) (\exp[(k/N_0)(N_0 \log(\bar{W}))] - 1). \quad (8a)$$

The resulting distribution will be exact if one also uses the migration rate $Nm = \bar{N}m$ in the equivalent soft selection model.

Equation (8a) defines a nonlinear transformation of the mean fitness. $N^* \log(\bar{W}^*)$ will have its maxima and minima at the same z as the old fitness function, but its value at these points will be different. To understand the effect of the transformation, it is helpful to use a Taylor expansion for small (k/N_0) :

$$N^* \log(\bar{W}^*) = N_0 \log(\bar{W}) + \left(\frac{k}{N_0}\right) N_0 \log(\bar{W}) \left(1 + \frac{N_0 \log(\bar{W})}{2}\right) + O((k/N_0)^2). \quad (8b)$$

$N^* \log(\bar{W}^*)$ is greater than $N_0 \log(\bar{W})$ for all positive $\log(\bar{W})$, and less than $N_0 \log(\bar{W})$ for small negative $\log(\bar{W})$: the effect of selection is increased by a factor $(1+k/N_0)$ for small $k \log(\bar{W})$. Thus, the effective asymmetry between the peaks is always increased by group selection, and the effective depth of the valley is increased for small $k \log(\bar{W})$. However, if the valley is sufficiently deep ($N_0 \log(\bar{W}) < -2$ for small k/N_0), group selection makes it shallower. This is illustrated in Fig. 5, which compares the distributions with hard and soft selection (solid and dotted lines). [The graph shows $\log(\psi)$, which equals $2N^* \log(\bar{W}^*)$.] Note that if selection is strong enough that hard selection makes the valley shallower, shifts will be rare. Thus, for the range of parameters in which the 'shifting balance' operates at a reasonable rate, one can regard interdemic selection simply as amplifying intrademic selection.

The rate of shifts from the lower peak to the higher peak, which determines the speed of the approach to equilibrium, is a function of the effective depth of the

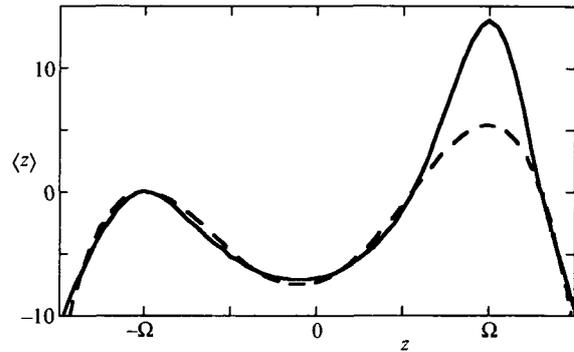


Fig. 5. The weighted distribution across demes, in the absence of gene flow. This is plotted on a log scale, as $\log[N(z)\psi(z|\bar{z}, \bar{N})]$, for $\alpha = 0.1$, $N_0s = 40$. The dotted line is for soft selection, whilst the solid line is for hard selection ($k/N_0 = 0.5$). The advantage of the higher peak is amplified by hard selection (r.h.s.). However, the depth of the valley is slightly reduced by hard selection. With weaker selection (N_0s), the valley depth would be slightly increased, rather than decreased [eqn (8)].

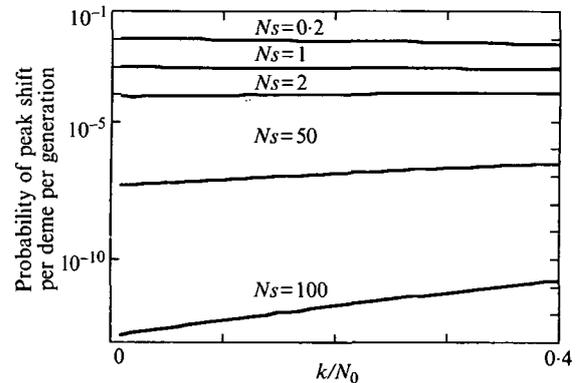


Fig. 6. The probability of a shift from the lower peak to the upper peak increases with k , provided that N_0s is large ($N_0s = 100$). For small values of N_0s ($N_0s < 10$) this probability decreases with k . (Values were calculated by numerical integration, as described in Barton & Rouhani, 1993; $\alpha = 0.1$.)

valley separating the peaks. With increasing k we expect the probability of a peak shift per deme to decrease for small N_0s , as the valley deepens, but no increase for large N_0s , as the valley becomes shallower. This is confirmed by Fig. 6.

The other effect of k is to increase the asymmetry between the two fitness peaks. The difference of the log probability of being at the two peaks is:

$$2N^* \Delta \log(\bar{W}^*) = \frac{4\alpha ks}{3} + \frac{2N_0}{k} \left[\exp\left(\frac{2\alpha ks}{3}\right) - 1 \right], \quad (9)$$

which is a monotonically increasing function of k . This increase in asymmetry increases the bias towards the higher peak. The importance of group selection in aiding adaptation is essentially determined by eqn (9).

It is tempting to try to find effective parameters α^* , Ns^* , which would give an equivalent soft selection model of the form analysed in Barton & Rouhani

(1992). However, this would constrain $\log(\psi)$ to follow a quartic polynomial; yet, even when group selection is weak [eqn (8*b*)], the effective log mean fitness is an eighth order polynomial. The shapes of the distributions with hard and soft selection are therefore substantially different especially when selection is strong.

5. The two-state approximation

Exact calculation of the equilibrium distribution requires numerical integration of eqns (1) and (6). However, when Ns is large enough that demes are usually near one or other adaptive peak, the distribution can be approximated by the sum of two Gaussians, which can be integrated explicitly. This gives an analytic expression for the relation between the mean of the migrant pool, and the mean of the consequent distribution. Barton & Rouhani (1993) have shown that this relation applies to any distribution of polygenic traits or allele frequencies which clusters around alternative adaptive peaks, and does not depend on details of the model of disruptive selection.

This gives a fairly simple expression for the relation between the mean across demes, and the mean in the migrant pool:

$$\langle z \rangle = \Omega \tanh \left[\frac{2m\bar{N}\Omega\bar{z}}{v} + N^*\Delta \log(\bar{W}^*) - \frac{\alpha}{2} - \frac{1}{4} \log \left(\frac{k/N_0 + 1}{k/N_0 + \exp(2\alpha ks/3)} \right) \right]. \quad (10)$$

Here, $2N^*\Delta \ln(\bar{W}^*)$ is the difference in log probability of being at the peaks [eqn (9)]. In the soft selection limit ($k = 0$) we obtain a result equivalent to eqn (8*b*) of Barton & Rouhani (1992), for large N_0s . The average population size \bar{N} can also be calculated using the Gaussian approximation. For small k/N_0 this is:

$$\langle N \rangle = N_0 \exp \left(\frac{\alpha ks}{3} \right) \frac{\cosh \left(\frac{2N_0 m \Omega \bar{z}}{v} + \frac{2(N_0 + k) s \alpha}{3} \right)}{\cosh \left(\frac{2N_0 m \Omega \bar{z}}{v} + \frac{2N_0 s \alpha}{3} \right)}. \quad (11)$$

Interdemic selection will have an appreciable effect on population size only when $ks\alpha$ is large. Clearly, this requires unacceptably high values of k when asymmetry and selection are weak.

6. The weak selection limit

When Ns is small, selection within demes is ineffective: the distribution \bar{W}^{2N} is almost flat. However, if migration is high enough ($m \gg s$), the system will behave as one panmictic population, and disruptive selection will push it towards either $-\Omega$ or $+\Omega$. We

argued (Barton & Rouhani, 1992) that just as with strong selection, there can be a strong bias towards the higher peak, even when all the demes start at the lower peak. This limit of very weak selection can be understood in terms of another 'effective mean fitness', which we term \bar{W}_{eff} :

$$\langle z \rangle - \bar{z} \approx \frac{v}{m} \frac{\partial \bar{W}_{\text{eff}}}{\partial \bar{z}},$$

where

$$\bar{W}(\bar{z})_{\text{eff}} = \int \bar{W}^*(z) \exp \left(-\frac{\bar{N}m}{v} (z - \bar{z})^2 \right) \sqrt{\frac{\bar{N}m}{\pi v}} dz. \quad (12)$$

This is derived by approximating $\log(\bar{W}^*)$ by $(\bar{W}^* - 1)$ in eqn (6*b*) [cf. eqn (10) in Barton & Rouhani, 1992]. Since the equilibria are where $\bar{z} = \langle z \rangle$, we see that these correspond to the stationary points of the graph of \bar{W}_{eff} against \bar{z} . This function is just the adaptive landscape that would be produced by adding $(v/2\bar{N}m)$ to the phenotypic variance. When the number of migrants is large, this addition is small, and so the modified adaptive landscape still has two peaks: there are thus two stable equilibria. However, once the number of migrants falls below a critical value, the increased variance smoothes the two peaks into one, so that the ensemble of demes has a single equilibrium. This qualitative change is similar to that described by Kirkpatrick (1982), who analysed the effects of changes in phenotypic variance on the evolution of a quantitative character under disruptive selection.

Since the transformation of eqn (8) reduces to a simple multiplication by $(1 + k/N_0)$ when selection is weak, we arrive at a similar expression to the soft selection model (Barton & Rouhani, 1993):

$$\langle z \rangle - \bar{z} = \frac{(N_0s + ks)v}{8\Omega^4 \bar{N}m} \left\{ 2(\Omega^2 - \bar{z}^2)(\bar{z} + \alpha\Omega) - \left(\frac{v}{\bar{N}m} \right) (3\bar{z} + \alpha\Omega) \right\}. \quad (13)$$

In the symmetric case ($\alpha = 0$), the critical rate of gene flow is $\bar{N}m_{\text{crit}} = 1.5(v/\Omega^2)$, and is independent of k . With asymmetry, this value increases, but is again independent of k . The thin line on the left of Fig. 4 shows this weak selection limit, for $\alpha = 0.1$. As N_0s decreases, the points in Fig. 4 do indeed approach the limit given by eqn (13).

7. Discussion

In this paper we analysed the effect of a form of group selection on the spread of a new adaptive peak in the third phase of Wright's 'shifting balance'. The essential conclusion was simple: even when the number of migrants increases disproportionately with mean fitness ($Nm = N_0m\bar{W}^k$, with $k = 10$, say, and $N_0 =$

100), the advantage accruing to the new peak through group selection is small. This is to be expected, since when selection is weak ($ks \ll 1$), the effect of selection on the number of migrants is small, whilst when selection is strong ($ks \approx 1$), it is likely to dominate over drift ($Ns \gg 1$), so that peak shifts become very rare. Our analysis shows that the group selection will only have an appreciable effect when the parameter k , which measures the weakness of density-dependent regulation, is comparable with the deme size, N . Then, density dependence is unlikely to be strong enough to counter demographic fluctuations, so that the population will be on the verge of extinction.

In order to simplify the analysis, we assumed that population size was a definite function, $N(z)$, of the genetic state of the deme. This will be reasonable only if density dependence acts much faster than selection, implying $ks \ll 1$. Since group selection is likely to be more effective for large ks , where population dynamics and population genetics act on the same timescale, and for large k/N , where demographic fluctuations are large, the obvious extension of our analysis is to consider joint variation in population size and genetic state. Such an analysis could be done by considering the joint distribution of N and z across demes; an explicit formula can be derived provided that selection is independent of density.

Our analysis is of a highly idealized model. However, we are confident that the conclusions apply much more widely. Our previous analysis of selection against heterozygotes gave similar results to that of the polygenic model considered here, and moreover, we obtained general conclusions in the limit of strong selection. In this paper, we showed how group selection could be understood in terms of an effective mean fitness'; the same argument applies to other models, and would also show that k has a significant effect only when comparable with N .

A more restrictive assumption is that group selection acts only through changes in population size. We expect that our conclusions would be similar if the rate of migration varied with mean fitness ($m \propto \bar{W}^k$, say). A stronger relation between mean fitness and number of emigrants can be imagined: for example, Crow *et al.* (1989) suggested that the number of emigrants might be zero when \bar{W} is below some threshold, and increase linearly from zero above the threshold. This might be so if, for example, there were a fixed number of territories, and if only homeless juveniles dispersed. However, we feel that in general, a change in mean fitness of a few percent is likely to change the number of emigrants by a similar percentage.

In a continuous population, the fitter peak may spread through the deterministic advance of a tension zone. The increased density caused by an increased mean fitness will increase its speed of advance, and make a new peak more likely to be established by chance (Rouhani & Barton, 1987; Barton & Hewitt,

1989). However, just as in this analysis, the effect is weak, and is likely to be negligible for those shifts that have an appreciable chance of establishment.

Group selection could in principle be much more effective if the new adaptive peak spread by colonization of vacant sites, rather than by infection of neighbouring populations, as is assumed here. In a comparison of these two processes, Lande (1985) found that group selection, in the form of different rates of extinction and colonization, was less important than selection between individuals. This conclusion depends on the relative importance of infection and of extinction/recolonization in the third phase, and warrants further investigation: the process of stochastic infection considered here may be relatively insensitive to group effects.

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