

Exploring individual quality in a wild population of red deer

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Summary

1. A wide range of measures are used to quantify ‘individual quality’, with the term often used but not defined.
2. Here we use detailed data from a population of red deer (*Cervus elaphus*) to assess whether frequently used measures of individual quality are well correlated, and therefore likely to lead to comparable ecological and evolutionary insight in analyses.
3. Correlations between measures were usually small, indicating that individuals may be considered high quality for one trait, but low quality for another.
4. By using principal component analysis, we illustrate that there are potentially many varied individual life-history tactics within a population.
5. This variation in tactics makes it challenging to characterize individual quality as a simple scalar; measures of heterogeneity in ecological studies should therefore be both species and question specific.

Key-words: fitness, individual heterogeneity, phenotypic variation, trade-offs

Introduction

According to the principle of resource allocation (Levins, 1968; Van Noordwijk & Dejong, 1986; Stearns, 1989), animals have to allocate limited energy to different activities, for example, survival and reproduction (Viallefont, Cooch & Cooke, 1995). Trade-offs are therefore expected between life-history traits (Stearns, 1989). However, positive correlations are often found where negative correlations are expected (Clutton-Brock, 1985; Van Noordwijk & Dejong, 1986; Yoccoz *et al.*, 2002; Moyes *et al.*, 2006). These correlations are explained by biologists with the argument that the amount of energy available to individuals varies substantially (Van Noordwijk & Dejong, 1986). As a result, we only expect trade-offs to be apparent when comparing individuals of similar energetic acquisition levels.

Because of the effects of variation in energy acquisition levels, it is necessary to correct for individual differences in order to investigate trade-offs (Cam & Monnat, 2000). The heterogeneity in performance in various life-history traits between individuals is generally referred to as ‘quality’.

Individual quality is assumed to be closely related to individual fitness. High-quality individuals are therefore expected to have higher fitness. Variation between individual quality and individual fitness may be greatest in harsh environments; in more favourable environments, it is possible that there is sufficient energy for all individuals to survive and reproduce successfully (Lomnicki, 1978; Leung & Forbes, 1997).

Quality is often referred to in ecological studies, but its measurement varies greatly across studies (Table 1). It can be regarded as a variable that continuously changes throughout life (such as annual body condition, annual reproductive success or body weight), or as a measure that is constant throughout life, such as frailty (Vaupel, Manton & Stallard, 1979; Link, Cooch & Cam, 2002; Table 1). Measures of quality that change with time within an individual can be used to provide insight into temporal variation in individual survival or reproduction probabilities in a given year, sometimes as a function of phenotypic traits (Link *et al.*, 2002). In contrast, a lifetime measure defines individual quality regardless of reproductive effort in a given year or environmental conditions.

There is currently no widely accepted method of measuring quality between studies or species. Various quantities have been used including morphological, behavioural and demographic

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Table 1. Measures used to describe individual quality. 'lme' indicates that the measure was used to estimate individual frailty measures from mixed effects models with individual as a random effect. 'v' indicates the example is variable and 'c' indicates a constant measure

Quality trait	Examples	Species	
Timing of reproduction	Arrival at breeding ground (c)	Pied flycatcher (<i>Ficedula hypoleuca</i>)	(Siitari & Huhta, 2002)
		Merlin (<i>Falco columbarius</i>)	(Espie <i>et al.</i> , 2004)
	Hatching date (c)	Leach's storm petrel (<i>Oceanodroma leucorhoa</i>)	(Blackmer <i>et al.</i> , 2005)
		Kentish plover (<i>Charadrius alexandrinus</i>)	(Amat, 2005)
	Laying date (c)	Tree swallow (<i>Tachycineta bicolor</i>)	(Ardia, 2005; Bowlin & Winkler, 2004)
		Common guillemot (<i>Uria aalge</i>)	(Lewis <i>et al.</i> , 2006)
	Laying date (lme) (v)	Common pochard (<i>Aythya ferina</i>)	(Blums <i>et al.</i> , 2005)
		Northern shoveler (<i>Anas clypeata</i>)	
		Tufted duck (<i>Aythya fuligula</i>)	
		Leach's storm petrel	(Blackmer <i>et al.</i> , 2005)
Reproductive effort	Lifetime reproductive success (c)	Red deer	(Moyes <i>et al.</i> , 2006)
	Proportional age-specific reproductive effort (v)	Common guillemot	(Lewis <i>et al.</i> , 2006)
	Chicks raised previously and number of previous breeding attempts (lme) (v)		
Maternal investment	Brood size (v)	Merlin	(Espie <i>et al.</i> , 2004)
		Common eider (<i>Somateria mollissima</i>)	(Hanssen, Folstad & Erikstad, 2006)
	Egg volume (v)	Leach's storm petrel	(Blackmer <i>et al.</i> , 2005)
		Kentish plover	(Amat, 2005)
Egg volume (lme) (c)	Oystercatcher (<i>Haematopus ostralegus</i>)	(van de Pol & Verhulst, 2006)	
Longevity	Survival (c)	Merlin	(Espie <i>et al.</i> , 2004)
	Juvenile body weight (c)	Roe deer (<i>Capreolus capreolus</i>)	(Pettorelli <i>et al.</i> , 2001)
	Age at maturity (c)	Mountain goats (<i>Oreamnos americanus</i>)	(Cote & Festa-Bianchet, 2001)
Parental ability Condition	Provisioning of young (v)	Blackbirds (<i>Turdus merula</i>)	(Preault <i>et al.</i> , 2005)
		American red squirrels (<i>Tamiasciurus hudsonicus</i>)	(Steury & Murray, 2003)
		Kentish plover	(Amat, 2005)
	Mass and wing index (v)	Common pochard Northern shoveler Tufted duck	(Blums <i>et al.</i> , 2005)
		Condition index (v)	<i>Microtus voles</i> (<i>M. agrestis</i> and <i>M. rossiaemeridionalis</i>)

factors (Table 1). Frequently reported positive correlations between life-history traits may not always relate to variation in quality between individuals. There is always more than one trade-off an individual can make when allocating resources; for example, individuals with high survival and reproductive probabilities could be 'lower quality' in terms of other traits: they could potentially produce late-born calves with low birth weight and reduced survival (Stearns, 1976). In this case, different quality measures would assign the same individual to different quality classes. If a measure of 'quality' is to be used in an ecological study, it is essential to ensure that a reliable estimator, specific to a study population, is used in order to account for the heterogeneity in individual quality when evaluating trade-offs between life-history traits.

In this paper, we assess whether the range of measures commonly used to account for phenotypic quality relate to

one another. A variety of different measures of quality are compared using data from a population of red deer (*Cervus elaphus*) on the Isle of Rum, Scotland (Clutton-Brock, Guinness & Albon, 1982). Red deer are ideal for researching these quality measures, as life histories vary widely between individuals; reproductive skipping is common and there is considerable variation in individual lifetime performance. The data set provides detailed accurate information on the life history of individuals. Eleven quality measures are used; correlations between each of the variables are estimated, and a multivariate statistical technique is used to elucidate patterns between these variables. We show that several of the principal components have clear interpretations in terms of different life-history tactics within the population and this variation in life-history tactics indicates that it is difficult to characterize individual quality as a simple scalar.

Methods

The red deer population on the Isle of Rum was used in these analyses because not only is the study incredibly detailed, with complete life-history information for most individuals in the study area, but also deer are long-lived and despite being iteroparous, individual life histories do vary and reproductive skipping is common (for more information on the study see Clutton-Brock *et al.*, 1982).

QUALITY MEASURES

Measures previously used to quantify quality in either red deer or other species were identified (see Table 1 for a list of measures and where they have been used). Quality measures that had been identified in previous studies were estimated for females with known dates of birth and death as described in detail below. Males were not included in the analysis as they spend a large proportion of their life outside the study area. An annual cull occurs on Rum outside the study area. As the island is unfenced, a few study females are shot each year as a result of them moving outside the area. These females were removed from this analysis (95 females removed from a sample of 456). Culling, as far as we are aware, does not select for individuals of a specific trait and therefore should not lead to bias in terms of individual quality. Only females that survived to at least age 3 were included in the analysis, because at 3 years individuals are able to reproduce and their survival is no longer dependent on current provisioning from their mother. All statistical analyses, including linear mixed effects models, linear regressions and multivariate methods were performed in R (R Development Core Team, 2008). The following quality measures were considered:

1. Longevity (LON), longevity was calculated as the age at death.
2. Lifetime breeding success (LBS), estimated as the total number of calves of the focal female, regardless of calf survival.
3. Lifetime reproductive success (LRS), the total number of offspring the focal female has successfully raised to one year of age. Individuals with one or more calves that had been shot were not included in this measure.
4. Lifetime individual contribution to population growth [$LP_{(i)}$], $P_{(i)}$ estimates a female's contribution to population growth over a time-step (Coulson *et al.*, 2006), and is an individual's annual realized fitness. These annual quantities are summed over the lifespan of the individual. The calculation for $P_{(i)}$ is:

$$P_{(i)} = \frac{S_{(i)} - \bar{S}_t}{N_t - 1} + \frac{f_{(i)} - \bar{f}_t}{N_t - 1}$$

where $S_{(i)}$ is the survival for a given individual i in time t (either 1 if they survive or 0 otherwise); \bar{S}_t is the mean survival at time t ; $f_{(i)}$ is the fecundity for a given individual i at time t ; \bar{f}_t is mean fecundity at time t ; and N_t is the population size at time t . Only females were included in the calculation of N_t . The lifetime contribution to population growth [$LP_{(i)}$] of each individual was defined as the sum of the individual's annual values.

5. Lifetime proportional age-specific reproductive effort (LPARE), PARE gives an indication of the reproductive effort of a female regardless of age at death and lifetime PARE is estimated as:

$$LPARE = \frac{\text{total number of calves}}{\text{age at death} - 2(\text{for years as immature})}$$

6. Residual birth weight (BW), as the time at which newly born calves are weighed varies, residual birth weight is estimated by linearly

regressing weight at capture against time of weighing in hours and subtracting the predicted value given the age at weighing from the capture weight (Catchpole *et al.*, 2004; Nussey *et al.*, 2005). The regression equation used in this analysis is:

$$BW = \text{capture weight (kg)} - [6.486 + 0.0154 \times \text{age at capture (hours)}]$$

7. Year-adjusted calf birth date (CBD), birth date (ordinal date) of the focal individual's calves is used to obtain a measure of quality for the mother. Frailty models have previously been used to account for differences in survival probability, by assuming that individuals differ in their frailty (Vaupel *et al.*, 1979). More recently, similar methods have been used to account for heterogeneity in reproduction and survival probabilities with age between individual kittiwakes (*Rissa tridactyla*) (Cam *et al.*, 2002), and also heterogeneity in the timing of egg production, corrected for age, between individual oystercatchers (van de Pol & Verhulst, 2006). Here we estimate these frailty measures by using individual identity as an additive random term on the intercept of a model of calf birth date (transformed on the log scale) regressed on year as a factor in a linear mixed effects model to obtain best linear unbiased predictions (BLUP; see Robinson, 1991) for each female. These BLUPs are used as a measure of frailty of the mother because consistently producing late-born calves may indicate maternal frailty, and are reported on the log scale.

8. Year-adjusted calf birth weight (CBW), frailty measures were estimated for each individual by using individual identity as an additive random term on the intercept of a model of calf residual birth weight (calculated using the same method as the focal individual's birth weight) regressed against year as a factor in a linear mixed effects model to obtain a BLUP for each female. These BLUPs are used as a measure of frailty of the mother because consistently producing small calves may indicate maternal frailty.

9. Year-adjusted calf survival (CS), frailty measures were estimated for each individual by using individual identity as an additive random term on the intercept of a model on a quasibinomial scale to compensate for overdispersion on a binomial scale (see Crawley, 2002 for further explanation of the quasibinomial scale) for calf survival against year as a factor. Generalized linear mixed models with penalized quasi-likelihood (glmmPQL from the MASS library in R Venables & Ripley, 2002) were used to obtain a BLUP for each female. These BLUPs are used as a measure of frailty of the mother, because consistently producing calves with low survival may indicate maternal frailty, and are reported on the logit scale.

10. Number of male calves (MC), producing male calves requires a greater relative investment than producing female calves in red deer (male calves have higher birth weight), and is also positively associated with dominance between hinds (Clutton-Brock, Albon & Guinness, 1986). The total number of male calves produced by the focal individual was therefore used.

11. Age of primiparity (AP), beginning to reproduce early in life can be costly (Clutton-Brock, Guinness & Albon, 1983; Tavecchia *et al.*, 2005). In red deer, most females reproduce for the first time between 3 and 6 years old, although some do delay reproduction further. The age at primiparity was taken for all females that bred.

COMPARING MEASURES OF INDIVIDUAL QUALITY

The Pearson's product-moment correlations between these measures were calculated. Principal component analysis (PCA) was used to identify patterns in the data. PCA is commonly used with multivariate data to reduce the number of variables without appreciably losing

Table 2. Correlation matrix of quality measures calculated using Pearson's product moment correlation (*represents statistical significance to 0.05). *N* is given below each correlation

LON	1											
	361											
LRS	0.63*	1										
	361	361										
LBS	0.88*	0.70*	1									
	361	361	361									
$LP_{(i)}$	0.44*	0.71*	0.53*	1								
	264	264	264	264								
BW	0.08	0.17*	0.12	0.14	1							
	210	210	210	189	210							
LPARE	0.24*	0.36*	0.57*	0.18*	0.07	1						
	361	361	361	264	210	361						
CBD	-0.08	-0.08	-0.11	-0.09	0.02	-0.09	1					
	295	295	295	217	189	295	295					
CBW	0.07	0.23*	0.10	0.34*	0.26*	0.07	-0.01	1				
	295	295	295	217	189	295	295	295				
CS	0.00*	0.41*	-0.03	0.59*	0.01	-0.05	-0.12*	0.33*	1			
	288	288	288	210	184	288	288	288	288			
AP	0.13*	-0.14*	-0.19*	-0.31*	-0.12	-0.56*	0.03	-0.15*	-0.08	1		
	344	344	344	248	201	344	295	295	288	344		
MC	0.69*	0.54*	0.80*	0.45*	0.10	0.46*	-0.13*	0.10	-0.03	-0.19*	1	
	361	361	361	264	210	361	295	295	288	344	361	
	LON	LRS	LBS	$LP_{(i)}$	BW	LPARE	CBD	CBW	CS	AP	MC	

information. This is achieved by finding a smaller number of uncorrelated indices (principal components) as linear combinations of the variables (Manly, 1986, p. 75; ter Braak, 1983). As the quality measures are on different scales, the analysis was based on the correlation matrix rather than the covariance matrix to prevent the scale of variables biasing the eigenvalues (Jolliffe, 2002). As deer are iteroparous, lifetime breeding success is strongly correlated with, and likely to be strongly dependent on, longevity. Similarly, $LP_{(i)}$ is very strongly dependent on both longevity and LRS. Therefore, as it is unnecessary to include parameters dependent on the same trait and in order to simplify the analysis, $LP_{(i)}$ and LBS were not included in the PCA.

Results

The variation within measures of quality was first explored by plotting frequency histograms along with the mean and the sample size (Fig. S1). The residual measures appear to be approximately normally distributed, as expected. Life-history measures such as longevity, LRS and LBS are not normally distributed. LBS, MC and $LP_{(i)}$ show similar distributions to longevity whereas LRS is heavily skewed to the right. Age at primiparity is most commonly at age 4; this distribution is leptokurtic and skewed to the right.

The correlation matrix (Table 2) shows that many of the highly correlated variables are strongly related to longevity, for example, LBS, MC, $LP_{(i)}$ and LRS. In contrast, correlations between variables not dependent on the age at death are relatively low. Calf birth weight and calf survival show some correlation, but perhaps not as much as would be expected given the effect of residual birth weight on calf survival (Clutton-Brock *et al.*, 1982; Catchpole *et al.*, 2004). LPARE is slightly correlated with the measures which are dependent

on longevity, despite not being directly dependent on age itself. This is not entirely surprising given that LPARE has previously been found to positively correlate with survival in older individuals (Moyes *et al.*, 2006). Given the positive correlation with survival, the correlation with longevity would perhaps be expected to be more pronounced.

PRINCIPAL COMPONENT ANALYSIS

Principal component analysis identified different dimensions of the data; the first component in the PCA, and therefore the projection with the greatest variance, relates to the positive correlations between quality measures (Table 3; Fig. S3). This first component includes all measures and all coefficients are greater than 0.15 in absolute value. The loadings of the measures related to longevity are greater than those of the other measures in this component. Therefore, despite this component appearing to relate to the positive correlations in the quality measures, this is largely focused on the contrast between the longevity-related measures. In this component, high longevity is associated with more calves, high birth weight, high calf birth weight and survival, earlier calf birth date, earlier primiparity, more male calves and high LPARE. This component accounts for 30.9% of the total variance for these variables (Table 4), indicating that a high proportion of the variance between these measures is not related to correlations as a result of what is commonly perceived to indicate individual quality. Components 2 to 5 explain a similar amount of variance to each other (Table 4), but focus on quite different aspects of the variance in the data. After the principal component scores were plotted against each other (Fig. S2), there appeared to be two outliers on the third principal component. These two

Table 3. Loadings of each component from the principal component analysis (PCA) of the potential quality measures. Fig. S3 represents the coordinates of the variables according to axis 1 and 2 of the PCA

Variable	1	2	3	4	5	6	7	8	9
LON	-0.422	0.146	0.540	0.035	0.011	0.121	0.128	0.202	0.660
LRS	-0.481	-0.209	0.182	-0.092	-0.140	0.352	-0.341	0.389	-0.521
BW	-0.171	-0.182	-0.199	0.663	0.528	0.385	0.002	-0.172	0.033
LPARE	-0.347	0.372	-0.434	0.014	-0.165	-0.109	-0.639	-0.198	0.257
CBD	0.161	0.007	0.136	0.616	-0.750	0.083	0.029	-0.073	-0.028
CBW	-0.281	-0.483	-0.080	0.250	0.019	-0.749	0.000	0.235	0.045
CS	-0.173	-0.641	-0.087	-0.322	-0.254	0.222	0.057	-0.526	0.233
AP	0.323	-0.158	0.587	0.060	0.213	-0.148	-0.611	-0.286	-0.012
MC	-0.448	0.308	0.265	0.035	0.037	-0.248	0.286	-0.565	-0.410

Table 4. Importance of components in PCA, including the variance and the proportion of variance explained by each component

Component	1	2	3	4	5	6	7	8	9
Variance	2.785	1.467	1.259	1.088	0.863	0.609	0.413	0.344	0.172
Proportion of variance	0.309	0.163	0.140	0.121	0.096	0.068	0.046	0.038	0.019
Cumulative proportion	0.309	0.472	0.612	0.733	0.829	0.897	0.943	0.981	1.000

individuals were both reasonably long-lived (11 and 18 years) with very late first age of primiparity (both aged 7). Removing these two individuals from the analysis did not result in differences in either the variance explained by each component or the interpretation of each component.

Generally with principal component analysis, as the objective is usually to reduce the number of parameters needed to explain the variance in the data set, the number of components that are required to explain adequately this variance needs to be considered (Jolliffe, 2002). However, in this case we are interested in examining the different dimensions of the data that the components identify in order to elucidate different life-history tactics in the population. For example, component 2 contrasts those individuals that reproduce frequently but have calves with low survival and low birth weight with those individuals that produce a small number of calves with high survival and high birth weight. Component 3 contrasts the long-lived, infrequently reproducing individuals with late primiparity, with the short-lived frequently reproducing individuals with early primiparity (Table 3). Components 4 to 9 explain less than 40% of the variance in total (Table 4) but do appear to elucidate further life-history tactics (Table 3).

Discussion

Some individuals perform consistently well on all quality measures and some consistently perform poorly, as identified by the first component in the PCA. This component therefore represents the typical good–poor quality projection. This is what would be hoped given that these measures are frequently used to indicate heterogeneity in individual quality. However, this component accounts for less than a third of the total

variance, and although all quality measures are included in the component, due to red deer being iteroparous the measures with most weight are those which are strongly dependent on longevity. This is supported by correlations between the variables; the correlations in general are very low, except between longevity-related traits. If quality in individuals was consistent across all traits, correlations would be expected to be high. These results indicate that different measures of quality can result in quite different predictions of quality for the same individual. It is interesting that we are able to interpret these components in terms of different credible tactics. We speculate that similar interpretations might arise from corresponding analyses of data on different species.

This variation in performance between quality measures within individual indicates that individuals vary in the trade-offs that they make by allocating energy to different traits. The second component contrasts the trade-off between frequent reproduction and investment in each offspring, and the third component contrasts the trade-off between longevity and reproduction. The fourth component in the PCA contrasts the trade-off between weight and offspring survival. Heavy individuals are considered to be high quality and the correlation between mother and calf birth weight is high. However, this may result in increased energy expenditure for somatic maintenance for the focal individual and for the growth of the calf (heavy individuals were also associated with late birth dates). Heavier individuals therefore encounter different trade-offs compared with lighter individuals, as they need to allocate a higher proportion of energy available to somatic maintenance. These results potentially indicate heterogeneity in the allocation of resources between individuals dependent on their relative phenotypic quality in different quality-related traits.

Individual quality is closely related to fitness. Fitness of an individual is defined as the propensity of its genes to be present in future generations (Fisher, 1930); high-quality individuals would therefore be assumed to have high fitness. If the sole aim of all individuals is to maximize their genetic contribution in future generations and therefore increase their fitness, it is surprising how variable the life-history tactics appear to be in a population. The correlation between individual quality measures and fitness is expected to vary with environmental harshness (Leung & Forbes, 1997; Lomnicki, 1978); therefore, comparing indices of quality may vary between good and poor environmental conditions. Resource allocation theory predicts negative correlations between life-history traits due to fixed available resources in terms of time, energy and nutrients (Partridge, 1987; Stearns, 1989; Van Noordwijk & Dejong, 1986). Positive correlations between life-history traits are therefore explained by variation in the amount of these fixed resources and the ability to acquire and utilize these resources effectively (Van Noordwijk & Dejong, 1986). Individual variation can result from differences in genotype, maternal investment (Gendreau, Cote & Festa-Bianchet, 2005; Holand *et al.*, 2006) or temporal and spatial heterogeneity in habitat and resources (Coulson *et al.*, 1997; Pettorelli *et al.*, 2003). It is therefore expected that individuals would vary in their relative ability to acquire or utilize the resources and their relative need for time, energy or nutrients (Stopher *et al.*, 2008). The presence of this variation would explain why individuals of the same species can adopt very different life-history tactics even if some measures of quality are of a very similar magnitude. The variation in the relative ability to acquire or utilize resources would be expected to be present between individuals of species other than red deer and therefore measuring quality would be expected to be problematic in most species.

It is common to include quality measures in life-history analyses in order to explain individual heterogeneity (Blums *et al.*, 2005; e.g. Viallefont *et al.*, 1995; e.g. Beauplet *et al.*, 2006). However, from these analyses it is evident that there is high intra-individual variation between quality measures. This is potentially due to different tactics that different individuals follow. For example, the finding of a positive correlation between lifetime age-specific reproductive effort and survival (Moyes *et al.*, 2006) could be due to frequently reproducing individuals being of higher quality and therefore also having higher survival, or due to frequently reproducing individuals investing relatively little in their offspring and therefore being able to allocate resources to somatic maintenance, or more likely the result is due to a combination of these two tactics and probably others. In addition, a trait may be advantageous in one situation but a hindrance in another situation. For example, larger females may be able to gain better access to higher-quality vegetation and to allocate increased resources to their offspring, but when the available vegetation is reduced, they may suffer more than a smaller female due to requiring a higher energetic intake for somatic maintenance. Including measures of quality in life-history models is essential for understanding trade-offs, but due to the complexity and

variability in these tactics, selection of appropriate measures to correct for quality and interpretation of the results can be difficult.

The lack of correlation between many of the measures commonly used to assess quality and the variability of life-history tactics can therefore lead to problems in trying to correct for quality when attempting to identify trade-offs between life-history traits. It is not appropriate to assume that one trait is related to individual quality, whereas instead it simply reflects an aspect of one of the many alternative life-history tactics. One alternative to attempting to correct for heterogeneity by using a known trait is to use random effects on the individual level. This then creates 'frailty' estimates for each individual (Vaupel *et al.*, 1979). This does serve to account for heterogeneity related to the particular trade-off or trait in question, but does not provide further information on the source of this variation or of the overall quality of an individual. For example, as in this analysis, frailty indices estimated from different traits do not correlate between individuals. When attempting to identify trade-offs, it is therefore necessary either to use a specific trait which explains a high proportion of the variance in the response to the trade-off or to use mixed-effects models to gain frailty estimates on the individual level and therefore a general response to the trade-off. The decision to use either frailty indices or a specific trait in an analysis should be appropriate to both the question and to the population.

There are alternative measures of quality, not included in these analyses, such as annual body weight, annual condition and dominance status. It is possible that these variables could provide a more reliable measure of quality. However, given that the correlation between the quality measures considered here in general are very low, further measures of quality would provide further information on life-history tactics and trade-offs of individuals with particular traits, but would still not provide consistent measures of quality. As the measures used in this analysis do not strongly correlate, it is very difficult to decide which of these measures or any alternative measures accurately capture variation in individual quality.

These analyses emphasize the complexity and variability of life-history tactics. Phenotypic heterogeneity is often regarded as variation in individual quality and is quantified using various demographic, behavioural and physiological measures. Many different measures are commonly used to estimate phenotypic quality and it would be assumed that these different measures are strongly related. However in this paper, it is shown that many of these measures do not strongly correlate, indicating the diversity of life-history tactics and trade-offs between individuals.

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Supporting information

Additional supporting information may be found in the online version of this article:

Fig. S1. Histograms for the quality measures, showing the sample size and means of each measure. The mean is not shown for CBD, CBW and CS as these are residuals and so the mean is approximately 0.

Fig. S2. Figures illustrating each component of the PCA relative to one another.

Fig. S3. Coordinates of variables according to component 1 and 2 of the PCA.

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