Review

Defining individual quality over lifetimes and selective contexts

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Individual quality has been measured as a variety of different traits and in several different contexts. However, the implications of such measurements in terms of overall fitness are less straightforward than has generally been appreciated. Here we outline some key issues in this regard that have yet to be addressed. Specifically, we consider the importance of both variation in selection on individual and multivariate suites of traits, and of context-specific plasticity in allocation strategies. We argue that an explicit life-history perspective is crucial for understanding variation in quality, as both the strength and direction of selection and an individual's response to it can vary within a breeding season. Hence, 'quality' is not a static characteristic that can be measured by taking longitudinal measures of single traits across a population, but rather a dynamic, multivariate suite of traits that is dependent not only on the selective context, but also on the nature and intensity of selection operating at any given time. We highlight these points by considering recent research on selection and plasticity.

Keywords: quality; life-history; plasticity; selection; quantitative genetics

1. INTRODUCTION

Variation in reproductive success is the central tenet of sexual selection, and a key principle underlying the entirety of evolutionary theory. Explanation of the factors driving this variation is therefore among the chief goals of ecology and evolutionary biology. Researchers especially seek to identify traits or suites of traits that grant increased fitness to individuals expressing those traits, relative to individuals that do not. Consequently, possession of such traits has frequently been considered to be an indication of individual 'quality' [1]. Understanding the components and correlates of quality has therefore been a priority, and to this end researchers have employed a variety of approaches ranging from manipulative experiments to correlative analyses. Despite this vigorous pursuit of the determinants of quality, progress in this area has been hampered by a lack of consistency in the way that quality has been conceptualized and measured. Most notably, the meaning of 'quality' frequently depends on whether the studies concerned are couched in behavioural, ecological, or evolutionary perspectives [1]. Within an evolutionary and sexual selection framework, for example, genetic quality is considered to be breeding value for total fitness [2]; behavioural studies, however, generally regard quality to be a specific trait or suite of traits that maximizes fitness (or correlates thereof) within a specific context, such as female choice or intrasexual competition [3]; while in ecological studies, quality is considered to comprise traits that maximize lifetime reproductive success [4,5].

The common thread linking all these fields is the use of the phenotype as a metric of quality, both because it is the target of selection and because an individual's phenotype is easily quantifiable relative to its genotype. In a recent review, Wilson & Nussey [1] state that the major problem with this approach is the difficulty in correctly identifying the traits of interest and the associated heritabilities. Moreover, they note that estimations of quality based on single traits may be hampered by trade-offs between those traits of interest and other potentially unmeasured traits, leading them to advocate a multivariate approach to the understanding of quality. While we agree that these are important areas of concern, we argue that the general problem is more insidious. We contend that 'quality' has moved beyond understanding how a suite of traits predict fitness, and is frequently used in place of fitness in situations where genetic contributions to future generations are unknown or difficult to measure (figure 1a). As a result, quality has become a vague surrogate for fitness itself, or a kind of 'potential' fitness (but note that genetic quality is distinct from phenotypic quality and equivalent to fitness [6]). For example, although survival is often considered to be a correlate of fitness [7], survival may be compromised in higher 'quality' males that expend relatively more energy on sexual displays [8]. A secondary problem is that even when phenotype–fitness correlations are correctly established, they are frequently derived from singular contexts and then generally assumed across contexts.

In this review, we critically examine the concept of quality and offer recommendations for its measurement and interpretation. We have three main goals. First, we provide a brief overview of quality and its components,

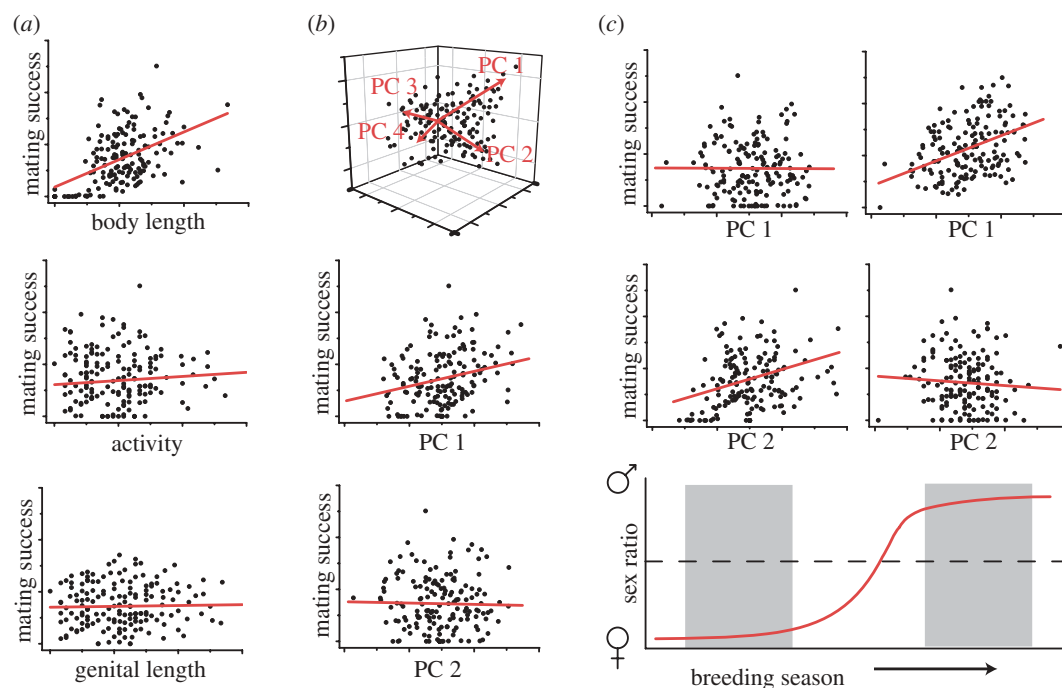* Author for correspondence (slailvaux@gmail.com).

Figure 1. Here we provide a hypothetical example based on a study on water striders (*Aquarius remigis*) by Sih *et al.* [88] using mating success as a measurement of fitness. In this species, males compete for mates and larger size confers increased competitive success and allows males to overcome female resistance. By contrast, females prefer smaller males resulting in opposing selection on male size. Several other species that fit this example can be found in [2]. (*a*) The traditional means by which researchers examine traits associated with fitness is by observing males and females within a particular context; i.e. competition for mates in a controlled setting. Multiple traits are then measured and analysed in a multiple regression with fitness as the dependent variable. This allows for determination of the measured traits that best predict fitness in a single context (male competition). Each slope determines both the relationship between the trait and fitness and the strength of selection on each trait. In this hypothetical waterstrider example, we use three potential traits: genital length, body length, and activity. Here, selection is stronger on body length than it is on activity or genital length. As a result, larger more active males would be considered higher quality. (*b*) Wilson & Nussey's [1] suggested approach would involve measuring as many traits as could be relevant and then placing all the traits in a principal component (PC) analysis. This would yield several uncorrelated axes that explain all the variation in the measured male traits, where the first axis (PC 1) explains the majority of variation in male traits and can be used in analyses to represent an axis of quality. Here, fitness is regressed on PC 1 demonstrating the correlation between the first component of male variation and fitness. Examination of other axes (PC 2) show weaker correlations with fitness if the axis comprises variation in traits that are not associated with fitness in a particular context. (*c*) The correlations between fitness and the two previous axes are examined at two different time frames within the breeding season where the sex ratio differs (highlighted in grey boxes). Early in the breeding season, the sex ratio is female biased resulting in a relaxation of intrasexual competition and a potential increase in female choice. As a result, traits associated with female preference (PC2) are favoured and selected for. By contrast, there is a male bias later in the breeding resulting in increased intrasexual competition favouring traits associated with competition (PC 1).

offering a view that is in some respects complementary to that presented by Wilson & Nussey [1], but which further challenges some of their underlying assumptions. We show that quality is founded on concepts derived from life-history theory, and as such must be interpreted within a life-history framework. Our second goal is to show how traits that appear valuable in one context may be costly in another. Although this has been the focus of several past reviews (e.g. [2,9]), it is especially pertinent to the issue of quality and has received little recognition in this context. In the same vein, we discuss how patterns of genetic correlations among traits may result in different responses to selection in different selective contexts, demonstrating the importance of understanding the underlying genetic variance and covariance among traits. Finally, we examine how individuals adaptively modify their allocation strategies in response to variation in environmental factors other than resource abundance, and discuss how ignoring the

rearing environment can lead to a misunderstanding regarding the traits associated with fitness and potential quality.

2. QUALITY VERSUS FITNESS

Fitness is unambiguously defined as the number of offspring an individual leaves over its lifetime [6,10]. However, given the difficulty in measuring lifetime reproductive success over multiple generations for most species, researchers have tended to adopt a simpler approach that uses a particular suite of phenotypic traits as potential predictors of fitness in a given context. Individuals expressing those traits at relatively higher levels are then considered to be of higher 'quality', and by implication, higher fitness [3]. In the terminology proposed by Wilson & Nussey [1], this conceptualization of quality can be described as 'the axis of phenotypic variation that best explains variance in individual fitness'

(figure 1b). Although this approach appears intuitive and obviates the need to measure fitness directly, it has some important implications which are not widely recognized. The first and perhaps most obvious is that phenotype–fitness correlations must be estimated or otherwise validated in different contexts, rather than simply assumed universally. Furthermore, even if potential fitness can be shown to be a function of one or several phenotypes, some attempt must be made to ascertain the shape of that function, as opposed to assuming it is linear (see [11] for an example using response–surface analysis). Indeed, studies have suggested that the frequency of nonlinear selection (whereby trait values at the upper end of a distribution do not necessarily result in greater fitness than mean trait values; see [12]) has been enormously underestimated within natural systems [13,14]. We argue that understanding the form and intensity of selection operating on traits related to quality is important even if one does not wish to make evolutionary inferences regarding those traits [1], precisely because of the posited close relationship between quality and fitness.

The second implication of the 'potential fitness' approach to quality has to do with life-history and condition dependence. Briefly, individuals vary in their ability to acquire resources in a variable environment. Allocation of those limited resources towards one trait precludes simultaneous allocation towards another, constituting the basis for life-history trade-offs [15]. However, individuals that acquire more resources are thereby able to allocate more energy towards fitness-enhancing phenotypes and tasks without necessarily compromising others [16]. This pool of acquired resources is referred to as condition [17], and traits which are affected by the differential allocation of those resources are considered to be condition-dependent [18]. Individuals that can express fitness-related traits at relatively higher levels compared with conspecifics are therefore considered to be both in better condition, and of better quality. Thus, condition is equated with quality, and hence indirectly with fitness. In addition to the above-mentioned caveats regarding possible or probable nonlinear selection (which may undermine the assumption that higher levels of trait expression equal greater potential fitness), and the fact that the costs associated with trait expression for individuals of differing condition may not be linear [19], the implications of quality as a life-history concept are not always explicitly acknowledged. Indeed, all of the caveats and pitfalls associated with the study of life-history traits apply to quality as well (e.g. [20–23]). For example, resource allocation, and hence trait expression (and especially trade-offs among traits), may often occur over far longer timescales than the average ecological study, a point which has been made at length elsewhere [6,8] but is seldom considered in studies of phenotypic quality. As a condition-dependent trait, quality is also inherently variable, and the sources of variation in quality have received little attention. Indeed, the measurement of condition is itself problematic as it requires an understanding of how the acquired resources are allocated to all metric and life-history traits throughout an individual's lifetime. This has led to development of indices of body-condition that replace the concept of condition [24–26], the ecological and evolutionary validity of which have been

questioned [27,28]. We therefore urge caution in drawing inferences regarding potential fitness from instances of condition dependence without a proper understanding of the relationships between condition and phenotype, and between phenotype and fitness. As a further point, the importance of allocation decisions relative to acquisition limitations are currently under scrutiny (see [29] for discussion). For example, variation in the social environment has also been posited to drive variation in continuous trait expression (e.g. [30,31]) along with other more well-known abiotic and biotic factors (e.g. temperature and predation [32,33]). Understanding other factors that are responsible for variation in trait expression and whether shifts in allocation are as important as acquisition differences in trait expression will provide insight into how traits are associated with quality [23,34].

A third major consequence of equating quality with potential fitness is that when doing so, the relationships between the phenotypes of interest and 'quality' cannot be generalized beyond the selective context within which they were measured. For example, competitive contexts not only fluctuate over an individual's lifetime [29], they also converge such that animals experience selection pressures from multiple contexts simultaneously [35]. This is demonstrated by studies showing variation in phenotype–fitness correlations when a wider range of relevant competitive contexts are examined [36–38], and studies demonstrating that traits associated with success in intrasexual competitions may not be the same traits that are favoured by females (reviewed in [39]; figure 1c). Consequently, it is important to understand how total selection (i.e. the sum of selection episodes) acts on traits [2] and how selection may change over time [40]. This integrative view implies that quality is an inherently dynamic attribute that cannot be easily quantified without understanding the ecology, behaviour and life history of the organism under study.

3. PERFORMANCE AND SELECTIVE CONTEXT
In order to ascertain the direction of total selection on a trait or suite of traits, different selective contexts must be considered. For secondary sexual traits, for example, the most pertinent selective contexts are typically male combat and female choice [3], while studies of non-sexually selected traits may focus on specific contexts, such as escape from predators [41]. However, for many kinds of traits several different selective contexts can be considered to be equally appropriate. To illustrate the disparity in 'quality' between the same traits in different competitive contexts, we consider the role of a whole-organism performance trait (jumping ability) in affecting male combat and female choice outcomes in an insect. We also consider the relationship between life-history traits and condition from a quantitative genetic perspective.

Whole-organism performance (any measure of an organism conducting a dynamic, ecologically relevant task such as locomotion [42]) has featured prominently in discussions of natural and sexual selection owing to the demonstrated links between performance and fitness components (reviewed in [41,43]). Within the context of male combat, performance has repeatedly been shown to influence combat outcomes in a variety of taxa

such that superior performers win fights against relatively poor performers, leading to speculation that performance is an important indicator of male quality [44]. By contrast, evidence for male performance capacities influencing female mating preferences is mixed (e.g. [45–47]). To demonstrate the importance of both competitive context and life history to the determination of male quality, we focus on recent work using the black field cricket, *Teleogryllus commodus*. Staged male–male contests in *T. commodus*, using individuals of known performance ability, showed that males exhibiting superior jumping ability tended to win fights against poorer jumpers, in combination with other factors such as bite force and body size [48]. Indeed, response–surface analysis showed that any selection occurring on jump performance during male contests is likely to be positive and directional. Taken on this evidence alone, jump performance might be considered to be an important facet of overall quality. Within the context of female choice, however, the most important determinant of mating success in this species is male attractiveness (as assessed directly by measurements of female mating preferences). If jump performance were indeed an important contributor to overall quality, then one might expect to find positive links between jumping and attractiveness, as well as jumping and male combat. Studies of genetic relationships among jumping and attractiveness offer no support for this prediction; indeed, when female choice was considered in *T. commodus* within an overall quantitative genetic/life-history framework, strong negative genetic correlations were found between male attractiveness and several measured life-history traits, including jumping ability and lifespan, indicating that males who are preferred by females tend to be poor jumpers with relatively short lifespans [49]. Together, these studies suggest that any selection on jumping ability in male combat situations will tend to be opposed by selection against jumping ability imposed by female mating preferences through this negative genetic correlation.

Within the context of the definition of quality proposed by Wilson & Nussey [1], this study also shows that there is in fact no single axis of among-individual heterogeneity that is positively correlated with fitness. Indeed, Lailvaux *et al.* [49] found statistical support for multiple significant dimensions of genetic variation, each of which is characterized by strong trade-offs among traits. This result strongly implies that individuals of different genotypes employ different resource allocation strategies in order to maximize their own fitness. A single axis of genetic quality (i.e. a specific combination of traits that confers high fitness) is therefore unlikely to exist in *T. commodus*, a finding which calls into question the notion of quality as a scalar abstraction of a multivariate phenotype [1]. It should be noted that the study described here focused on genetic variation, as opposed to the phenotypic variation described by Wilson and Nussey; however, we feel that this is appropriate given that the response to phenotypic selection (and hence, in this case, lifetime reproductive success) is determined in part by the available additive genetic variation [50–52]. Indeed, examination of the phenotypic variation alone is potentially misleading, given that the phenotypic ($\mathbf{P}$) and genotypic ($\mathbf{G}$) variance–covariance matrices are not necessarily equivalent. Although Cheverud [53] made

the controversial conjecture that $\mathbf{P}$ may in some cases be an accurate proxy for $\mathbf{G}$, this concordance is likely to hold only if $\mathbf{P}$ is derived from large samples; consequently, unless $\mathbf{P}$ is estimated from many hundreds of individuals (in some circumstances, arguably as many as would be measured in a moderately sized breeding design), the major axes of phenotypic and genotypic variation may not necessarily always correspond ([53]; see also [54]). Further research into this area using other species and/or trait combinations would be extremely useful in properly evaluating this definition of quality. However, the findings of Hall *et al.* [48] and Lailvaux *et al.* [49] do agree with Wilson and Nussey's [1] assertion that single traits (such as jump performance) are unlikely to act as indicators of, or proxies for, genetic quality, in this case, specifically because their value in terms of fitness may vary depending on the selective context.

4. PHENOTYPE-ENVIRONMENT MATCHING THROUGH ADAPTIVE PLASTICITY

Genetic approaches, such as those described above, have played an important role in understanding phenotypic evolution. However, an individual's phenotype is ultimately a result of interactions between its genotype and the environment it develops in and inhabits, particularly in the case of condition-dependent traits. How the genotype is expressed and whether the resulting variation in condition-dependent traits is a consequence of either adaptive or non-adaptive processes will depend on the role of the environment in the interaction. For example, the expression of condition-dependent traits can be a result of limitations imposed by the environment (e.g. resource availability, stress) on genetically determined allocation strategies. As the traits are not expressed at their optimal trait value owing to these limitations, the reduced trait expression results in a decrease in fitness, suggesting that the shifts in allocation are non-adaptive. By contrast, phenotypes can be a result of shifts in allocation strategies in response to cues that reliably signal future competitive challenges. Such shifts in allocation are considered adaptive because they result in increased fitness as phenotypes are matched to the specific competitive environment (developmental plasticity [33,55]).

Differentiating between the two processes has important implications for whether traits can be used as reliable predictors of fitness, and therefore, whether they can be considered indicators of quality [56]. If the expression of condition-dependent traits is limited by some environmental factor, then variation in trait expression is a consequence of the genotype being susceptible to environmental variation. If females prefer higher trait values, then traits can become indicators of individual 'quality' as they reliably predict fitness (i.e. condition dependence; [18]). By contrast, if genotypes are responding to specific environmental cues resulting in shifts in allocation strategies, then an individual's 'quality' can no longer be determined by the value of particular traits alone as their expression is environment dependent and requires context to be relevant.

Adaptive developmental shifts are common throughout animal taxa [32,33,55,57]. Here we focus on studies of plasticity resulting in continuous phenotypic variation rather than discrete traits (i.e. polyphenisms) to

complement the examples above. The majority of factors known to modify individual allocation strategies occur on large scales, affecting entire populations equally (e.g. predator presence [58]; photoperiod [59]). For example, individuals can allocate resources towards faster development if the breeding season is ending [60], the predation risk is high [61,62], or if resources are diminishing [63,64]. In the same manner, individuals can allocate resources towards the production of traits that minimize predation events if predation risks are high (e.g. [65]). Trait expression is thus dependent upon the relative strength of the different selection pressures an individual will experience.

Differences in the relative strength of selection between populations will result in different phenotypic optima, and thus, different estimates of quality. For example, female mosquitofish (*Gambusia spp.*) generally prefer males with larger gonopodia [66]. Larger gonopodia however, reduce burst swimming speed and become costly under high predation rates [67]. Gonopodium size as a predictor of male quality in *Gambusia* thus depends on the relative intensity of natural (predation) and sexual (female choice) selection. In such examples, inter-population differences in the relative strength of selection pressures will prohibit inter-population comparisons of quality owing to different phenotype–fitness correlations. However, if environments vary at a large enough scale to encompass an entire population, individuals within the same population experience the same diverse selection pressures, and phenotype–fitness correlations should exist for each specific competitive context. As long as the context is known and explicitly stated, traits may still be reliable predictors of future fitness and indicators of quality in particular contexts.

Environments, however, are not limited to large-scale variation and factors can vary in the social environment on much smaller temporal and spatial scales. For example, the social environment can vary as a function of variation in sex differences in maturity rates [68], immigration/emigration rates [69], time of arrival to breeding grounds [70], predation rates [71] and differences in mating optima between the sexes [72]. As the strength and direction of sexual selection is dependent upon the operational sex ratio and population density [73,74], the selective environment experienced by individuals within a population will differ throughout the breeding season (e.g. [75–77]). Because phenotype–fitness correlations are strongly dependent upon the social context [37,78], individuals that shift their ontogeny to match the competitive context they are most likely to encounter should have increased fitness [79].

Although relatively less examined, several studies have demonstrated shifts in allocation in response to acoustic, pheromonal, tactile and visual cues of the social environment that signal the intensity of sexual selection. Studies of socially induced developmental plasticity show that individuals respond to the social environment and alter their resource allocation towards size and weight [80,81], developmental rate [30,31], sperm number [82,83] and body condition [30,84]—continuous traits that are often used as predictors of fitness. Individuals generally allocate more resources towards traits that increase competitive success such as growth and sperm when competition is likely to be more intense, but

sacrifice these traits to mature more quickly when competition is lessened [30,31,80]. Such shifts allow immature individuals to capitalize on the social environment by either developing traits that best match the adult competitive context they are most likely to encounter or by maturing at a more appropriate time. Although most commonly seen in invertebrates where individuals only experience a portion of the entire breeding season [30,80,82], examples also occur in relatively longer-lived vertebrates [31,81]. These studies suggest that using traits as assays of quality without knowing the juvenile context and instead using population-wide averages of contexts will result in an overestimate of the importance of a phenotype in phenotype–fitness correlations and a misunderstanding of the traits that affect fitness. Small-scale environmental variation, such as variation in the social environment, makes identifying quality significantly more difficult since trait expression is context-dependent, and it is the context that needs to be determined before trait quality can be established. Furthermore, environmentally imposed adaptive developmental shifts can secondarily feed back to generate further shifts in selection [29,85], making contexts more difficult to deduce.

If adaptive shifts in allocation strategies allow individuals to increase their fitness in a variable environment [32,33,55,57], the developmental system leading to trait expression may then play an important role in determining quality. Under such a scenario, females may not be selecting mates based on a specific suite of traits, but may be mating with males that allocate resources to those life-history traits that match the competitive environment, allowing them to subvert rivals. Thus, 'quality' could just as easily be considered the ability to read the environment and develop the phenotype that best matches the context. In other words, individual reaction norms themselves may be under selection and can be critical to fitness [55,86,87].

5. CONCLUSION

The concept of male quality is relevant to many different areas of ecology and evolution, and consequently has been considered from as many different perspectives. However, it is most commonly used to imply the potential for future fitness. Our intention in this article is to clarify the conditions and criteria required for a trait or group of traits to capture some aspect of true quality (i.e. component or clear determinant of overall lifetime reproductive success). Picking up on the points made by Wilson & Nussey [1] that quality is likely to be a multi-variate phenomenon, we have illustrated the importance of considering both the selective context and plasticity in determining a trait's true value in terms of breeding value for total fitness. We argue that estimations of quality should incorporate the environmental and selective context in which traits are measured, and must be conducted over an appropriate timescale in order to capture important potential shifts in resource allocation. Indeed, the study of quality within a variety of social, environmental and selective milieu and over individual life-histories is likely to be a fruitful area of future research. Simply increasing the number of traits in the analysis as suggested by Wilson & Nussey [1] will not

improve our understanding of the traits associated with overall quality, as correlations between phenotypes shift depending on context-specific allocation patterns and adding traits does not clarify contexts. The quantitative models comparing phenotypic variance/covariance matrices within lifetimes as suggested by Wilson & Nussey [1] are an excellent start, but the validity of such models will depend on our understanding of varying contexts within individual lifetimes both within and between populations.

Given that the proper usage and measurement of individual quality requires numerous caveats and assumptions, as we have shown, we suggest that researchers in this field adhere as far as possible to recommendations put forward by Hunt *et al.* [6] and approach the estimation of fitness from the perspective of genetic quality wherever feasible. The use of this term is advantageous in that it has an explicit and specific definition, namely the breeding value for total fitness [6]. However, we recognize that even an estimate of total fitness may be difficult or otherwise impossible to obtain for many species. In these cases, we urge researchers to bear in mind the limitations of inferring fitness from phenotypic measurements, and to interpret any such inferences within the appropriate life history and selective contexts.

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