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Conflicting selection pressures and life history trade-offs

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SUMMARY

We review studies of natural selection in wild populations in which selection has acted in opposite directions at different stages of the life history. For example, the phenotype with highest probability of survival may have the lowest reproductive success. We discuss two important implications of these findings. First, measurements of opposing selection confirm that evolution of traits is governed by a balance of conflicting fitness advantages. Second, studies of opposing selection are informative about mechanisms underlying life history trade-offs. We outline difficulties in measuring opposing selection, particularly the problem that patterns of selection may be masked by the positive effects of nutrition on size of metric traits and fitness components. We discuss some solutions to these problems, and present a statistical technique to help disentangle direct selection from nutritional effects. Finally, we show how fluctuations in selection pressures lead to norms of reaction for life history traits in the absence of developmental plasticity.

1. INTRODUCTION

Natural selection is common in wild populations (see Endler 1986; Manly 1985). Here we draw attention to studies in which selection has been discovered to act in opposite directions on a trait at different life history stages. For example, on Mandarte Island, British Columbia, immature female song sparrows having long beaks survived better over their first winter than shorter-beaked individuals, but short-beaked adult females had higher reproductive success (Schluter & Smith 1986).

We identify two broad implications of such discoveries. First, the presence of opposing selection pressures directly confirms the common perception that phenotypic evolution is governed by a balance between conflicting fitness advantages. Second, the results show how the value of a metric trait which maximizes one fitness component (e.g. survival) may differ greatly from the value maximizing another (e.g. adult fecundity). Fitness components comprise the set of life history traits, and studies of opposing selection on metric traits are therefore informative about phenotypic mechanisms underlying life history trade-offs. We suggest that studies of selection in wild populations can complement traditional approaches to the study of life history evolution.

2. CONFLICTING NATURAL SELECTION PRESSURES ON METRIC TRAITS

We define natural selection as non-random variation among phenotypes in one or more components of

fitness. We define the components of fitness to be synonymous with life history traits; they include survival, fecundity, mating success and age at maturity. More formally, a life history trait (fitness component) is any character correlated with total fitness when all other traits are held constant. For example, higher survival is always advantageous, all else being equal, and we therefore include survival in the set of life history traits. Beak length, however, should not be correlated with total fitness when all other traits, including fecundity and survival, are held constant. We refer to these other phenotypic traits, including morphological, behavioural and physiological traits, as 'metric traits', after Falconer (1989).

Direct demonstrations of opposing selection pressures at different life history stages are summarized in table 1. The list is confined to observations from wild populations, and includes all examples that we found in a survey of the literature. Bird studies outnumber others, probably because of their determinate growth and the relative ease with which they may be measured, marked and subsequently observed in the wild. The list includes two studies of germination date in annual plants. This is a metric trait rather than a fitness component, under the definition given above, because it does not refer to age at first breeding (which is a fitness component) but to time within a season (during which all individuals breed). In this case, germination time provides no intrinsic fitness advantage. We also include two examples of selection on enzyme morphs. Although these are arguably not phenotypic traits, we presume that their fitness consequences derive from their association with specific morphological, physio-

Table 1. *Opposing selection pressures identified on metric traits in the wild*

(Life history traits refer to the fitness components whose performance is enhanced (1) and reduced (2) by an increase in the metric trait. Order of life history traits is arbitrary for polymorphic traits. Mating success refers to the rate at which individuals obtain a mate.)

organism	metric trait	life history trait 1	life history trait 2	reference
Darwin's finch ^a	body size	adult survival	age at 1st reprod.	Price (1984)
Darwin's finch ^a	body size	adult survival	juvenile survival	Price & Grant (1984)
song sparrow ^a	beak length	juvenile survival	fecundity	Schluter & Smith (1986)
Darwin's finch ^a	plumage colour	fecundity	survival	Grant (1990)
swallow ^{a, b}	tail-length	mating success	future fecundity	Møller (1988, 1989a)
herring gull	body-size	survival (non-breeding)	survival (breeding)	Monaghan & Metcalfe (1986)
Arctic skua ^a	plumage colour	age at 1st reprod.	mating success	O'Donald (1983)
house sparrow ^a	plumage badge size	mating success	adult survival	Møller (1989b)
red deer ^a	enzyme morph	juvenile survival	age at 1st reprod.	Pemberton <i>et al.</i> (1991)
dragonfly	hindwing length	mating success	survival	Koenig & Albano (1987)
damsel fly	body size	adult survival	mating success	Anholt (1991)
barnacle ^c	shell form	survival	fecundity	Lively (1986a, b)
snail	shell size	fecundity	survival	Bantock & Bayley (1973)
wild oat ^a	enzyme morph	survival	fecundity	Clegg & Allard (1973)
blue-eyed Mary	germination date	winter survival	spring survival	Kalisz (1986)
<i>Leavenworthia</i>	germination date	fecundity	survival	Baskin & Baskin (1972)
jewelweed	cotyledon area	fecundity	survival	Stewart & Schoen (1987)

^a Traits known to be heritable.

^b Opposing selection pressures identified only by experiment.

^c Known to show adaptive phenotypic plasticity of metric trait.

logical or behavioural (i.e. metric) traits as yet unmeasured.

Although many studies have observed selection in nature (Endler 1986), few have reported selection over more than one life history stage. When directional selection is present on a trait at one life stage, three patterns are possible at any other stage: no directional selection, selection in the opposite direction to that seen at the first life stage (i.e. opposing selection), and selection in the same direction to that at the first stage (complementary selection). Examples of all three patterns are known, occasionally from the same field study (e.g. Kalisz 1986). However, unknown biases in reporting, sampling error and technical difficulties in measuring selection make it difficult to assess the relative frequency of the three types. For example, biases may arise if some components of fitness (e.g. fecundity) are more difficult to measure than other components (e.g. mating success). Another major problem is the tendency of opposing selection to be masked by nutritional effects. For example, good nutrition may enhance both survival and fecundity as well as size of body parts, giving the false impression that size itself is under complementary directional selection. This problem is discussed more fully below and in Appendix 1. Note also that if a trait is associated with several fitness components (three, for example), then only a subset of the associations can be in opposing directions (two); the rest must be complementary.

Despite these problems, opposing selection appears to be relatively common in nature (table 1). We located only five examples in which selection was studied over two or more life stages, and complementary selection, but no opposing selection, was observed: body size in an *Anolis* lizard (Trivers 1976);

wing length in the scorpionfly (Thornhill 1983); tarsus length in a flycatcher (Alatalo & Lundberg 1986); horn length in a fungus beetle (Conner 1988), and leaf length in a perennial grass (Scheiner 1989). Subsequent analyses (Arnold & Wade 1984; Alatalo *et al.* 1990) have suggested that masking effects of nutrition may be important in some of these cases. Both opposing selection and complementary selection were present in two examples (Price 1984; Kalisz 1986; cf. table 1). Thus, as a first estimate, opposing selection appears to be more frequent than complementary selection.

Variability in selection intensities is the hallmark of virtually all field studies of natural selection, and the studies in table 1 were no exception. Two types of variability were shown. First, traits subject to strong selection in one year (or place) experienced weak or no selection in another (Kalisz 1986; Schluter & Smith 1986; Stewart & Schoen 1987; Anholt 1991). Second, the direction of the association between a given trait and a fitness component fluctuated between years or locations (Stewart & Schoen 1987).

The conflict between selection pressures on metric traits can be summarized in a simplified path diagram (figure 1). We focus on survival and fecundity for purposes of illustration only; the same idea can be applied to other fitness components. β_1 and β_2 are directional selection coefficients from separate linear regressions of survival and fecundity on the phenotypic (metric) trait (Lande & Arnold 1983). When the two selection pressures on the trait conflict, these coefficients are of opposite sign ($\beta_1 \times \beta_2 < 0$). An example of selection giving rise to this conflict is shown in the top half of figure 2.

We add a third path to figure 1 to incorporate the possibility that each increment to fecundity causes a

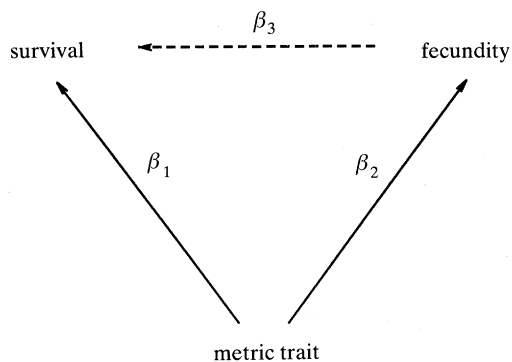


Figure 1. Path diagram summarizing the main causal links between survival, fecundity and a phenotypic metric trait. β_1 and β_2 are the linear selection intensities on the metric trait, which are of opposite sign when the survival and fecundity advantages of the trait conflict ($\beta_1 \times \beta_2 < 0$). The dashed line and β_3 represent the possible reduction in survival stemming directly from an increase in fecundity.

reduction in fitness components at later life stages. For example, brood enlargement in blue tits may reduce the future survival of parents caring for the young (Nur 1984), and induced fruiting in an orchid reduces fecundity in subsequent years (Primack & Hall 1990). These effects are mediated through physiological, morphological and behavioural changes that affect the fitness components in opposite ways (for example, induced fruiting in orchids led to a reduction in growth and hence size relative to control plants), but they are consequences of the increment to fecundity itself. The full correlation between survival and a metric trait (figure 1) depends on β_1 and $\beta_2 \times \beta_3$ (and also on the effects of correlated metric traits on survival and fecundity, whose paths of influence are not illustrated, for simplicity). This third path is not always applicable; for example $\beta_3 = 0$ when pre-reproductive survival is of interest.

3. PROBLEMS WHEN METRIC TRAITS ARE CORRELATED

Before discussing the implications of opposing selection, we first mention a difficulty encountered in attempts to precisely determine patterns of selection on traits. The problem is that the true target of selection may not be among the metric traits measured (Lande & Arnold 1983; Mitchell-Olds & Shaw 1987; Crespi & Bookstein 1989). This problem is not unique to studies of opposing selection, but special difficulties worth mentioning arise in this case. For example, in any given breeding season, male Arctic skuas with dark plumage obtain a mate earlier in the year than males with pale plumage (table 1; O'Donald 1983). However, this apparent selection on plumage coloration may stem indirectly from a tendency in females to mate with older males (Baker & Parker 1979).

This problem of unmeasured, correlated characters is ubiquitous in observational studies of selection, and careful choice of traits on the basis of their presumed function is needed to minimize it. The most promising

approach to measure selection on a specific trait is to manipulate it experimentally, independently of the rest of the phenotype, as was done by Møller (1988, 1989*a*) in his study of tail length in the swallow (table 1), although this is not always feasible.

The task of identifying targets of selection is particularly difficult when size in metric traits is correlated with the overall condition or nutritional health of the individual, and this nutrition also elevates both survival and fecundity directly (Price *et al.* 1988; Price & Liou 1989; Alatalo *et al.* 1990). This mechanism could be represented in figure 1 by the addition of a new trait ('nutrition') directly connected to all three original nodes by arrows with positive coefficients. In this case the correlation between each fitness component and the metric trait is a function of both the direct selection intensities β and nutrition. Nutrition is a special kind of correlated trait because it is strongly affected by local environment, and although it may affect the size of other heritable metric traits, nutrition may not itself be heritable.

Most crucially, because it positively affects the metric trait as well as the two fitness components, nutrition may mask opposing selection pressures. An excellent example is provided by the swallow. Møller (1988, 1989*a*, 1991) showed that tail length in the male swallow is positively correlated with both survival and mating success, suggesting that the tail is under persistent selection pressure to increase. However, this pattern proved to be spurious when tail length was manipulated independently of nutritional state of the male: long tails enhanced mating success (Møller 1988) but may have reduced survival and subsequent fecundity (Møller 1989*a*). The true pattern of selection on tail length in unmanipulated birds was hidden by the fact that males in better health or nutrition grow longer tails as well as survive and reproduce better than males in poor nutrition. Nutrition-dependent expression of metric traits and fitness components is probably common (Price *et al.* 1988; Zeh & Zeh 1988; Price & Liou 1989; Alatalo *et al.* 1990; Rowe & Ludwig 1991). The phenomenon may be especially prevalent in organisms with indeterminate growth (for example, insects and plants), in which most of the variation among individuals in size-related traits may be nutrition based (e.g. Roach & Wulff 1987).

It is known that the effects of nutrition can mask trade-offs between life history traits (Lande 1982; Reznick 1985; van Noordwijk & de Jong 1986; Partridge & Harvey 1988; Stearns 1989). However, nutrition's equally confounding effects on measures of selection in the wild are less widely appreciated. The swallow example shows that conflicting selection pressures are particularly prone to masking effects, and lead us to suggest that the frequency of cases of opposing selection on metric traits in nature is underestimated by the number of studies recorded thus far. Møller's (1988, 1989*a*) experiments reveal the power of phenotypic manipulations to tease apart selection on specific traits from the effect of nutrition and other correlated characters. A second, indirect, method that may be used when experiments are not possible is discussed in Appendix 1.

4. SELECTION AND THE EVOLUTION OF METRIC TRAITS

The view that morphological and other phenotypic traits are under conflicting selection pressures is a central concept in evolutionary ecology (Krebs & Davies 1984; Pianka 1988; Ricklefs 1990). Direct measurements of selection provide powerful evidence of this principle (table 1). They show that the phenotypic values at which survival and fecundity (or other fitness components) are maximized often lie to either side of the population mean. Traits are pulled in alternate directions at different stages of the life history, and the point at which these conflicts are balanced may lie in the vicinity of the observed population mean.

Phenotypic selection pressures are relevant to the evolutionary dynamics of natural populations when variation in the metric trait has a genetic component. Traits under opposing selection pressures are known to be heritable in about half of the cases (table 1); a genetic component remains to be verified in the other half. Populations may thus appear to be evolutionarily stable over the long term, but the finer measurements summarized in table 1 reveal that the mean values of traits lurch and wobble continuously over time. Studies by Gibbs & Grant (1987) on Galápagos finches show that selection pressures on heritable morphological traits oscillate between generations. The present survey of studies shows that similar oscillations occur between life stages within a generation.

5. CONFLICTING SELECTION PRESSURES AND LIFE HISTORY TRADE-OFFS

Fitness components are synonymous with life history traits, and selection pressures on heritable metric traits therefore identify mechanisms underlying life history

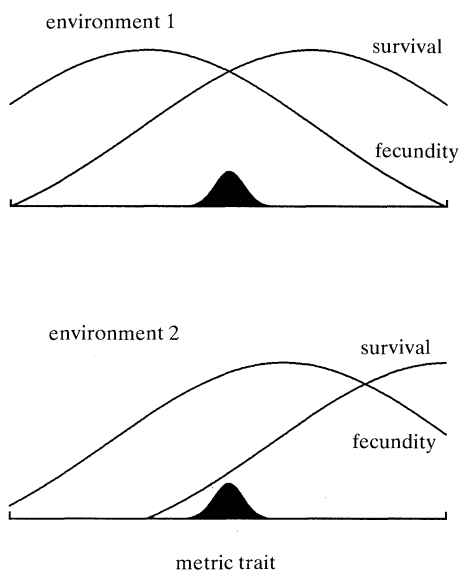


Figure 2. Hypothetical example of selection on a metric trait in two environments or time periods. The shaded curve shows the distribution of the trait in the population, assumed to be the same in the two environments. The top curves are fitness functions for survival and fecundity.

evolution. We doubt that there is a gene directly for survival (or other life history trait); rather, individuals in a population differ in survival either because of chance, or because they differ in one or more aspects of morphology, physiology and behaviour, metric traits that may have a partly genetic basis. The measurement of selection on underlying metric traits is therefore a useful way to identify trade-offs between life history traits: the demonstration that even one metric trait cannot be optimized simultaneously for survival and fecundity (table 1) is equivalent to a demonstration that survival and fecundity themselves cannot be simultaneously maximized.

The model of opposing selection (figure 2) is also a useful basis for evaluating and comparing other methods to identify life history trade-offs. These include the measurement of genetic correlations among life history traits, and the manipulation of fecundity (Reznick 1985; Partridge & Harvey 1988). Below, we briefly note the link between the latter two methods and patterns of opposing selection on underlying metric traits.

The method of genetic correlations considers that life history traits have an additive genetic component, and asks whether individuals with a high genetic value for survival also have a low genetic value for fecundity. This information is preferable to a measure of the phenotypic correlation between survival and fecundity, as a negative genetic correlation can be masked by the positive effects of nutrition (see above). Our approach is closely related to this method because, as has been argued elsewhere (Price & Schluter 1991), underlying heritable metric traits impart the genetic component to life history traits. Hence, selection on metric traits, and the heritability and genetic correlations between these traits, are the source of genetic correlations between fitness components (Price & Schluter 1991).

All else being equal, opposing survival and fecundity selection on a heritable metric trait such as beak length (figures 1 and 2) yields a negative genetic correlation between survival and fecundity (Schluter & Smith 1986; Price & Schluter 1991). However, the actual genetic correlation will be determined by the selection pressures accumulated over all heritable metric traits, with less predictable results. For example, if parasite resistance is heritable and has a strong positive effect on both survival and fecundity, then the net genetic correlation between the fitness components may be positive despite the fact that beak length is under conflicting selection pressures. Hence, although many metric traits in the organism may be subject to opposing selection, with the result that neither survival nor fecundity is maximized, the genetic correlation will not necessarily reveal it. This problem has been modelled by van Noordwijk & de Jong (1986) and Houle (1991).

Experimental manipulation of fecundity, such as adding eggs or young to the nest of individual birds and noting subsequent survival of the parents (see, for example, Nur 1984; Gustafsson & Sutherland 1988; Pettifor *et al.* 1988), is another common approach to investigating life history trade-offs. This approach illuminates only part of the trade-off between survival

and fecundity, as we show in figure 1: the experiment can determine whether or not β_3 is negative, but the manipulation bypasses consideration of the changes in organism design that would otherwise be necessary to produce that extra nestling, and the possibly negative consequences of that design to survival (β_1 in figure 1).

Reznick (1985) has criticized the fecundity manipulation as 'phenotypic', arguing that only genetic trade-offs are relevant to life history evolution. We demur, and consider the fecundity manipulation as analogous to a selection experiment, much like Møller's (1988, 1989*a*) on tail length of the swallow, the chief utility of which lies in its ability to identify the fitness consequences of variation in specific traits. Individual survival depends on underlying phenotype by all paths in figure 1 (β_1 and $\beta_2 \times \beta_3$, plus paths through other metric traits not illustrated); the genetic correlation between survival and fecundity also depends on these same paths. Only by manipulating fecundity independently of the underlying metric trait are we able to measure β_3 alone. However, the manipulative approach measures only one part of the survival-fecundity trade-off. Perhaps most of the burden of reproduction lies instead in the traits that organisms must carry around with them in order to reach the point of reproducing successfully. If so, then a conceivably large portion of the survival cost associated with reproduction (β_1) may be paid well before breeding begins.

6. SELECTION, GENOTYPE-ENVIRONMENT INTERACTION AND REACTION NORMS

The alternative phenotypes that a given genotype produces across a range of environments are labelled its 'norm of reaction' (Stearns 1989). Reaction norms are ubiquitous in life history traits, and as a result genetic variances and correlations between these traits are

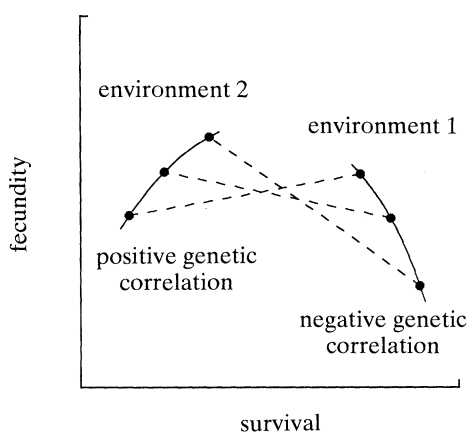


Figure 3. Genotype-environment interaction in life history traits arising from fluctuating selection on a metric trait (figure 2). Solid lines give mean survival and fecundity of different genotypes for the metric trait in two environments. The slope of the line shows the sign of the genetic correlation between survival and fecundity. A dashed line connects the same genotype in the two environments, and describes its norm of reaction.

highly dependent on the environment in which they are measured (Stearns 1989; Stearns *et al.* 1991). Such genotype-environment interactions in life history traits are generally thought to result from developmental plasticity in the organism's underlying phenotype. Consideration of fluctuating selection on heritable metric traits reveals an alternative mechanism, whereby genetic correlations between life history traits may even change sign in the absence of developmental plasticity.

We illustrate this mechanism by comparing the selection pressures acting on a heritable trait in alternative environments (figure 2; e.g. different locations or years of a field study). Survival and fecundity are presumed to depend on a metric trait in different ways. For example, a large beak in a finch may be advantageous to survival in the non-breeding season because it helps crack large seeds, but a small beak may be best in the breeding season when parents forage for insects to feed to their young. Fluctuations in the sizes of seeds and insects may lead to different patterns of selection in different years (figure 2). For simplicity, we assume that the metric trait does not itself change in response to these environments. The mean survival and fecundity of genotypes of alternate beak size can then be calculated from the fitness functions in figure 2, producing the results shown in figure 3. In this example, the genetic correlation changes sign simply as a consequence of an altered pattern of selection. Moreover, all the complexities of interpreting the shifting pattern of genetic correlations vanish when selection pressures on the underlying trait are understood.

The few studies of selection on metric traits that have been replicated across environments or years (Kalisz 1986; Schluter & Smith 1986; Gibbs & Grant 1987; Scheiner 1989; Anholt 1991) suggest that fluctuating selection pressures are the rule in nature. Hence, it may be worthwhile to partition the causes of genotype-environment interaction in life history traits into components, one attributable to developmental plasticity in the organism and a second to variation in selection pressures. In birds there may be restricted plasticity in morphology, in which case fluctuating selection on these traits may be the main cause of variation in life history trade-offs. In contrast, phenotypic plasticity probably dominates variation in behavioural traits, in which case studies of selection alone will not identify the causes of variation in measures of life history. An outstanding example of a joint approach, in which variable selection and developmental plasticity were both measured and found to be large, is that of shell form in the acorn barnacle (Lively 1986*a, b*). Levels of genetic variation in this trait are not yet known.

7. CONCLUSION

It is commonly recognized that heritable phenotypic traits mediate life history evolution (Partridge & Harvey 1988; Stearns 1989). It is less commonly recognized that this mediation is equivalent to natural selection on morphology, physiology and behaviour,

and that the growing number of demonstrations of conflicting selection pressures (table 1) provide examples of mechanisms in nature for life history trade-offs. Clearly, not all mechanisms of life history evolution will be discovered by field studies of opposing selection: many phenotypic traits under selection are extremely plastic, and others are difficult to observe and measure. Nevertheless, if life history trade-offs are common then opposing selection pressures on metric traits are also common, and there should be much to gain from studying them. We suggest that the link between selection studies and the study of life histories will grow as further field studies of selection are conducted.

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APPENDIX 1. DISENTANGLING DIRECT SELECTION FROM EFFECTS OF NUTRITION

The problem of nutrition masking patterns of natural selection is probably widespread. Experimental manipulation is one way in which effects of nutrition can be controlled for, but this will not always be possible. Here we show how one may statistically distinguish natural selection directly on a trait z from the effect of nutrition n , when nutrition cannot be measured. The gist of the method was suggested and applied by Alatalo *et al.* (1990) in their illuminating 'bubble plot' (their figure 1), and requires measurements on relatives. It has also been used with some success on song sparrows (W. M. Hochachka, unpublished results). Consider the following regression model of natural selection:

$$\omega - 1 = \beta z + \delta n + \text{random error}, \quad (1)$$

where ω is relative fitness, $\omega = W/\mu_w$; W is the fitness component (e.g. survival, measured as a binary (0, 1) variable, or reproductive success, measured as number of offspring), and μ_w is the mean of W . β is the intensity of directional selection on the trait z , and δ is the effect of nutrition on relative fitness. The trait z is assumed to consist of three independent components:

$$z = x + n + e; \quad (2)$$

an additive genetic term x , a component n attributable to nutrition, and a random error term e . Therefore, z and n are correlated with $\text{Cov}(z, n) = \delta_n^2$, where σ^2 refers to variance (Price *et al.* 1988).

A univariate regression of ω on z would have the slope $\beta + \delta_n^2/\sigma_z^2$ (cf. equation 1). Hence, if z has a nutrition component, its covariance with fitness may represent the effect of nutrition (δ) rather than direct selection (β) on the trait z . If n is measurable, its effect may be disentangled from natural selection on z with a multiple regression of ω on z and n (Lande & Arnold 1983). The following steps may be taken when n is not measurable, provided that z is heritable and n is not. First, carry out a regression of z on the same trait z' in a relative (e.g. offspring measurement z on midparent

measurement z'). Let H refer to the slope of this regression. Second, compute the deviation d of each individual measurement z from the regression line:

$$d = z - Hz'. \quad (3)$$

Finally, carry out a multiple regression of $\omega - 1$ on z and d . It can be shown that the partial regression coefficient for z is β , the intensity of directional selection. The partial regression coefficient for d is $\delta\sigma_n^2/\sigma_a^2$. Thus the terms β and δ of the selection model are separated, and their significance to fitness is now evaluated.

The above result may seem counterintuitive because d is not nutrition itself, but like z is a sum of genetic, environmental and nutrition components. However, when z is held constant, residual covariation between d and fitness can arise only through variation in the nutrition part, and the rate at which fitness increases with d depends on δ and the fraction of the variance in d attributable to nutrition. Hence, the partial regression coefficient for d evaluates the magnitude of δ (scaled by σ_n^2/σ_a^2) disentangled from selection on z . Similarly, when d is statistically held constant, the rate at which fitness changes with variation in z depends only on the magnitude of β , the selection intensity.

The above partial regression coefficients were determined by calculating $P^{-1}s$, where P is the matrix of variances and covariances between z and d , and s is a vector whose two entries are $\text{Cov}(\omega, z)$ and $\text{Cov}(\omega, d)$. We made use of the following substitutions:

$$\text{Cov}(\omega, z) = \beta\sigma_z^2 + \delta\sigma_n^2, \quad (4)$$

$$\text{Cov}(\omega, d) = \beta\sigma_a^2 + \delta\sigma_n^2 \quad \text{and} \quad (5)$$

$$\text{Cov}(z, d) = \delta_a^2. \quad (6)$$

This derivation makes a number of assumptions, and hence results from its application should be interpreted cautiously. In particular, we assume that selection is linear (equation 1); this may often be achieved with a suitable transformation of the data. We also assume that components of variation are additive and uncorrelated (equation 2), that nutrition is non-heritable, and that environmental and maternal sources of resemblance among relatives are absent (i.e. that the resemblance is entirely genetically based). The method will be most successful when the heritability of the trait is moderate or high.

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