

Comparing the effects of genetic drift and fluctuating selection on genotype frequency changes in the scarlet tiger moth

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One of the recurring arguments in evolutionary biology is whether evolution occurs principally through natural selection or through neutral processes such as genetic drift. A 60-year-long time series of changes in the genotype frequency of a colour polymorphism of the scarlet tiger moth, *Callimorpha dominula*, was used to compare the relative effects of genetic drift and variable natural selection. The analysis showed that most of the variation in frequency was the result of genetic drift. In addition, although selection was acting, mean fitness barely increased. This supports the 'Red Queen's hypothesis' that long-term improvements in fitness may not occur, because populations have to keep pace with changes in the environment.

Keywords: genetic drift; fluctuating selection; scarlet tiger moth; Bayesian analysis

1. INTRODUCTION

One of the many debates in evolutionary biology has surrounded the importance of genetic drift on populations. The problem came to the fore in the 1960s and 1970s, after the theoretical framework for neutral evolution had been worked out (Kimura 1983) and it had been shown that populations harboured a great deal of natural variation (Lewontin 1974). The two sides of the debate are often identified by the names of two of the early pioneers in population genetics, R. A. Fisher (the figurehead of the selectionist camp) and Sewell Wright (the chief drift). One exchange was over changes in the frequencies of a colour polymorphism in a population of the scarlet tiger moth, *Callimorpha (Panaxia) dominula*. Fisher & Ford (1947) analysed these changes and argued that the population size was too large for the changes in the frequencies to be ascribed to drift and concluded that fluctuating selection must be acting so Wright was wrong about drift. Wright (1948) replied by arguing first that multiple factors could affect a population, and second that the effective population size might be much smaller than the census population size if, for example, mortality affected whole groups of larvae rather than just individuals. Although group level mortality is unlikely, because eggs of *C. dominula* are not laid in batches (Sheppard 1951), the more general point that effective population size can be much smaller than the actual population size is valid. Remarkably, the population at the centre of the debate has, with the exception of a 10-year hiatus, been followed over the subsequent 60 years.

The dialectic between the selectionist and neutral positions has still not been resolved. The neutral position requires that populations are small and fragmented, but even under these conditions selection can be effective in causing phenotypic divergence between populations (Koskinen *et al.* 2002). Fluctuating selection has been observed in *Daphnia* (Lynch 1987), where drift can be

ignored because the effective population size is effectively infinite. For smaller populations, the importance of the contributions of directional selection, fluctuating selection and genetic drift to the population's evolution can be difficult to evaluate. If only phenotypic divergence is observed, then little can be said about the pattern of selection, as both directional and fluctuating selection can cause divergence in gene frequencies (Lynch 1987).

In his original criticism of Fisher and Ford (1947), Wright (1948) emphasized that several factors operate in real populations. However, whenever allele frequency changes have been analysed, this has largely been done by testing whether the changes can be explained by genetic drift alone (e.g. Fisher & Ford 1947; Mueller *et al.* 1985; Manly 1985). A better approach is to follow Wright's thinking and estimate what proportion of the variation in allele frequencies is the result of drift, and what is the result of selection. In particular, if selection is not constant and varies randomly over time, then the patterns of allele frequency change may look identical to those resulting from drift. The only way to separate them is to use an estimate of the (drift) effective population size, ideally from data on changes in allele frequencies of neutral genetic markers.

The main focus of this paper is to try to resolve the original debate about the dynamics of the *medionigra* polymorphism, by estimating the relative strengths of the forces of selection and drift in the Cothill population of *C. dominula*. The approach takes advantage of both the extra data that have been collected, and of advances in statistics and model-fitting techniques that have expanded the range of models that can be fitted to data.

A number of subsidiary questions can also be tackled within the same analysis. Some years after the original debate, Wright (1978) suggested that the selective regime changed around 1968, with the *medionigra* genotype having a lower mean fitness before then, subsequently fluctuating

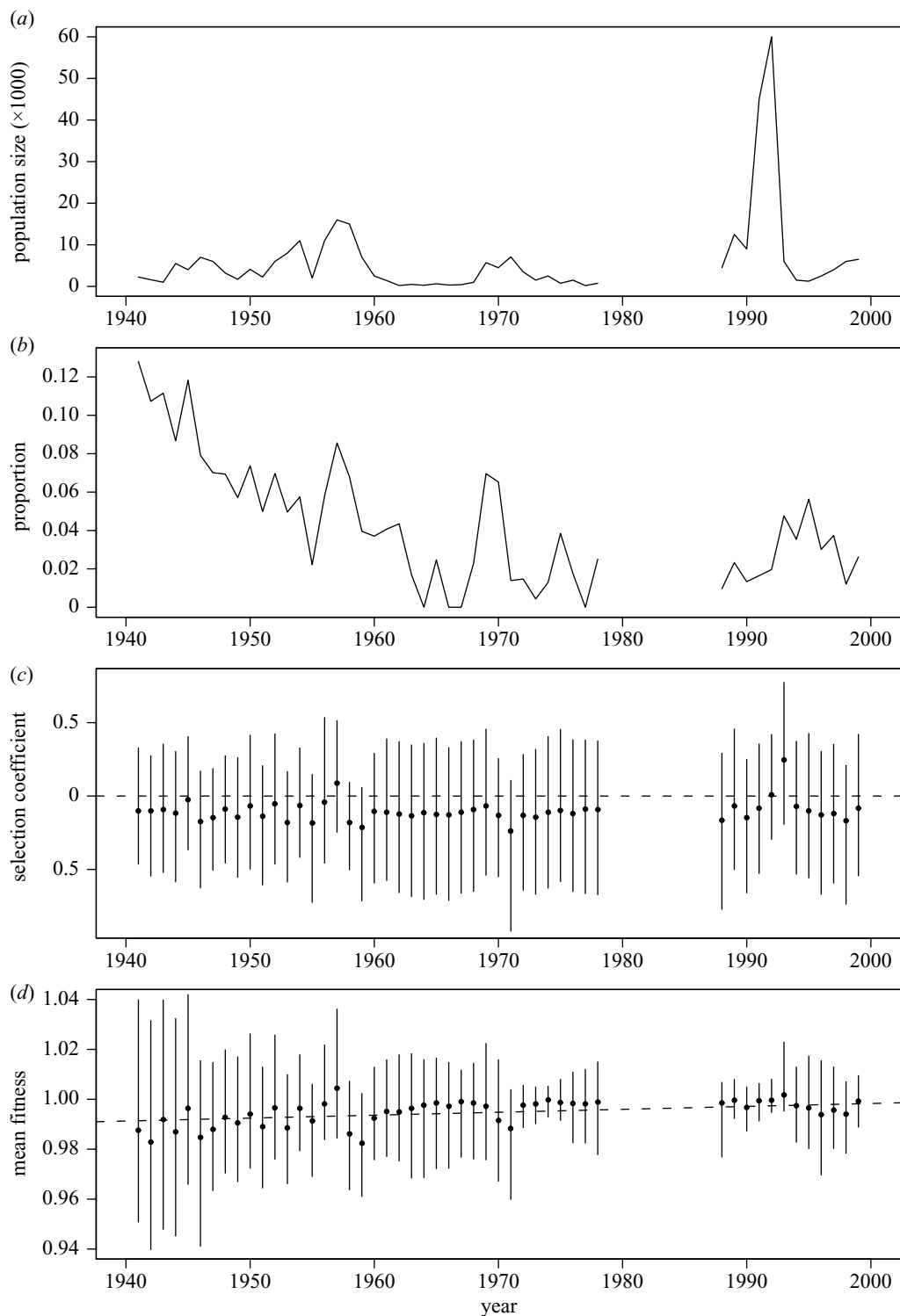


Figure 1. Time series plots of (a) estimated population size, (b) relative frequency of the *medionigra* genotype, (c) estimates of log of the selection coefficients, (d) estimated mean fitness. (c, d) posterior mode and 95% HPDI.

around zero. This explanation appears rather *ad hoc*, so frequency-dependent selection has been advocated as an alternative explanation of the pattern of genotype frequency changes (Cook & Jones 1996). This is supported by empirical evidence for the occurrence of disassortative mating (Sheppard & Cook 1962), which can give rise to frequency-dependent selection. Expression of the phenotype may also be affected by temperature (e.g. if it is partly determined by the environment; Goulson & Owen 1997),

in which case there should be a relationship between temperature and the estimated selection coefficient. Fitness can also be affected by density (e.g. O'Hara & Brown 1996). The effects of all of these factors are also investigated here.

2. MATERIAL AND METHODS

The scarlet tiger moth is a large day-flying arctiid moth. The population was studied in Cothill Fen, a 40 ha alkaline fen, *ca.*

8 km southwest of Oxford (map reference 51 31 44 N, 01 19 46 W). The population is effectively closed (Cook & Jones 1996), with the nearest population *ca* 1.5 km away (Sheppard 1951). The population was sampled during the adult flight period (July), where mark–recapture studies were used to estimate the population size (Fisher & Ford 1947), as well as the genotype frequencies. More details about the biology of *C. dominula* and the habitat are given by Fisher & Ford (1947). Jones (1989) reviews work on this population, and Cook & Jones (1996) review work on this and other *C. dominula* populations.

The polymorphism used by Fisher & Ford (1947) is in the pattern of spots on the wings of the moth, which is controlled by a single biallelic gene. The typical homozygous form (*dominula*) has several spots on the forewing. The other homozygote (*bimacula*) is distinguished by having only two spots on each forewing. The heterozygote (*medionigra*) is an intermediate between these two forms, with a reduction in the spots on the forewings, and a black or yellow spot on the hind wing (Fisher & Ford 1947; Jones 1989). Although the polymorphism can be induced environmentally (Goulson & Owen 1997), this does not occur under conditions experienced by the moths on the site (Jones 2000).

The frequencies of these three morphs have been recorded in samples since 1939 (Jones 1989, 2000). At the same time, the population size has been estimated since 1941 (mainly by mark–recapture; Jones 1993), with estimates varying between about 200 and 60 000 individuals (figure 1a). The frequency of the *medionigra* genotype has been a few per cent (figure 1b), and the *bimacula* genotype is very rare (indeed it has not been caught since 1959). Because of this rarity, there is little information in the data about the dynamics of the *bimacula* genotype, so although these dynamics are included in the model, the results of the analysis as regards this genotype are not reported.

The changes in genotype frequencies were modelled by modifying a simple selection model. If the relative frequency of the *a* genotype ($a \in \{1, 2, 3\}$ where 1 is *dominula*, 2 is *medionigra* and 3 is *bimacula*) at time t is $p(a, t)$, then the expected proportion at time t , after selection, is given by

$$E[p(a, t)] = \begin{cases} \frac{q_{t-1}^2}{\bar{w}} & a = 1 \\ \frac{w(2, t)2q_{t-1}(1 - q_{t-1})}{\bar{w}} & a = 2, \\ \frac{w(3, t)(1 - q_{t-1})^2}{\bar{w}} & a = 3 \end{cases} \quad (2.1)$$

where $w(a, t)$ is the relative fitness of allele a at time t (note that $w(1, t) = 1, \forall t$). The term q_t is the frequency of the *dominula* allele at time t ($q_t = p(1, t) + p(2, t)$), and the mean fitness is $w = q_{t-1}^2 + w(2, t)2q_{t-1}(1 - q_{t-1}) + w(3, t)(1 - q_{t-1})^2$. It is assumed that the relative fitnesses follow a log-normal distribution, i.e. for $a = 2, 3$, $\log[w(a, t)] \sim N(\eta_a, \sigma_a^2)$. Drift also creates variation in the genotype frequencies, and here it is modelled in a way that preserves the concept of (drift) effective population size (Mueller *et al.* 1985). If the effective population size at time t is $N_e(t)$, then the effective number of individuals with the *a* genotype, $\lambda(a, t)$, is drawn from a Poisson distribution with mean $N_e(t)E[p(a, t)]$. The term $p(a, t)$ is then calculated as $\lambda(a, t)/\sum_i \lambda(i, t)$. The numbers of the different genotypes caught in the sampling are then assumed to follow a multinomial distribution with $p(a, t)$ as given above.

An important statistic here is the proportion of variation resulting from selection, which can be calculated from the variances resulting from drift and selection. The contribution of selection to the variance is $\sigma_w^2 = \sigma_a^2 e^{2\eta_a} q(t)^2 (1 - q(t))^2$, and that of drift is $\sigma_d^2 = q(t)(1 - q(t))/2N_e(t)$ (Wright 1948). The proportion of

variation resulting from selection is then

$$\rho = \frac{\sigma_w^2}{\sigma_w^2 + \sigma_d^2} = \frac{1}{1 + (2N_e(t)\sigma_a^2 e^{2\eta_a} q(t)(1 - q(t)))^{-1}}. \quad (2.2)$$

The model requires the frequencies of the three morphs and $N_e(t)$, the effective population size (which measures the effects of genetic drift) as inputs. Although the effective population size has not been measured, it can be estimated by using a model that assumes that the females are singly mated, and that there is variation in offspring produced, and in the total population size in each year (see Appendix A).

No data were collected between 1979 and 1987, so there are no data on the population size. In addition, the relative strength of selection is evaluated by predicting it for the year 2000 (see below). This needs an estimate of the total population size. Therefore, an AR(1) model for the log of the population size was fitted, i.e.

$$\mu_p(t) = \rho(N(t-1) - \mu_0) + \mu_0, \quad (2.3a)$$

$$\log(N(t)) \sim N(\mu_p(t), \sigma_p^2), \quad (2.3b)$$

so that μ_0 is the overall mean population size, $\mu_p(t)$ is the expected log population size at time t , ρ is the auto-correlation, and σ_p^2 is the variance in log population size.

The model was fitted to the data using a Bayesian approach (Gelman *et al.* 2003), which allows specification of uncertainty in the parameter values (through a prior distribution), and then the data can be used to update this uncertainty (to give a posterior distribution). In the first two years there was no estimate of population size, so these were not used in the main analysis, but the 1940 data were used to give a prior for the initial allele frequency, a beta(8465, 577) distribution. The priors for the mean (η_a) and variance (σ_a^2) of the selection coefficients were chosen to be uninformative, the mean was given a normal distribution prior with mean 0 and variance 100, and the variance was given an inverse gamma distribution with a shape and scale of 0.01. The model in Appendix A produces point estimates of $N_e(t)$. The uncertainty in these estimates was approximated by assuming that the prior distribution for $N_e(t)$ was a non-central χ^2 distribution, i.e.

$$\frac{vN_e(t)}{\tilde{N}_e(t)} \sim \chi_v^2,$$

where $\tilde{N}_e(t)$ is the point estimate and v is the degrees of freedom parameter. A value of 10 was used for v . This includes all sources of uncertainty in the estimation of $N_e(t)$: that coming from the estimation of $N(t)$ (both the error, and any bias resulting from the sampling methods), as well as that from the estimation of the other parameters. Missing data (e.g. between 1979 and 1987) were estimated through multiple imputation (Gelman *et al.* 2003).

The population dynamic model was fitted simultaneously with the rest of the model. Terms μ_0 and $\mu_p(1)$ were given normally distributed priors, with mean 0 and variance 100, σ_p^2 was given an inverse gamma distribution with a shape and scale of 0.01, and $(\psi + 1)/2$ was given a beta(2, 2) prior distribution.

The analysis depends on the estimated values of $N_e(t)$, so if the model is wrong, then the estimates will also be incorrect. Sensitivity to this was assessed by fitting models, where $N_e(t)$ was estimated as a ratio $N_e(t)/N_T(t)$, with $N_T(t)$ estimated as above, and $N_e(t)/N_T(t)$ estimated as a parameter, with a tight prior distribution (specifically a beta(d , $100 - d$) distribution, with d varied in different estimations to alter the mean value of $N_e(t)/N_T(t)$).

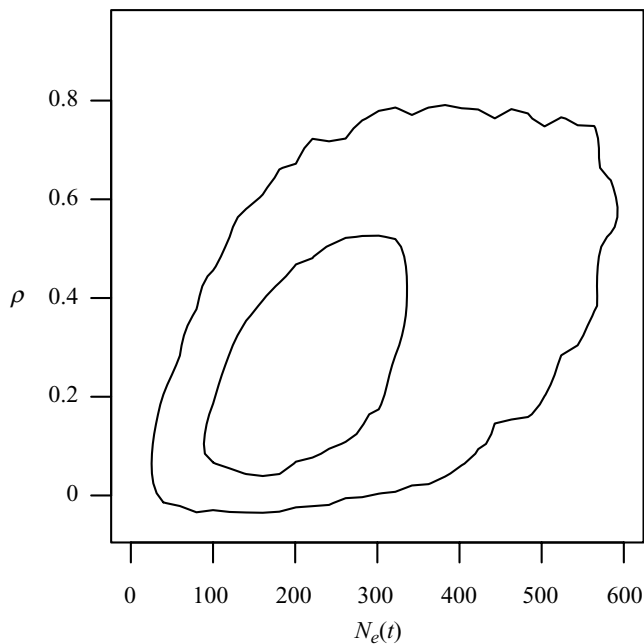


Figure 2. Joint posterior density of variation in the frequency of the *medionigra* genotype resulting from selection (ρ) and predicted effective population size ($N_e(t)$): 50% and 95% contours. Density at $\rho < 0$ is an artefact of the smoothing.

The model was fitted to the data by MCMC simulation using the WINBUGS package (Spiegelhalter *et al.* 1999). Two chains were run and after a burn-in of 10 000 iterations, every tenth iteration of the next 50 000 iterations was taken to give 10 000 values. The parameter estimates were summarized through their posterior mode (i.e. the most likely value, equivalent to a maximum-likelihood estimate), and their 95% highest posterior density interval (HPDI). These are confidence intervals in which 95% of the distribution with the highest density is contained. The proportion of variation resulting from selection was calculated for the year 2000 by simulating $N(2000)$ and $p(2000)$ with the model.

The effects of time, frequency, log density and temperature on the selection coefficients were examined by using a model-checking approach. Density was measured as $N_T(t)$ (which is proportional to density if the area is constant). The minimum June temperature in Oxford was used (data taken from <http://www.metoffice.com/climate/uk/stationdata/index.html>). June is the month when the wing pattern is most likely to be affected by temperature (Cook & Jones 1996). The minimum temperature was used as this gave a stronger result than either the maximum or mid-point temperature. The posterior for $\log[w(2, t)]$ was simultaneously regressed against all four factors. This was done for each MCMC draw from the posterior distribution, to obtain the posterior distribution of the regression parameters (i.e. including the uncertainty about the parameters). Point estimates were used for $N_T(t)$, which means that the variance in the parameters of the regression was underestimated, as they did not include the uncertainty in the estimates of $N_T(t)$.

3. RESULTS

The selection coefficient varied between years (figure 1c), and the estimate of the proportion of variation in the frequency of the *medionigra* genotype resulting from selection (ρ) had a mode of 28.8% (95% HPDI: 2.2% to 66.3%). Most of this variation therefore appears to be the

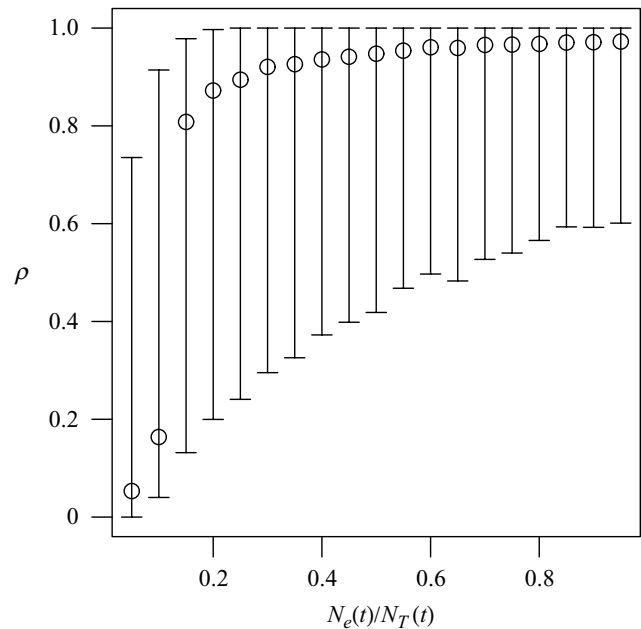


Figure 3. Effect of the ratio of effective to total population size ($N_e(t)/N_T(t)$) on the proportion of variation in the frequency of the *medionigra* genotype resulting from selection (ρ): posterior modes and 96% HPDIs.

result of drift, although there is considerable uncertainty. This can be seen in the joint posterior distribution of ρ and $N_e(t)$ (figure 2), where the posterior correlation between the variables is only 0.48. This is a result of the uncertainty in the other parameters used in the calculation of ρ . The data suggest that the *medionigra* genotype is less fit overall. The posterior mode mean fitness (i.e. $\exp(\eta_a)$) was 0.88 (95% HPDI 0.77 to 1.004), with 2.9% of the density above 1.

The ratio $N_e(t)/N_T(t)$ has to be small for drift to have a large effect on genotype frequency (figure 3). The figure is drawn for the posterior predictive population size in 2000, so the conclusion depends on this size: with a smaller population size (so that $N_e(t)$ is smaller), drift will be more important. For the main analysis, the ratio varies between years, but it is less than 0.1 in 42 of the 50 years for which it can be calculated.

The ratio of the effects of selection and drift depends on the population sizes in the current and previous years (see Appendix A). Not surprisingly, the effect of drift decreased as the current population size is increased (figure 4a). The wide confidence limits are in part the result of marginalizing over the previous population size. When the current population size is fixed, the relative strength of selection is positively correlated with the previous year's population size (figure 4b; the pattern is qualitatively the same for other values of the current population size).

Time, frequency, temperature and density had little effect on fitness (table 1). Altogether, they explain 8.7% (HPDI: 0.47 to 25.5%) of the variation, and there was no consistency in the direction of the effect (i.e. the HPDIs contain both positive and negative values). Frequency dependence is interesting because if there is any effect, then it is probably for a higher frequency of the *bimacula* allele to favour the *medionigra* genotype, which is the opposite direction to that suggested by Cook & Jones (1996). There is

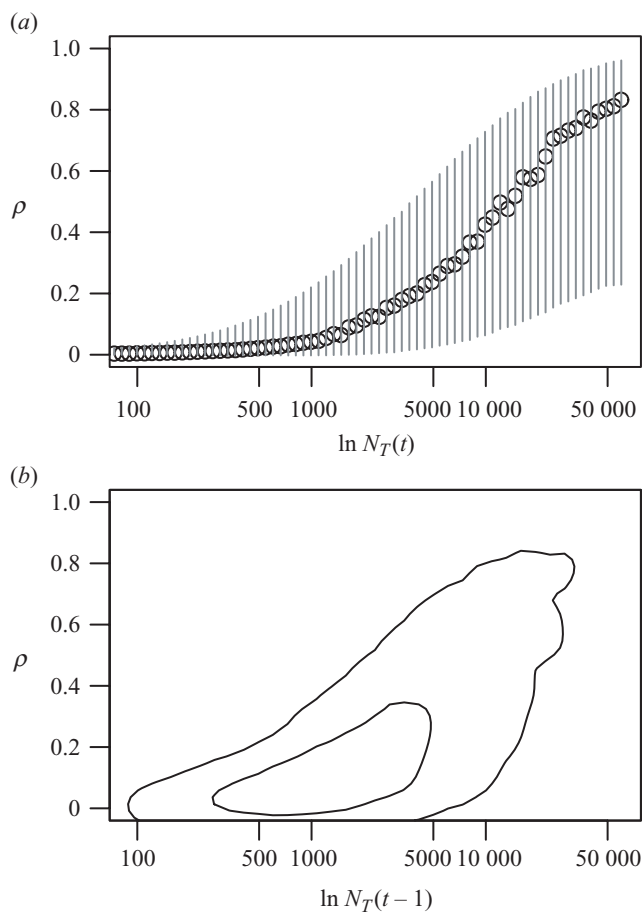


Figure 4. The relationship between the proportion of variation in the frequency of the *medionigra* genotype resulting from selection (ρ) and (a) posterior modes and 96% HPDIs for the current population size (marginalized over the previous population size), and (b) 50% and 95% contours for the previous population size (for a current population size of 6500, the estimated population size in 1999). Density at $\rho < 0$ is an artefact of the smoothing.

also no visible evidence for a change in the fitness of the *medionigra* genotype in 1968. When a model with a change point is fitted (i.e. where the mean fitness, η_a , is different either side of the point), then the posterior distribution for the position of the change point is uniform, the same as the prior distribution, and the posteriors for η_a before and after the change point are the same (prior 95% CI: 1942.48 to 1998.53, posterior 95% CI: 1942.40 to 1998.55; note that a HPDI cannot be uniquely defined for a uniform distribution).

One usual consequence of selection is an increase in the mean fitness of a population, as less fit individuals are removed. For this data, however, there is almost no increase (figure 1d, posterior mode for slope: 1.17×10^{-4} , HPDI: -1.41×10^{-4} to 2.98×10^{-4}), with changes in mean fitness dominated by changes resulting from environmental variation. Indeed, the posterior mode for the time taken to increase by 1 standard deviation is 79 years (only the part of the posterior distribution for the regression line for which the slope is positive is used). In other words, three-quarters of a century of steady improvement can be undone by a single moderately bad year.

Table 1. Posterior mode (95% HPDIs) for estimated slopes and r^2 for regressions of annual selection coefficients against year, frequency of *bimacula* allele, population size (density) and temperature.

factor	slope ($\times 10^{-3}$)	p
year	1.29 (−2.34 to 8.41)	0.16
frequency of <i>dominula</i> allele	36.8 (−45.1 to 264)	0.10
density	1.60×10^{-3} (-3.00×10^{-3} to 9.04×10^{-3})	0.19
temperature	2.85 (−61.1 to 87.2)	0.41

4. DISCUSSION

The main result is that both drift and selection are significant factors affecting changes in the allele frequency of the *medionigra* gene. Because the selection coefficients vary so much, the mean fitness of the population barely changes.

This is, of course, only one gene in one population, and the forces of drift and selection will act differently on different genes and populations. The phenotype seen here is clearly visible to human eyes, so one may expect that the phenotype would be visible to selection (or at least to predators) as well. Other polymorphic genes will be more or less visible to selection, and so drift will be more or less important. However, selection can even be detected in allozymes (Mueller *et al.* 1985). The temporal scale of variation can also be important (Gilchrist 1995). Annual variations such as those estimated here will have little effect on species with a longer lifespan (such as humans), whereas species with much shorter lifespans can track fluctuations within a year (Via & Shaw 1996). Another consideration has to be the size of a population—species that live in smaller populations will be more susceptible to the effects of drift, but fluctuating selection will still be important in large populations (e.g. Lynch *et al.* 1987). With all of these factors operating, the importance of fluctuating selection has to be assessed empirically, in a variety of systems.

The mean fitness of the species did not change over a long period of time (figure 1d). Instead, the population is evolving just to keep up with the environment, and there is always the threat that a particularly large perturbation will send the *medionigra* allele to extinction. This is a corollary of the Red Queen's hypothesis (Van Valen 1973). Van Valen (1973) developed the original hypothesis on the basis of the observation that extinction rates within a taxon remain approximately constant. The same conclusion can be drawn here, suggesting that the view of evolution as a process of trying to keep up with the environment can be used at different levels. Indeed, what may be viewed as a process of evolutionary improvement over the short time scale of this study may, over the geological time scale, be seen as just another fluctuation in a long sequence of erratic fluctuations.

Previous investigations on the moth have shown that the *medionigra* genotype is less fertile than the wild-type *dominula* and also that there is disassociative mating, with males tending to mate with females of a different phenotype (Sheppard & Cook 1962). The relative fitness of the *medionigra* genotype varies considerably between years, which suggests that experimental results showing that the

medionigra genotype is less fertile (Sheppard & Cook 1962) are contingent on the conditions of the study, and so may (or may not!) have little relevance in the field. A puzzle still remains over the frequency dependence, as disassociative mating would favour the *medionigra* genotype more when it was rarer, whereas there is little or no effect in the field—and even if there is an effect, it is most likely to be in the opposite direction. Again, this may simply be the result of a difference between the laboratory and the field, but the resolution of this should be left to those who understand moth biology and behaviour.

The analysis leads to rejection of the hypotheses that the fitness of the *medionigra* genotype is affected by temperature, allele frequency or a change in the environment. Why, then, were these mechanisms proposed? An inspection of figure 1*b* leads to the idea that there is a linear decrease in the frequency, followed (after 1969) by a period when there is no overall change in the frequency. If there were consistent selection against the *medionigra* genotype, then a curved relationship would be expected, and when the relative frequency is sufficiently low, it becomes difficult to separate out the reduction in frequency from the random noise. The conclusion here is that more than visual inspection of data is needed, and explicit hypotheses (such as those proposed by Wright (1978), and Cook & Jones 1996) need to be tested statistically.

What of the original argument between Fisher and Wright? In one sense, Fisher has been vindicated—this population is

...subjected from generation to generation to selective intensities capable of producing greater fluctuations in gene-ratios than could be ascribed to random sampling.

(Fisher & Ford 1947, p. 168)

However, the conclusion that this is fatal to Wright's position is not vindicated. Both fluctuating selection and genetic drift have their effects on the population, and the appropriate problem is estimating the relative effects of the two factors. A real appreciation of the relative roles of selection and drift can come about only through empirical studies of changes in allele frequencies in different genes from different populations and species.

I thank Laurent Lehmann for developing the model of N_e , the many field workers who have collected the data (see Cook & Jones (1996) for an incomplete list; D. A. and H. C. Jones have collected the data since 1988), and also David Jones, Mike Fowler and David Lesbarrères for their comments on the manuscript.

APPENDIX A: CALCULATION OF $N_e(t)$

If $P(t)$ is the rate of coalescence at time t , then the coalescent effective population size at time t , $N_e(t)$, is $1/P(t)$. A closed, randomly mating diploid population is assumed with a total population size of $N_T(t)$ at time t , but a constant sex ratio p (proportion of males). The number of offspring produced by each female has a mean of $\mu(t)$ and variance σ^2 . The rate of coalescence is

$$P(t) = \frac{1}{4} \left(\frac{P_f(t)}{2} + \frac{P_m(t)}{2} \right), \quad (\text{A } 1)$$

where $P_f(t)$ and $P_m(t)$ are the coalescence rates for females and males (e.g. Rousset 2004). When each female is mated

singly, the male coalescence rate is

$$P_m(t) = P_f(t) + \frac{1 - P_f(t)}{pn(t-1)} \quad (\text{A } 2)$$

(Balloux & Lehmann 2003). The female coalescence rate, $P_f(t)$, is the expectation of the number of pairs of offspring descending from a single female relative to the total number of pairs of offspring in the population. We define $n_f(t) = (1 - p) N_T(t)$, so that

$$\begin{aligned} P_f(t) &= \sum_M \frac{\sum_{i=1}^{n_f(t-1)} m_i(m_i - 1)}{n_f(t-1)\mu(t-1)(n_f(t-1)\mu(t-1) - 1)} \\ &\quad \times P(M_1 = m_1, \dots, M_n = m_n | n_f(t-1)\mu(t-1)) \\ &= E_M \left(\frac{\sum_{i=1}^{n_f(t-1)} m_i(m_i)}{n_f(t-1)\mu(t-1)(n_f(t-1)\mu(t-1) - 1)} \right), \quad (\text{A } 3) \end{aligned}$$

where $M = (m_1, \dots, m_{n_f(t)})$ is a vector of the number of offspring of each female. This is conditioned on the number of females and the mean number of offspring produced. Then,

$$\begin{aligned} P_f(t) &= \frac{\sum_{i=1}^{n_f(t-1)} (E(m_i^2) - E(m_i))}{n_f(t-1)\mu(t-1)(n_f(t-1)\mu(t-1) - 1)} \\ &= \frac{\sum_{i=1}^{n_f(t-1)} (\sigma^2 + E^2(m_i) - E(m_i))}{n_f(t-1)\mu(t-1)(n_f(t-1)\mu(t-1) - 1)} \end{aligned}$$

By definition $E(m_i) = \mu(t-1)$, so we get

$$\begin{aligned} P_f(t) &= \frac{n_f(t-1) \left(\sigma^2 + \mu(t-1)^2 - \mu(t-1) \right)}{n_f(t-1)\mu(t-1)(n_f(t-1)\mu(t-1) - 1)} \\ &= \frac{\sigma^2 + \mu(t-1)^2 - \mu(t-1)}{\mu(t-1)(1-p)n(t-1)\mu(t-1) - 1}. \quad (\text{A } 4) \end{aligned}$$

Given values of $N_T(t)$, p , $\mu(t)$ and σ^2 , $N_e(t)$ is calculated by plugging them into (A 4), calculating $P_m(t)$ from (2), hence $P(t)$ from 1, and $N_e(t) = 1/P(t)$.

Estimates of $N_T(t)$, the total population, are available from the literature (Jones 1989, 2000). A value of 0.5 is used for p , which is around the mean estimate from 3 years (Jones 1993), but the results are insensitive to deviations from this. By definition we have

$$\mu(t) = \frac{N_T(t+1)}{n_f(t)} = \frac{N_T(t+1)}{(1-p)N_T(t)},$$

which can be easily calculated. For the initial year, it was assumed that $N_T(0) = N_T(1)$. The variance in offspring, σ^2 was estimated from data on variance in the number of eggs (Sheppard 1951). This has a mean that is far in excess of the largest $\mu(t)$. To compensate for this, it was assumed that $\sigma^2 \propto \mu$, as is the case for Poisson and negative binomial distributions, so that σ_μ^2 is calculated as the estimated variance in egg number divided by the mean number of eggs. The variance at time t is then $\sigma_\mu^2 \mu(t)$.

REFERENCES

- Balloux, F. & Lehmann, L. 2003 Random mating with a finite number of matings. *Genetics* **165**, 2313–2315.
Cook, L. M. & Jones, D. A. 1996 The *medionigra* gene in the moth *Panaxia dominula*: the case for selection. *Phil. Trans. R. Soc. B* **351**, 1623–1634.

- Fisher, R. A. & Ford, E. B. 1947 The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. *Heredity* **1**, 143–174.
- Gelman, A., Carlin, J. B., Stern, H. S. & Rubin, D. B. 2003 *Bayesian data analysis*, 2nd edn. London: Chapman & Hall/CRC.
- Gilchrist, G. W. 1995 Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. *Am. Nat.* **146**, 252–270.
- Goulson, D. & Owen, D. F. 1997 Long-term studies of the medionigra polymorphism in the moth *Panaxia dominula*: a critique. *Oikos* **80**, 613–617.
- Jones, D. A. 1989 50 years of studying the scarlet tiger moth. *Trends Ecol. Evol.* **4**, 298–301.
- Jones, D. A. 1993 The phenotype and frequency of *f. medionigra* of *Panaxia dominula* L. (Lepidoptera: Arctiidae) at Cothill, Oxfordshire, England, 1988–1991. *Biol. J. Linn. Soc.* **49**, 305–316.
- Jones, D. A. 2000 Temperatures in the Cothill habitat of *Panaxia (Callimorpha) dominula* L. (the scarlet tiger moth). *Heredity* **84**, 578–586.
- Kimura, M. 1983 *The neutral theory of molecular evolution*. Cambridge University Press.
- Koskinen, M. T., Haugen, T. O. & Primmer, C. R. 2002 Contemporary fisherian life-history evolution in small salmonid populations. *Nature* **419**, 826–830.
- Lewontin, R. C. 1974 *The genetic basis of evolutionary change*. Columbia University Press.
- Lynch, M. 1987 The consequences of fluctuating selection for isozyme polymorphisms in *Daphnia*. *Genetics* **115**, 657–669.
- Manly, B. F. J. 1985 *The statistics of natural selection*. London: Chapman & Hall.
- Mueller, L. D., Wilcox, B. A., Ehrlich, P. R., Heckel, D. G. & Murphy, D. D. 1985 A direct assessment of the role of genetic drift in determining allele frequency variation in populations of *Euphydryas editha*. *Genetics* **110**, 495–511.
- O'Hara, R. B. & Brown, J. K. M. 1996 Frequency- and density-dependent selection in wheat powdery mildew. *Heredity* **77**, 439–447.
- Rousset, F. 2004 *Genetic structure and selection in subdivided populations*. Princeton University Press.
- Sheppard, P. H. 1951 A quantitative study of two populations of the moth *Panaxia dominula* (L.). *Heredity* **5**, 349–378.
- Sheppard, P. H. & Cook, L. M. 1962 The manifold effects of the *medionigra* gene of the moth *Panaxia dominula* and the maintainance of a polymorphism. *Heredity* **17**, 415–426.
- Speigelhalter, D. J., Thomas, A. & Best, N. G. 1999 *WINBUGS version 1.2 user manual*. Cambridge: MRC Biostatistics Unit.
- Van Valen, L. 1973 A new evolutionary law. *Evol. Theory* **1**, 1–30.
- Via, S. & Shaw, A. J. 1996 Short-term evolution in the size and shape of pea aphids. *Evolution* **50**, 163–173.
- Wright, S. 1948 On the roles of directed and random changes in gene frequency in the genetics of populations. *Evolution* **2**, 279–294.
- Wright, S. 1978 *Evolution and the genetics of populations. Vol. 4, variability within and among natural populations*. University of Chicago Press.

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.