

# What is individual quality? An evolutionary perspective

Alastair J. Wilson and Daniel H. Nussey

Institute of Evolutionary Biology, Ashworth Laboratories, University of Edinburgh, The King's Buildings, West Mains Road, Edinburgh EH9 3JT, UK

**In studies of population ecology, demography and life history evolution, among-individual differences in traits associated with survival and reproduction are often attributed to variation in 'individual quality'. However, often intuitive quality is rarely defined explicitly, and we argue that this can result in ambiguity about what quality actually is. Here we consider the various ways in which the concept of quality is currently applied, and show that subtle differences in intended meaning have very important consequences when the goal is to draw evolutionary inferences. We also propose a novel approach that is consistent with all current ecological uses, but also allows the concept of quality to be integrated with existing evolutionary theory.**

## Defining individual quality

Population and evolutionary ecologists frequently highlight differences in 'individual quality' to explain variation among individuals in traits associated with survival and reproduction. Despite enormous interest in the causes and consequences of individual heterogeneity [1–4], 'individual quality' remains a somewhat elusive concept within ecology [5,6]. At the heart of the problem is that researchers in different fields often invest the term with subtle, but potentially important differences in meaning. Consequently, if not carefully defined 'individual quality' is a rather ambiguous term. From an evolutionary perspective, heterogeneity among individuals is of central importance as it is the necessary starting point for adaptive phenotypic evolution. This is because natural selection can only occur if individuals vary in both phenotype and fitness, while a response to selection depends on this variation having a genetic basis [7]. Despite the efforts of ecologists and evolutionary biologists to explore among-individual heterogeneity in fitness and fitness-related traits, it is not currently clear how the concept of 'individual quality' relates to evolutionary theory.

Here we argue that the primary reasons for this lack of integration are that the term is often used without explicit definition, and that quality can mean somewhat different things to different people. Having been unable to locate a formal definition in the literature, we adopt a working definition of quality as being an axis of among-individual heterogeneity that is positively correlated with fitness. This working definition is based on our view that current meanings (either stated or implied) and uses appear totally

consistent in two fundamental respects; firstly, quality varies among individuals within a population; and secondly, high quality individuals have greater fitness than low quality ones. However, for an evolutionary biologist this working definition leaves a lot of important questions unanswered. For example, exactly how does individual quality relate to evolutionary fitness? Can quality have a genetic basis of variation, or is it a consequence of environmental effects alone? If reproductive costs and allocation trade-offs can be masked by variation in individual quality, then should we try to control for quality differences before attempting to draw evolutionary inferences from observed relationships between life history traits? If so, then how should empiricists actually define and measure an individual's quality?

In what follows we present a personal view of 'individual quality' in which we argue that the above questions need to be addressed if the relationship between quality and evolutionary processes is to be resolved. This article presents an evolutionary perspective on a topic that has primarily been the preserve of ecologists to date. It is neither our intention to provide a full review of the ecological literature on the subject, nor to be prescriptive about how quality should be used by ecologists. We also recognise that not all researchers will see the need to shoehorn quality into a form more digestible to evolutionary biologists. Nevertheless, it is our hope that this article will stimulate discussion and thought as to what exactly is meant by 'individual quality', how we can measure it, and what implications it has for phenotypic evolution.

## What are the relationships between quality, phenotype and fitness?

Evolutionary theory generally distinguishes between phenotypic traits and fitness. A trait is expected to evolve if it is heritable and under selection [7], requirements that are formally fulfilled by the presence of genetic covariance between the trait and fitness [8]. Among-individual heterogeneity in both a trait and in fitness is therefore a prerequisite for phenotypic evolution because, by definition, the covariance between two quantities is zero if either one of them does not vary. While the fitness of an individual is defined as its genetic contribution to future generations, empirical estimation is difficult since no single parameter is universally suitable [9–11]. In practice empiricists usually use proxies of fitness such as lifetime breeding success, or components of fitness such as litter size or survival meaning that, to some extent, the distinction

Corresponding author: Wilson, A.J. (alastair.wilson@ed.ac.uk).

between traits and fitness becomes arbitrary. For example, litter size might be treated as a measure of fitness in one study, but as a phenotypic trait under selection in another. Nevertheless, the distinction has practical utility since we can use statistical parameters describing the covariation of a trait and fitness to measure natural selection [12].

So, where does individual quality fit into this evolutionary framework? Is it a phenotypic trait or is it fitness, and does it matter? That individual quality is the same as fitness is sometimes implied [13] and poses no real difficulties for evolutionary interpretation aside from the potential for semantic confusion. We would argue fitness is a better defined and more widely understood concept than individual quality, albeit similarly awkward to estimate empirically [9–11]. However, quality is more generally viewed as a property of the phenotype that is positively, but not necessarily perfectly, correlated with fitness. Three uses of the term are common in the literature and we have illustrated these in Figure 1. First, quality is

often used to describe heterogeneity in a measured trait that is known (or assumed) to be under positive selection [14–16]. Second, quality can be defined as a scalar abstraction of the multivariate (measured) phenotype [6,17,18]. Third, quality is sometimes used to encapsulate the idea of one or more important but unmeasured traits that contribute to fitness variation [19].

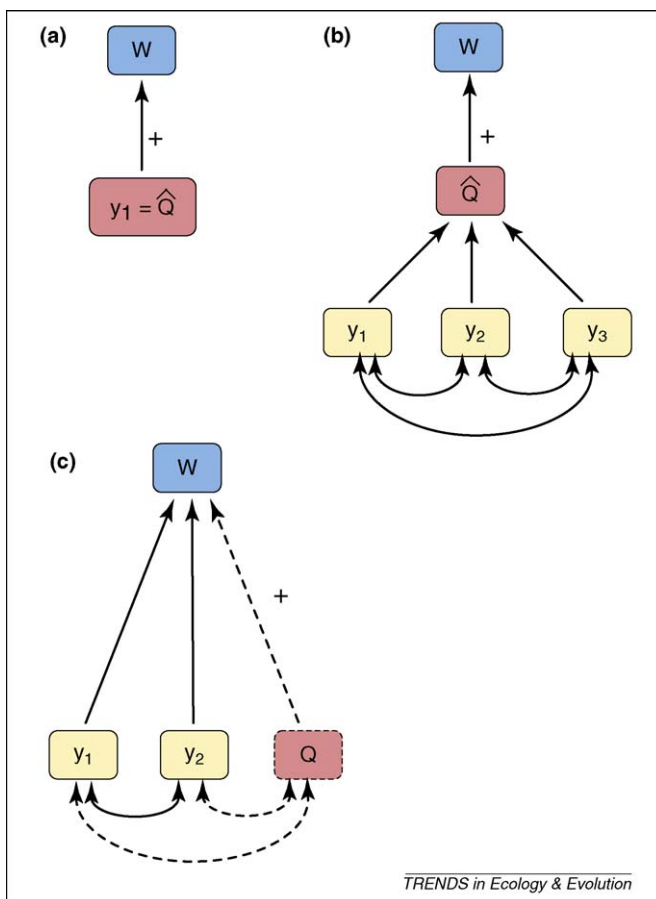
#### Quality as among-individual heterogeneity in a single trait

Individual variation in a single phenotypic trait is often used as a proxy or indicator of variation in individual quality (Figure 1a). A range of traits have been employed to capture quality including breeding phenology, measures of reproductive effort or success, body condition indices and longevity [6,15,16,20–22]. From an evolutionary perspective, the assumption made here is that, all else being equal, an individual with a higher trait value and therefore higher quality is expected to have higher fitness. Here, quality equates to a trait under positive directional selection, although the selection is often assumed rather than empirically estimated. We see two difficulties with this approach to measuring quality. First, within a population, two putative indicators of ‘quality’ might be only weakly correlated [6,23], which in our view undermines the validity of using a single trait to measure quality. If two indicators yield different biological conclusions then how should we choose between them? Or should we conclude that neither is sufficient to describe quality on its own? Second, since different traits are necessarily used according to the organism being studied, it is not clear that the concept of ‘quality’ as measured in one study will bear any relation to ‘quality’ measured in another. Thus, one cannot generalise conclusions across studies.

#### Quality as a scalar abstraction of a multiple phenotypic traits

If we accept that quality cannot adequately be inferred from a single indicator trait, then perhaps it can be captured by measuring multiple traits and then reducing the information into a scalar variable (Figure 1b). The use of multiple measured traits to assess individual quality is an interesting development applied in several recent studies [6,17,18]. For example, Hamel *et al.* [17] employed a composite measure of quality derived from a suite of fitness-related traits to several ungulate populations. Traits used included longevity, breeding success in final reproductive episode, and adult mass. Their method defined individual quality from principal component analysis (PCA) of multivariate phenotypic variation. Determined in this way ‘quality’ becomes an axis of variation in multivariate phenotype space that, to be consistent with our working definition, would have to be positively correlated with fitness.

We think that an increased use of multivariate methods would greatly benefit empirical studies of ‘quality’. However, there are unresolved issues that need careful consideration. Which traits should be included in the analysis? Should any be excluded? Which axis of variation should be defined as quality – the most important one (i.e. PC1 from a PCA), or perhaps the axis most closely correlated with



**Figure 1.** Schematic diagram representing the three prevalent uses of individual quality in the literature. **(a)** In empirical studies to date an individual's quality ( $Q$ ) has most commonly been assessed from a single trait ( $y_1$ ) known to be positively (denoted with +) correlated with fitness ( $W$ ). An individual's estimated quality  $\hat{Q}$  is therefore equal to its phenotypic value at  $y_1$ . **(b)** An alternative is to define quality in such a way that it is estimated from a set of multiple measured traits (e.g.  $y_1$  to  $y_3$ ). Here quality becomes a scalar abstraction of the multivariate phenotype which is causally (and positively) related to fitness. **(c)** In the third common use, individual quality is not estimated but is instead viewed as an unmeasured trait that is causally and positively related to fitness. As we discuss in the text, the potential presence of such a trait causes difficulties when attempting to make evolutionary inferences from observed covariance among fitness-related traits that have actually been measured (e.g.  $y_1$ ,  $y_2$ ). Solid boxes (or lines) denote measured variables (or pathways). Dashed lines are assumed relationships.

fitness? Should major axes of variation be summarised in the phenotypic covariance matrix or in the corresponding correlation matrix (as used by Hamel *et al.* [17]). Being standardised, using the correlation matrix will protect against potentially misleading scale effects (e.g. if different traits are measured in different units) but will be insensitive to biologically interesting differences in variance levels among fitness-related traits. The results of any empirical analysis will depend on these decisions and comparison across studies will remain difficult if the traits used, or their relationships to fitness, differ. Nevertheless, the application of multivariate statistics is potentially a very useful advance for empirical studies and, as we discuss later, could provide a useful approach for integrating ecological and evolutionary perspectives on ‘quality.’

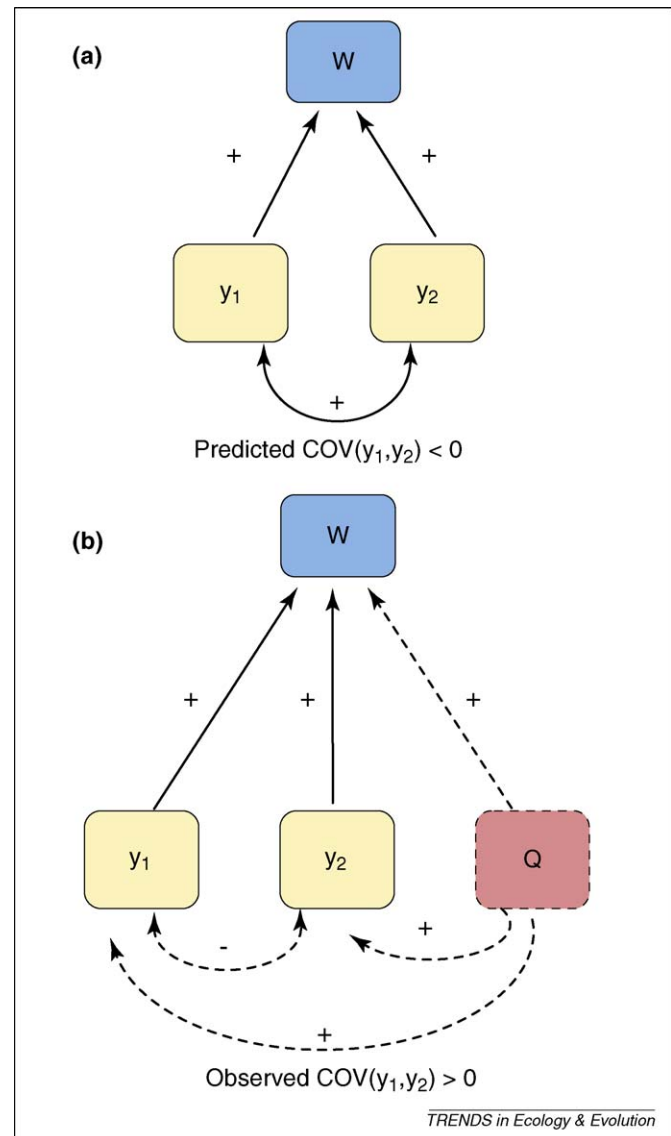
#### Quality as an unmeasured trait

It is often stated that ‘quality’ differences among individuals can mask patterns arising from important biological processes such as ageing, phenotypic plasticity and resource allocation trade-offs [1,4,24–26]. As these processes are properly seen as occurring within individuals, a growing body of research has developed tools that utilise longitudinal data to separate between- and within-individual variation in order to elucidate their relative contributions to ecological and evolutionary processes [27–30]. However, individual quality is still frequently invoked as an unmeasured variable that can obscure the expected relationship between traits, or between a trait and a covariate such as age or the environment in ecological studies (Figure 1c). One area in which quality is used in this way relates to the detection of trade-offs among life history traits (Figure 2). This use of quality can be particularly problematic in an evolutionary context, where trade-offs are commonly thought of as sources of evolutionary constraint [31]. We return to this point later but before doing so it is first necessary to consider another area of uncertainty: is there genetic variation for individual quality?

#### Does variation in quality have an important genetic basis?

As we have provisionally defined it, quality varies among individuals and is positively correlated with fitness. Quality is therefore under selection. A question that arises for an evolutionary biologist is whether quality is heritable since, if this were the case, we would expect it to evolve. In principle, and provided we can first agree on an empirical measure of quality to use, we could answer this question by estimating its heritability (i.e. the proportion of variance in quality explained by genetic effects [7]). Quantitative genetics offers powerful statistical tools to do this, and recent applications of these tools have demonstrated their utility for empirical studies of heterogeneity in natural populations [32,33]. However, they can only be applied in systems where the relatedness between individuals is known [33] and obtaining such information can be extremely challenging in field studies.

Our reading of the evolutionary ecology literature suggests that assumptions are often made, either explicitly or implicitly, regarding the genetic basis of variation in



**Figure 2.** Reproductive costs versus the ‘Individual Quality’ hypothesis. **(a)** If reproduction has fitness costs then current reproductive effort ( $y_1$ ) should negatively impact on some aspect of future performance (e.g. post-reproductive survival,  $y_2$ ), leading to an expectation of negative covariance between  $y_1$  and  $y_2$  (assuming that both traits are causally positively associated with fitness,  $W$ ). **(b)** Costs of reproduction might be masked by variation in individual quality  $Q$  (often viewed as trait of covariate positively related to resource acquisition). If  $Q$  is positively correlated with both  $y_1$  and  $y_2$  it could result in a net positive covariance between the traits at the population level even when within-individual covariance is negative. Note that  $Q$  here is unmeasured and usually thought of as a missing trait, but it could equally be thought of as a composite of all unmeasured traits and environmental covariates (see text). Solid boxes (or lines) denote measured variables (or pathways). Dashed lines are assumed relationships. Positive and negative relationships are respectively denoted + and –.

individual quality. Two common but contrasting positions are particularly prevalent. In studies of mate choice and sexual selection, individual quality is often held to have an important genetic basis of variation. For example, the good-genes or ‘sexy sons’ hypothesis posits that females should choose mates of high (genetic) quality in order to increase the expected fitness of their offspring [34]. This requires that a male character used as a basis for female choice should provide reliable information as to the expected genetic merit (with respect to fitness) of a male’s potential offspring [35]. Many tests of this hypothesis assume that offspring fitness and focal male trait (i.e.,

the indicator of quality) are both heritable and positively genetically correlated with each other, without supporting quantitative genetic evidence.

Conversely, the term ‘individual quality’ is often used to describe environmentally-induced heterogeneity in life history traits which, as has long been recognised, can complicate and potentially bias the measurement of ecologically and evolutionary important processes [4,24,29,30]. For example, cohort and maternal effects can have important and long lasting influences on reproductive performance and survival as well as profound effects on population demographics and dynamics [36]. Observed phenotypic heterogeneity might also reflect differences in resource acquisition among individuals, perhaps arising from spatial heterogeneity in the environment. While it might seem intuitive that such effects would have no genetic basis, this need not always be the case. For example, it is well established that maternal effects can have a heritable basis [37,38] and it is not difficult to imagine a hypothetical scenario in which resource availability would itself be heritable as a consequence of genotype–environment correlations [7]. This could happen if, for example, the outcome of competition for resource patches was mediated by a heritable trait (e.g. body size).

Thus quality is sometimes assumed to be a property of the genotype (e.g. in studies of mate choice [39]) and sometimes of the environment an individual experiences (e.g. in studies of life history trade-offs [6]). This dichotomy is important because it leads to divergent views on the role of quality in phenotypic evolution. Is quality an important axis of variation in its own right, or is it something we need to control for if we want to reveal those patterns of phenotypic variation that do tell us about evolutionary processes [6]? If researchers wish to draw evolutionary inferences from their data, then making assumptions about the genetic basis of variation in quality might be unavoidable. However, when the heritability of a trait or traits associated with individual quality is unknown there is a real need to better recognise, and state, the dependence of biological conclusions on any assumption made.

### Is quality fixed or can it vary?

Demographic models of capture–mark–recapture data that incorporate among-individual variation in vital rates (i.e. survival and fecundity) sometimes distinguish between fixed and dynamic sources of heterogeneity. Fixed differences in vital rates are sometimes said to reflect differences in individual quality [28] arising from features of an individual’s phenotype that are determined at birth [28,40]. This has led to the suggestion that the presence of quality effects could be tested for comparing observed life history data to a null model of dynamic heterogeneity generated by stochastic processes alone [28].

This concept of quality as a fixed property of an individual is potentially at odds with the use of fitness-related indicators discussed earlier since, for example, an animal’s fecundity typically varies among-reproductive episodes. To an extent the dichotomy between fixed and dynamic heterogeneity is related to the earlier question of whether quality differences are genetically determined. For example, genetic variation for quality should result in

some individuals receiving good genes and therefore showing consistently higher fecundity across reproductive events. In contrast, if quality is taken to mean environmentally determined ‘condition’ then we might clearly expect it to vary over an individual’s lifetime according to the environment experienced. However, there is no direct equivalence between fixed and genetic effects since while an individual’s genotype might not change over its lifetime the phenotypic consequences of a particular genotype certainly can (e.g. through genotype-by-environment and/or genotype-by-age interactions [41,42]). Conversely, quantitative genetic analyses of longitudinal data routinely demonstrate ‘permanent environment’ effects on the phenotype that arise from non-genetic (or at least non-additive genetic) sources. In addition, a distinction is sometimes also made between intrinsic (e.g. genetic) and extrinsic sources of heterogeneity, with only the latter being regarded as individual quality (e.g. [43]). However, this does not necessarily yield an expectation with respect to permanence either. For example, while Kempnaers *et al.* [44] argue that intrinsic quality differences could arise from maternal effects, maternal effects frequently decline over ontogeny [45]. Indeed age itself is sometimes cited as an intrinsic source of quality variation [43,46].

While an individual’s quality need not be defined as a constant, if quality is not, at least to some extent, repeatable then it is difficult to argue a case for its existence. For example, imagine a scenario where individual quality varies as a reaction norm of either an intrinsic (e.g. age) or extrinsic (e.g. resource abundance) variable. In this case, quality would vary, but would nonetheless be correlated within individuals across measurements. In practice, if using longitudinal data to discriminate between within- and among-individual patterns of phenotypic covariance (e.g. to look for a trade-off) then the decision as to whether sources of heterogeneity among individuals (i.e. quality) are treated as constant or variable will often be a modelling decision to be decided on statistical grounds.

### Reproductive costs versus the ‘individual quality’ hypothesis

There is an increasing tendency among evolutionary ecologists to posit the existence of reproductive costs, manifest as a trade-off between current reproductive effort and future fitness components [47], versus heterogeneity in individual quality as alternative hypotheses to be discriminated from patterns of phenotypic covariance (e.g. [13,48,49]). When total resources are limited, allocation to one fitness component or activity (e.g. reproduction effort) should reduce the available allocation to another (e.g. somatic maintenance) resulting in an observable cost (e.g. decreased survival probability) [47]. While this generates an equilibrium expectation of negative genetic, and hence phenotypic, covariance between traits involved in the trade-off (Figure 2a), it has long been recognised that this pattern could easily be obscured by variation in a third unmeasured trait that we might view as ‘quality’ (Figure 2b). For this reason, patterns of phenotypic covariance might not provide an accurate picture of within-individual (and potentially genetic) associations among traits [50,51]. For example, if individuals vary in levels

of resource acquisition then we would expect those 'high quality' individuals with more resources to be able to allocate more to all traits [26]. Thus it can be argued that negative covariance between traits (e.g. reproductive success in consecutive breeding seasons) provides evidence of a cost of reproduction, while positive covariance implies that there is variation in individual quality [13,52].

Although seductive, we feel there are some major pitfalls with this as a premise for empirical investigations. First, the alternative hypotheses are not mutually exclusive. In a recent investigation of reproductive costs in reindeer, Weladji *et al.* [19] identified two extreme scenarios, a 'cost only' scenario in which reproductive effort was predicted to negatively co-vary with future fitness components, and a 'quality only' scenario in which the covariance was predicted to be positive. In this case the data supported the latter scenario more than the former. However, a general problem is that there is no clear expectation for the sign of the covariance if both costs and quality variation are present, and we cannot infer the magnitude of the costs even when negative covariance is found. Equally, if positive covariance leads to the conclusion that a cost is being masked by quality (rather than the cost is absent), then it is important to recognise the presence of the posited trade-off is an *a priori* assumption of the study rather than a hypothesis being tested.

Second, the poor fit to the data of a model involving two traits (Figure 2a) cannot in itself prove that a second model (Figure 2b) involving a third unmeasured trait (i.e. quality) is better. Thus, if quality is seen as an unmeasured trait then in this context it risks becoming nothing more than a term to describe a hypothetical source of positive covariance that would reconcile our *a priori* expectations with seemingly contradictory results. We are not trying to argue that the 'individual quality' hypothesis has no merit here, but rather that properly testing it requires that quality be defined and empirically measured. Certainly stronger conclusions can be justified from those studies of reproductive costs that include a measure of individual quality allowing the more complex model (Figure 2b) to be parameterised. Thus if quality is an unmeasured trait (or traits) related to resource acquisition [26], then the challenge for empiricists must be to identify and measure it.

Third, even if confounding effects of 'quality' could be completely accounted for, the presumed negative genetic relationships among life history traits might not always be there to uncover. Genetic correlations are unfortunately difficult to measure with precision, particularly in field studies. However, considerable progress has been made over recent years [33] and empirical support for the common view that negative genetic correlations among pairs of life history traits act as ubiquitous sources of evolutionary constraint is equivocal at best [33,53]. In the absence of genetic variance for resource acquisition [54], negative genetic correlations between at least some pairs of (positively selected) life history traits are expected under optimal equilibrium conditions. However, such optimal equilibrium conditions are assumed far more frequently than tested in evolutionary ecology [55] and will not always hold. Furthermore, the genetic correlations between any two traits at equilibrium will depend on patterns of genetic

covariance with, and selection on, other traits which might not have been measured [56].

### Integrating evolutionary and ecological views: a possible way forward?

We have argued above that any empirical test of the 'individual quality hypothesis' properly requires that quality be defined in such a way that it can be measured. We have also argued that using single traits to measure individual quality will often be unsatisfactory. How then can we move the concept of quality forward and potentially integrate evolutionary and ecological perspectives? One solution could lie in the further development of the multivariate approaches recently used in field studies of ungulates [17,18]. In those studies, principal components analysis was used to identify the main axes of variation within a set of fitness related traits. A useful variation on this approach might be to define quality, not simply as one or two major axes of variation among putative fitness-related traits, but rather as *the axis of phenotypic variation that best explains variance in individual fitness*. To do this requires that one of the measured 'traits' can be designated as an appropriate proxy for individual fitness (e.g. lifetime reproductive success), while the remaining traits comprise the phenotype. Then, the axis of phenotypic variation best explaining differences in fitness (i.e. the axis of 'quality') would be given by a vector  $\beta$  that contains the partial regression coefficients from a multiple regression of traits on fitness [57]. Under this approach, 'quality' becomes an idealised axis of phenotypic variation along which fitness would change importantly, rather than an axis that is necessarily important in the observed data. The crucial question that arises from this new approach is: how well do the main axes of variation in the measured phenotype correspond with the idealised axis of quality measured by  $\beta$ ? This question can be answered by applying standard quantitative genetic methods [58,59] to the variance-covariance matrix of phenotypic traits  $\mathbf{P}$  (as opposed to the additive genetic matrix  $\mathbf{G}$  more normally used). This idea is developed in more detail in Box 1.

A useful point to recognise is that for analytical purposes there is really little distinction between a trait included in the multivariate phenotype and an environmental covariate. Thus any continuously measured environmental variable (age, experience etc.) that might influence fitness and can be assigned to an individual can be included in the matrix  $\mathbf{P}$  and used to estimate  $\beta$ . Additional complexity arising from environmental variation can be incorporated by, for example, estimating  $\beta$  and  $\mathbf{P}$  in environment-specific data subsets. Alternatively, selection and/or phenotypic (co)variance structures can be modelled as continuous functions of environmental covariates [41,60]. In this way models can be readily constructed that enable an individual's quality to vary within its lifetime. This flexibility accommodates the alternative treatments in the ecological literature whereby quality is sometimes viewed as a source of fixed heterogeneity [28] but is sometimes viewed as dynamic and free to vary with environmental conditions or age [43,46].

Estimating individual quality from  $\beta$  in this way does require that a suitable proxy of fitness is available and we

### Box 1. Determining the importance of individual quality

If quality is defined as the axis of phenotypic variation that best explains variance in individual fitness, it can be determined from the vector of partial regression coefficients of traits on fitness,  $\beta$ . This is the vector of selection; an integral part of quantitative genetic theory [57]. Having estimated  $\beta$ , we can ask whether or not heterogeneity in quality is a salient feature of a population. One way to do this is by determining the angle ( $\theta$ ) between  $\beta$  and one or more principal components (eigenvectors) of the phenotypic covariance matrix  $\mathbf{P}$ . A simple two-trait illustration of this idea is shown in Figure 1.

Points in the two panels of Figure 1 represent individuals measured at two traits involved in a putative trade-off and the black line indicates the major axis of phenotypic variance. The blue arrow denotes the vector of selection, or 'quality', with positive selection on both traits. In panel (a) the vector of selection corresponds poorly with the major axis of phenotypic variation (large angle  $\theta$ ), and we would conclude that heterogeneity in 'quality' is not a salient feature of this population. In contrast, panel (b) shows a good correspondence (small  $\theta$ ) between the vector of selection and the major axis of phenotypic variation, consistent with important heterogeneity in 'quality'.  $\theta$  can range from  $90^\circ$  when  $\beta$  is orthogonal to the axis of phenotypic variation to  $0^\circ$  if they are perfectly aligned. If  $\theta = 0^\circ$ , then

quality itself is the major axis of observed phenotypic variance. A complementary, and in some ways more direct approach is to simply estimate the amount of total phenotypic variance in the  $\mathbf{P}$  that is explained by the vector of quality  $\beta$ . This is possible by evaluating the matrix product  $\beta^T \cdot \mathbf{P} \cdot \beta$  which could then be standardised for comparison across studies by expressing it as a proportion of the total variance in  $\mathbf{P}$  (determined as sum of the diagonal elements in  $\mathbf{P}$  or, equivalently, as the sum of the eigenvalues of  $\mathbf{P}$ ).

Defining individual quality from  $\beta$  would standardise its meaning, interpretation and prediction. An individual's quality would simply be its predicted fitness given its observed phenotype and the estimated partial regression coefficients in  $\beta$ . However, if key fitness-related traits are not included then the estimate of selection gradients obtained from the regression model (and hence the vector defining quality) will be biased [66,67]. Frustratingly, this introduces a potentially circular problem for the 'individual quality' hypothesis: while quality is commonly invoked when unmeasured traits are suspected, defining it from the multivariate phenotype will require us to assume that we have measured all the relevant traits. Nevertheless, by first recognising that this assumption is inherent, we can at least acknowledge the impact that any violation might have on conclusions from real-world studies.

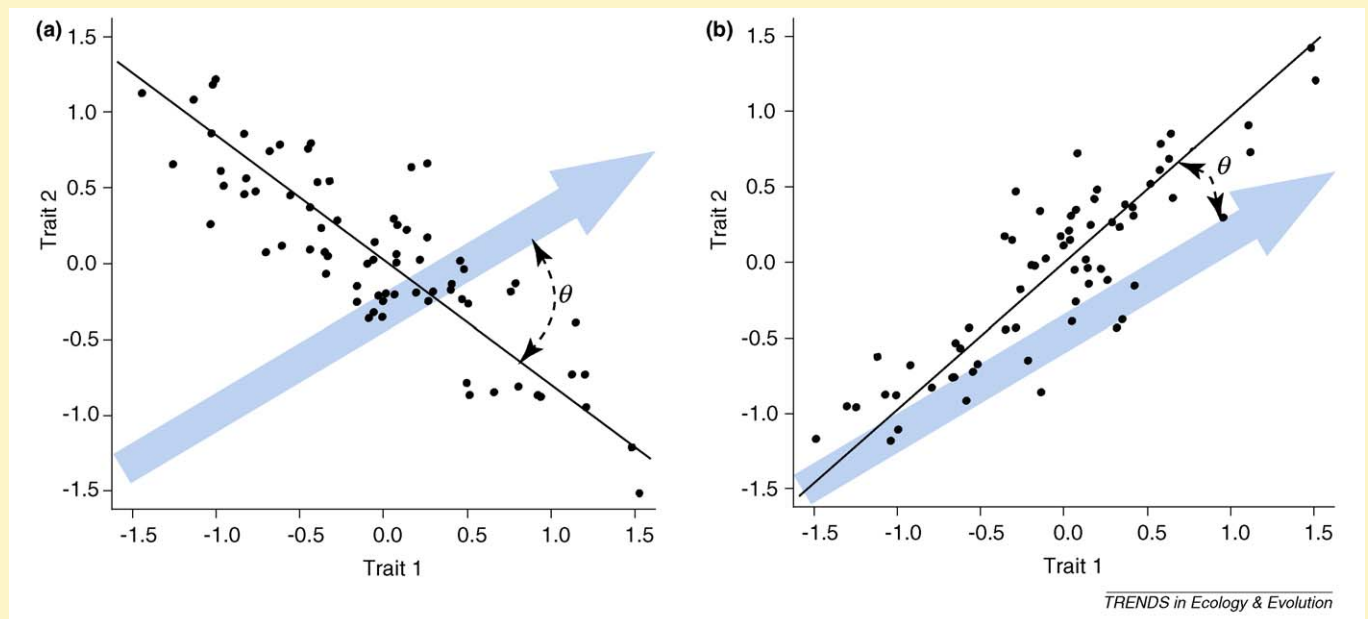


Figure 1. Quality as the vector of selection on a bivariate phenotype.

admit that this will limit empirical applicability. While estimating quality does not require that any assumptions be made about the genetic basis of quality variation, we reiterate that making evolutionary inferences will. If heterogeneity in quality has a purely environmental origin [6] then we expect no evolutionary response since quality will be variable but not heritable. Conversely, if there is genetic variance in the direction defined by the vector of selection (i.e. genetic variance in quality) we would predict an evolutionary response. Importantly, this means that while quality can mask trade-offs as discussed earlier, if it does have a strong genetic basis of variation, then conditioning on quality to test a putative trade-off would remove (rather than reveal) the covariance patterns of primary evolutionary significance.

Interestingly, in a quantitative genetic analysis of big-horn sheep, Coltman *et al.* [61] estimated both phenotypic

and genetic correlations among fitness-related traits and found them universally positive. Eigenvector decomposition of the additive genetic matrix ( $\mathbf{G}$ ) revealed a first principal component consistent with the presence of (genetic) variance for an underlying 'condition' trait on which other aspects of phenotype depend (although subsequent principal components offered some support for antagonistic effects [61]). Rowe and Houle [62] have also made the point that if condition (or quality) is influenced by a large number of loci it will represent a large mutational target that could contribute to the maintenance of genetic variance.

### Conclusions

Individual quality is a concept that can mean different things to different people. Current uses are consistent with each other to the extent that quality is necessarily both

variable and positively correlated with fitness, but beyond this the term has little consistent meaning. We have not argued here that any particular use or definition of quality is correct, and in fact we see no insurmountable difficulties with pluralism of meaning. However, the price for this flexibility is obviously the risk of being misunderstood and this seems particularly likely when drawing evolutionary conclusions about 'quality'. To avoid confusion we suggest there is a need for authors to state more explicitly what they mean by individual quality in any given context.

We have also argued that there are difficulties with an uncritical acceptance of quality differences as a general explanation for the failure to detect trade-offs. Natural selection does not act on single traits alone, but it seems equally unlikely that it will act to optimise trait pairs in isolation from the full (multivariate) phenotype either. Therefore, we certainly should not expect that a trade-off between two life history traits will always be apparent from phenotypic observations: relevant correlated traits and features of the environment will often remain unmeasured [26]. Nevertheless, we should avoid the trap of equating a lack of negative covariance with the necessary existence of an unmeasured, and sometimes unmeasurable, axis of individual quality. Used in this way, 'quality' could become nothing more than a euphemism for unmeasured traits. Unmeasured traits certainly pose challenges for quantitatively estimating evolutionary parameters [63] and one can never know if all relevant traits and covariates have been accounted for [25,31]. Sometimes the best we can manage is to recognise and acknowledge this when interpreting patterns of covariance, although coupling phenotypic observations to experimental manipulations is useful wherever possible [25,64]. Additionally, since trade-offs and reproductive costs are properly measured within-individuals, the use of longitudinal data and statistical methods that disentangle within- from among-individual effects is essential [1,30,65].

In conclusion, we believe differences in intended meaning often prevent clear interpretation of the evolutionary implications of heterogeneity in quality. Our understanding of phenotypic evolution, as encapsulated by quantitative genetics, is based on traits and fitness, the covariance between them (i.e. selection), and the genetic component of that covariance. If we want to use quality in an evolutionary context then it might be useful to define it in a way that can be more readily interpreted within this existing framework for studying heterogeneity. We have shown how this could be achieved if quality is defined from the vector of selection  $\beta$ . It is our belief that integration of ecological and quantitative genetic perspectives would help researchers from both traditions to define this elusive concept in a more rigorous and consistent manner, thus facilitating our wider understanding of the causes and consequences of heterogeneity within ecology and evolution.

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