ELSEVIER

Research Focus

When environmental variation short-circuits natural selection

Loeske E.B. Kruuk[1], Juha Merilä[2] and Ben C. Sheldon[3]

[1]Institute of Cell, Animal and Population Biology, Ashworth Laboratories, King's Buildings, West Mains Road, University of Edinburgh EH9 3JT, UK
[2]Ecological Genetics Research Unit, Department of Ecology and Systematics, University of Helsinki, Finland
[3]Edward Grey Institute, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

The development of a coherent framework for measuring natural selection was one of the major advances in evolutionary biology in the 1970s and 1980s. However, for evolution to occur, natural selection must act on underlying genetic variation, whereas most measurements of natural selection are limited to phenotypes. Two new papers now show that environmentally induced covariances between phenotypes and fitness can frequently lead to the systematic overestimation of the strength of natural selection.

Evolutionary biologists spend a lot of time measuring selection because it is the predominant force driving evolution: if we are to understand evolution, we need to understand what drives it. An elegant theoretical framework exists with which to quantify selection pressures on phenotypic traits, generate and test theoretical predictions, and thereby summarize important evolutionary processes with a few key parameter estimates. However, this quantitative framework for describing natural selection can be seriously short-circuited by the presence of confounding environmental covariance between fitness and the focal trait. Two recent studies [1,2] focus on this problem, presenting alternative ways of tackling the bias and then using experimental data to provide an estimate, for the first time, of its prevalence.

From the relationship between a quantitative phenotypic trait and individual fitness (or some component of the latter), we can quantify the force of selection on that trait. Specifically, selection will induce a change in the mean of a trait that is equal to the covariance between the trait and fitness [3]. In the natural world, selection rarely acts on a single trait in isolation, but the extension to a multivariate case is straightforward [4]. Thus, with the publication of simple methods for estimating selection from a multiple regression of fitness measures on phenotypic traits, estimates of selection gradients (Box 1) have become commonplace in the evolutionary literature: for example, a recent review reports >2500 estimates from a survey of studies published between 1984 and 1997 [5]. These estimates can be combined with those of the heritability of, and genetic correlations between, traits to predict changes in future generations, and hence patterns of microevolution.

So far so good. But the underlying assumption behind

the selection analyses is that there is a causal connection between fitness and the trait in question. This need not be so: consider a situation in which some environmental variable – say, resource availability – affects the size of the focal trait, but also, independently, affects fitness (Fig. 1). Price *et al.* [6] discuss such a scenario in relation to avian breeding time: birds in good condition can breed early and can also produce large healthy broods, generating an association between breeding time and fitness that gives an artificial impression of selection for early breeding time. In their paper, Stinchcombe *et al.* [1] consider a situation in which soil nitrogen content determines first the concentration of nitrogen-based defensive alkaloids, and second plant growth rate and hence fitness. Thus, there is a positive correlation between alkaloid concentration and fitness, although alkaloid concentration might confer no selective benefits whatsoever. In such cases, these correlations would generate a positive selection gradient in any standard selection analysis, and hence a misguided expectation of evolution if the trait is heritable; in reality, fitness differences are only associated with the environmental component of the trait (Fig. 1).

Although there is a long history to this concern (both Darwin and Fisher discussed examples of environmental covariance between phenotypes and fitness), quite how

Box 1. Definitions

Selection gradient
A measure of the strength of selection on a trait, taken from the relationship between the trait and fitness. From a multiple regression of relative fitness (i.e. with a mean of one) on all measured traits, each partial regression coefficient gives the selection gradient on that trait, accounting for selection on the other traits. If phenotypic data are used, the estimate is a phenotypic selection gradient; if genotypic data are used, it is a genotypic selection gradient. The trait data are often standardized to unit standard deviance, so that the selection gradient gives the proportional change of fitness for a change of one standard deviation in the trait.

Genotypic measures
From measures of individual phenotypes, genotypic value can be inferred in several ways: for example, using family means [1,2] or, if pedigree information and the phenotypes of relatives are available, best linear unbiased estimators (BLUPS) of breeding values, which are the sum of the additive effects of the genes of an individual (or twice the expected deviation of the offspring of an individual from the population mean) [13].

Corresponding author: Loeske E.B. Kruuk (Loeske.Kruuk@ed.ac.uk).
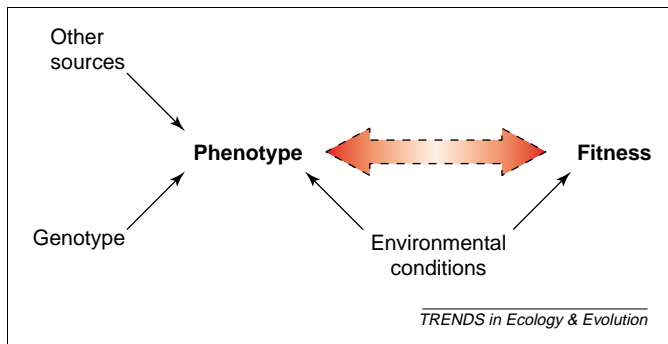
Fig. 1. How environmental covariance can generate a biased impression of selection on a phenotypic trait. The phenotype of an individual is determined by its genotype and by environmental conditions, and possibly by other factors. Environmental conditions (or an environmentally determined trait, such as nutritional state) are correlated both with the expression of the phenotypic trait and with fitness, giving the impression of selection on the trait. Single-headed arrows show causality, and the double-headed arrow shows the resulting statistical correlation between fitness and the trait.

widespread and serious the problem might be has never previously been evaluated. Rausher [7] showed that it could be quantified by comparing selection gradients (Box 1) on phenotypes with those on some measure of genotypic value. In the absence of any confounding environmental covariance, selection gradients on phenotypic values should be the same as on genotypic values (simply because the genotypic value of an individual equals the expected phenotypic value); whereas if environmental covariance is a problem, they will differ. Stinchcombe *et al.* [1] expand on some of the details of this approach and apply the method to data from experimental studies of three species of annual plants. Although the populations that they consider were grown in a spatially replicated, randomised design (in which confounding environmental covariance should have been minimized), they reach the alarming conclusion that, for the range of traits analyzed, nearly 25% of selection gradients were biased by environmental covariance. This suggests that, in general, our view of the magnitude of selection on phenotypic traits might be seriously distorted.

Scheiner *et al.* [2] pick up the theme and apply the Rausher approach to a further three data sets, again from plant experiments. They also find extensive evidence for environmental covariance, this time in 34% of traits considered. However, they then compare these results with those obtained from a path analysis [8], as an illustration of how path analyses can be less prone to bias than is the regression approach.

Given full measurements of all the relevant variables, a path analysis can provide a more accurate (and thus efficient) representation of patterns of causation [8]. Rather than considering all possible traits as potentially affecting fitness and potentially being correlated, a path analysis allows for some traits to have effects simply on other traits, which then, in turn, can affect fitness. No statistical power is therefore wasted in estimating a nonexistent effect of the initial trait on fitness, when, in truth, its only effect is on other traits. Scheiner *et al.* compare the agreement between phenotypic and genotypic selection gradients (i.e. the extent of bias) estimated from path analyses with that from multiple regression, and show that the path analyses give a better agreement than

does the latter [2]. This suggests that, at least for their data sets, path analysis is less sensitive to the potential bias caused by environmental covariance.

The subject inevitably throws up a few knotty statistical issues. Stinchcombe *et al.* argue for the use of nonstandardized selection gradients, on the grounds that phenotypic and genotypic gradients must be measured in the same units for a valid comparison. This is understandable, although the two ratios should only differ by a factor equal to the square root of the heritability in the case of equal nonstandardized values. Reporting only nonstandardized values would make comparisons with other studies (in the manner of [5]) impossible, because the units of nonstandardized selection gradients depend on the arbitrary choice of scale of measurement. Thus, a sensible strategy would be to report both, which is what they do in their paper. Statistical power also raises its head: using family means (to estimate genotypic values) gives fewer data points than do individual observations and, proving that an effect (here, selection on the genetic component) does not exist is far trickier than proving that it does. On this issue, path analyses certainly cause less concern [2]. However, the measurements of all important pathways that a path analysis requires might not be feasible in many studies, particularly those of free-living organisms, such as wild animals, rather than sessile plants; it is not clear whether a badly specified path analysis might send a study further off course than would the less intricate multiple regression.

A further difficulty is that finding a measure of genotype is not always straightforward, in contrast to the simplicity of the Lande–Arnold regression on phenotypes. Here, both papers use family means of one form or other. However, for long-term studies with multiple generations and pedigree information, it is possible to estimate breeding values (Box 1). This has been shown to be feasible for several studies of wild populations (e.g. [9–11]), and will become more so with the ever-increasing availability of molecular data with which to construct pedigrees. Furthermore, the genotypic regression analysis also has the great benefit of giving estimates that can be combined with a variance–covariance matrix to predict the shape of evolutionary responses in the different traits (note that estimates from path analyses cannot be used this way).

The main reason for worrying about any of this is that biased estimates of selection will generate over-ambitious predictions for the efficacy of selection. Great expectations for a phenotypic response might be wildly exaggerated if selection estimates are inflated by environmental covariances. Thus, the concept offers one possible explanation as to why evolution by natural selection rarely follows (quantitatively) its expected trajectories, in contrast to the well behaved responses to artificial selection that are observed in animal and plant breeding schemes. Overestimates of selection gradients can explain the wide-spread lack of a predicted response to directional selection on heritable traits in wild populations [12] and, thus, the persistence of genetic variation in such traits (sexually selected traits being an obvious example [10]). Furthermore, indications of any consistent, nonrandom, environmental influences on fitness should ultimately help to improve our understanding of a biological system.

Churlish though it might seem to muddy the elegant simplicity of the Robertson–Price/Lande–Arnold approach for describing selection, these recent studies underline the need for more caution in describing the forces of natural selection. They provide strong evidence that environmental covariances can bias our estimates of selection; in doing so, the results highlight the benefits to be gained by considering genetic, rather than simply phenotypic, measures when trying to understand the evolution of quantitative traits. They also provide a potential explanation for the widespread lack of correspondence between predicted and observed evolutionary trajectories in natural populations [12].

References
1 Stinchcombe, J.R. *et al.* (2002) Testing for environmentally induced bias in phenotypic estimates of natural selection: theory and practice. *Am. Nat.* 160, 511–523
2 Scheiner, S.M. *et al.* (2002) Reducing environmental bias when measuring natural selection. *Evolution* 56, 2156–2167
3 Robertson, A. (1966) A mathematical model of the culling process in dairy cattle. *Anim. Prod.* 8, 95–108
4 Lande, R. and Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution* 37, 1210–1226
5 Kingsolver, J.G. *et al.* (2001) The strength of phenotypic selection in natural populations. *Am. Nat.* 157, 245–261
6 Price, T. *et al.* (1988) Directional selection and the evolution of breeding date in birds. *Science* 240, 798–799
7 Rausher, M.D. (1992) The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution* 46, 616–626
8 Shipley, B. (2000) *Cause and Correlation in Biology*, Cambridge University Press
9 Merilä, J. *et al.* (2001) Natural selection on the genetical component of variance in body condition in a wild bird population. *J. Evol. Biol.* 14, 918–929
10 Kruuk, L.E.B. *et al.* (2002) Antler size in red deer: heritability and selection but no evolution. *Evolution* 56, 1683–1695
11 Sheldon, B.C. *et al.* (2003) Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution* 57, 406–420
12 Merilä, J. *et al.* (2001) Explaining stasis: microevolutionary studies of natural populations. *Genetica* 112, 119–222
13 Lynch, M. and Walsh, B. (1998) *Genetics and Analysis of Quantitative Traits*, Sinuaer

Slow burn: the insidious effects of surface fires on tropical forests

William F. Laurance

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá

Accidental surface fires are emerging as one of the most pervasive threats to tropical forests. Although unimpressive in appearance, these fires can have surprisingly potent impacts on rainforest plant and animal communities, as demonstrated by recent studies led by Jos Barlow and Carlos Peres in central Amazonia. Even worse, surface fires greatly increase the likelihood of far larger conflagrations that can lead to complete forest destruction.

Each year, thousands of fires are lit in the humid tropics, to raze vast expanses of forest for ranching and slash-and-burn farming. Although highly destructive to natural ecosystems, these intentional fires are now being rivaled in terms of their ecological impacts by a more subtle menace: accidental surface fires.

Surface fires are deceptively unimpressive, creeping along the forest floor as a thin ribbon of flames and rarely exceeding 20 cm in height (Fig. 1). Unlike fast-burning intentional fires, which are lit after vegetation has been slashed and felled to dry out forests and increase flammability, surface fires merely consume the leaf and woody litter and generate only modest heat, covering as little as 150 m in a day [1].

Nevertheless, surface fires are deadly to many rain-forest plants, which typically have thin (< 1-cm thick) bark and thus are highly vulnerable to heat stress [2,3]. Studies conducted 1–2 years after a surface fire suggest that the

Fig. 1. A surface fire creeping through the rainforest understorey in eastern Amazonia. Reproduced with permission from Mark A. Cochrane.

Corresponding author: William F. Laurance (laurancew@tivoli.si.edu).