

Estimating individual contributions to population growth: evolutionary fitness in ecological time

T. Coulson^{1,*}, T. G. Benton², P. Lundberg³, S. R. X. Dall⁴,
B. E. Kendall⁵ and J.-M. Gaillard⁶

¹*Division of Biology and Centre for Population Biology, Faculty of Life Sciences, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, UK*

²*School of Biology, University of Leeds, Leeds LS2 9JT, UK*

³*Department of Theoretical Ecology, Ecology Building, Lund University, 223 62 Lund, Sweden*

⁴*Centre for Ecology and Conservation, University of Exeter in Cornwall, Tremough Campus, Penryn TR10 9EZ, UK*

⁵*Donald Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106-5131, USA*

⁶*UMR 5558, "Biometrie et Biologie Evolutive" UCB Lyon 1, 43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France*

Ecological and evolutionary change is generated by variation in individual performance. Biologists have consequently long been interested in decomposing change measured at the population level into contributions from individuals, the traits they express and the alleles they carry. We present a novel method of estimating individual contributions to population growth and changes in distributions of quantitative traits and alleles. An individual's contribution to population growth is an individual's realized annual fitness. We demonstrate how the quantities we develop can be used to address a range of empirical questions, and provide an application to a detailed dataset of Soay sheep. The approach provides results that are consistent with those obtained using lifetime estimates of individual performance, yet is substantially more powerful as it allows lifetime performance to be decomposed into annual survival and fecundity contributions.

Keywords: de-lifing; selection; fitness; cohort effects; demography

You've been given a great gift, George. A chance to see what the world would be like without you—Clarence (Henry Travers) in the 1946 film 'It's a Wonderful Life'.

1. INTRODUCTION

Most theory about evolutionary change is concerned with understanding changes in allele, strategy and heritable trait distributions (Fisher 1930; Falconer 1960; Lewontin 1974; Lande 1982; Maynard-Smith 1982). A commonly used approach is to assess the performance of alleles, strategies or traits by estimating their fitness. This approach defines fitness as the expected representation of a replicating entity within a population at some distant point in the future (Hamilton 1964; Dawkins 1982; Metz *et al.* 1992; Benton & Grant 2000; Shertzer & Ellner 2002). Fitness is, therefore, theoretically considered as a long-term measure of relative performance (Fisher 1930; Lande 1982; Charlesworth 1994). Many empirical tests of evolutionary theory, including estimates of selection and responses to selection, use generation-based proxies for

fitness to characterize performance. The fitness of alleles, traits or strategies is typically estimated by measuring the lifetime performance of the individual in which they occur: lifetime reproductive success (LRS: the number of offspring produced over the lifespan) is one such measure (Clutton-Brock 1988). Another reason that per generation fitness measures are favoured is that in most formal evolutionary biology they permit selection to be distinguished from the response to selection (Fisher 1930; Arnold & Wade 1984). Longer term estimators of fitness confound heritability and selection; however, estimators of fitness measures on time scales shorter than the generation do not.

The per-generation based approach has proven illuminating; however, there are empirical issues in using these metrics to estimate selection and evolutionary change in the field, including: (i) difficulties in collecting sufficient data to satisfy the long-term assumptions of most theoretical models (Grafen 1988), (ii) substantial variation in generation times between cohorts and individuals in iteroparous species (Kruuk *et al.* 1999) and (iii) a failure to correct for environmental and ecological variation during the lifespan that may influence the performance of an individual in a specific genotypic or phenotypic state in a year (Coulson *et al.* 2003). These problems have hampered attempts to reconcile predicted and observed micro-evolutionary change in the wild using theory-derived measures (Merila *et al.* 2001b). The motivation

* Author for correspondence (t.coulson@imperial.ac.uk).

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behind the work developed in this paper is to develop measures of individual performance that can be used to empirically link ecological and evolutionary change. We start by justifying the use of non-generational measures; we then present novel empirical methods before applying them to data from Soay sheep.

2. NON-GENERATIONAL MEASURES OF EVOLUTIONARY CHANGE

Despite the evocative lexicon of evolutionary biology (see Dawkins 1982 for an excellent discussion of this) biologists do not consider individuals 'following strategies' or 'making decisions' that actively 'trade-off' current and future performance (Krebs & Davies 1997; Roff 2002). Instead, apparent trade-offs within life histories are the result of continuous past selection on individual decision rules: an organism may decide to breed now or not, perhaps based on its current state; it generally does not decide between breeding now or later. Another way of phrasing this is evolution not concerned with per generation fitness (Caswell 2001, p. 295)—selection is a continuous process that operates on the distribution of phenotypic traits within a population at a point in time, and it may generate a response to selection at the genetic level which can be recorded as a change in allele frequencies. Given this, an alternative approach to the analysis of micro-evolutionary change is to consider time in shorter intervals than the generation (Metz *et al.* 1992; Benton & Grant 2000; Engen *et al.* in press). Empirically this is frequently done: selection gradients are frequently calculated between a trait and one component of fitness like juvenile survival in one year (Kingsolver *et al.* 2001). One drawback of this approach is that selection can operate via survival and fecundity simultaneously (Lande 1982) and the relative importance of selection via one component of fitness can vary over time (Coulson *et al.* 2003). Consequently, there is no reason to expect that selection estimated using only one demographic rate will have much utility in predicting evolutionary change. A powerful way around this drawback, which has not been widely applied, is to estimate selection between a trait and all demographic rates, and to sum together all the selection gradients, each weighted by the association of the demographic rate with population growth (Lande 1982; van Tienderen 2000; Coulson *et al.* 2003). One problem with this approach is it requires the estimation of large numbers of selection gradients which could introduce error in the overall estimate of the strength of selection. The approach we develop here estimates individual fitness over a time step in such a way it averages to give mean fitness over the time step. This approach simplifies the estimation of selection on a trait via all demographic rates by reducing the number of selection gradients that need to be calculated.

The measures we develop are concerned with describing temporal changes in distributions. Various statistics can be used to characterize temporal changes in distributions. For example, the area under a distribution (the 'size' of the distribution) will change as the population the distribution describes changes in size. Understanding changes in the size of trait or allele distributions is the domain of population ecology, but is central to evolutionary ecology as well. Changes other than the size of the

distribution can be characterized with changes in the moments of the distribution like the mean, the variance, the skew and the kurtosis as long as the distribution describes a continuously distributed trait. Changes in the frequency of alleles or discretely distributed traits are best characterized by changes in the relative heights of the bars of the histograms depicting the distribution at two points in time. In §§3–5, we demonstrate how individual contributions to population growth, moments of continuously distributed traits and relative frequencies of alleles or discretely distributed traits can be calculated by removing individual demographic performances, trait values and genotypes and recalculating summary statistics.

3. INDIVIDUAL CONTRIBUTIONS TO POPULATION GROWTH $p_{t(i)}$

The approach we develop allows the estimation of an individual's contribution to population growth over a time step from life history and population data. This quantity is an individual's annual realized fitness.

We first calculate how a population would have performed with the focal individual removed over the time step t to $t+1$. We do this by retrospectively removing the individual and any offspring that it produced between time t and $t+1$ that were still alive at time $t+1$ from the data and recalculating population growth. The mechanics of this approach is the same as jackknifing; however, jackknifing is a specific statistical tool, so from here on we term the method 'de-lifing'.

The number of surviving offspring produced over a time step, that are still alive at the end of the time step, plus one if the parent survived, is a measure with a long pedigree in population biology (Watson & Galton 1874; Caswell 2001; Lande *et al.* 2003); we refer to this quantity as individual performance and denote it ξ . For each individual within a population at each time we remove ξ and recalculate population growth. This approach takes the realized population growth over a time period and asks how each individual contributed to it directly. The method does not estimate what the consequences of removing an individual would be on the performance of other individuals. Of course, if a dominant individual or territory holder really was removed from a population it could alter dominance hierarchies or territory tenure. We are not attempting to estimate these consequences (the quote at the beginning of the paper should not be taken too literally)—we are specifically working with the *realized* population growth and estimating *direct* (relative) individual performance given the environment they experienced. We denote population growth with individual i 's contribution removed $w_{t(-i)}$. If N is population size it is straightforward to calculate,

$$w_{t(-i)} = \frac{N_{t+1} - \xi_{t(i)}}{N_t - 1}. \quad (3.1)$$

The logic behind this equation is that population growth between time t and $t+1$ (w_t) is the population size in year $t+1$ divided by population size in year t . If individual i is removed at time t then the population size at that point would be the denominator in equation (3.1) ($N_t - 1$). If individual i and any surviving offspring are removed at time $t+1$ the population size would be the numerator in equation (3.1) ($N_{t+1} - \xi_{t(i)}$). This equation considers time

Table 1. Demonstration of how to calculate $p_{t(i)}$ from individual performance data. ($N_t=9$ —the number of rows in the table.)

ID	age	survive ($s_{t(i)}$)	recruits ($f_{t(i)}$)	$\xi_{t(i)}$	$(s_{t(i)} - \bar{s})/(N_t - 1)$	$(f_{t(i)} - \bar{f})/(N_t - 1)$	$p_{t(i)}$
A	1	0	0	0	-0.0833	-0.1389	-0.2222
B	1	1	0	1	0.0417	-0.1389	-0.0972
C	1	1	0	1	0.0417	-0.1389	-0.0972
D	2	0	2	2	-0.0833	0.1111	0.0278
E	2	1	1	2	0.0417	-0.0139	0.0278
F	2	1	2	3	0.0417	0.1111	0.1528
G	3	0	2	2	-0.0833	0.1111	0.0278
H	3	1	2	3	0.0417	0.1111	0.1528
I	3	1	1	2	0.0417	-0.0139	0.0278
totals		6	10	16 (N_{t+1})	0	0	0
means		0.667 (\bar{s})	1.111 (\bar{f})	1.778 (w_t)	0	0	0

as discrete and assumes that the time interval chosen is shorter than the time it would take for a newborn to grow to reproduce itself. If changes over a time period longer than this are of interest, we suggest decomposing this longer interval into steps that only include one breeding season.

An individual's contribution to population growth, $p_{t(i)}$, is calculated by subtracting $w_{t(-i)}$ from w_t . We denote this quantity $p_{t(i)}$

$$p_{ti} = w_t - \frac{N_{t+1} - \xi_{t(i)}}{N_t - 1}, \quad (3.2)$$

which can be re-arranged to give

$$p_{ti} = \frac{\xi_{t(i)} - w_t}{N_t - 1}, \quad (3.3)$$

from this arrangement it is clear that the numerator provides the residual performance of individual i , and the denominator the number of competitors within the population. The logic for correcting by the number of competitors within the population is that an individual with a $\xi_{t(i)}=3$ living in a population with a $w_t=0.97$ will make a greater contribution to population growth if the population is small (for example, 100 individuals) rather than large (1000 individuals). An alternative matrix and vector formulation for the calculation of $p_{t(i)}$ is provided in the electronic supplementary material.

We can further break down $p_{t(i)}$ values into the contribution of an individual's survival or reproduction to population growth. If we write $\xi_{t(i)} = s_{t(i)} + f_{t(i)}$ where $s_{t(i)}$ is a binary variable representing whether individual i survives from year t to $t+1$ and $f_{t(i)}$ is the number of offspring produced by individual i in year t that survive to year $t+1$ and define \bar{s}_t and \bar{f}_t as the means of $s_{t(i)}$ and $f_{t(i)}$ then

$$p_{ti} = \frac{s_{t(i)} - \bar{s}_t}{N_t - 1} + \frac{f_{t(i)} - \bar{f}_t}{N_t - 1}. \quad (3.4)$$

The survival or fecundity components on the right-hand side of equation (3.4) can be summed across individuals within the same state and weighted by $(N_t - 1)/(N_t - x)$ where x is the number of individuals within the class, to give the contribution of state-specific survival or fecundity to population growth. Table 1 provides an example of the calculation of $p_{t(i)}$ from data. This example considers only the female component of this theoretical population; however, if we considered a two sex population the number of recruits produced would be multiplied by

1/2. From table 1 it can be seen that $p_{t(i)}$ can be positive or negative. A negative value represents an individual that performed worse than the population mean while a positive value represents one that performed better.

An important property of the $p_{t(i)}$ statistic is that a weighted sum across individuals within the same state (age, size, etc.) can be calculated to give the contribution of individuals within a specific state to population growth. For example, individuals D, E and F in table 1 are all age two, which makes the total contribution of two year olds to population growth $= (0.0278 + 0.0278 + 0.1528) \times 8/6 = 0.2779$. Because $p_{t(i)}$ values are corrected for population size they can also be summed across years.

There are two other properties of $p_{t(i)}$ that should be noted. First, the opportunity for variation in individual contributions to population growth is dependent on life history. In a life history where females can only produce one offspring in each year a female has four ways in which she can contribute to population growth: (i) surviving and producing a recruit, (ii) surviving and failing to produce a recruit, (iii) failing to survive but producing a recruit and (iv) failing to survive and failing to produce a recruit. Although there are four ways a female can contribute to population growth, two ways of contributing will produce the same value of $p_{t(i)}$. In terms of w the way an individual can contribute to change is best thought of in terms of the number of individuals contributed to next year's population. In our example, a female can either: (i) reduce population size by one individual in year $t+1$ by dying and not reproducing, (ii) increase population size by one individual by surviving and reproducing or (iii) have no effect on population size by either surviving and not reproducing or reproducing but not surviving. In species, where a female can produce more than one offspring the opportunity to contribute to population growth is greater.

A second interesting property is that the opportunity for an individual to contribute to population growth is a function of population size. This is because when the population consists of a few individuals one individual can have a large influence on mean performance, while this is not the case for very large populations. For any life history, as population size goes up the maximum potential contribution an individual can make in any one time step goes down. If $w=1$ exactly then $N_{t+1}=N_t \equiv N$, and the maximum value of $p_{t(i)}$ for a life history where an individual can only produce one offspring at each breeding attempt is $1 - (N-2)/(N-1) = 1/(N-1)$. For the variance, if the survival probability is g , then the reproduction

probability must be $(1-q)$, and so (if reproduction and survival are independent) the variance in individual performance will be $2q(1-q)$. Thus, $\text{var}(p) = 2q(1-q)/(N-1)$.

4. INDIVIDUAL CONTRIBUTIONS TO TEMPORAL CHANGES IN THE DISTRIBUTIONS OF CONTINUOUS TRAITS (c_i)

A similar de-lifing approach can be used to estimate individual contributions to temporal changes in the frequency distribution of continuous traits like size. At two points in time, t and $t+1$, the frequency distributions of the trait of interest are characterized with moments of the distribution (mean \bar{x} , variance σ^2 , skew s^3 , kurtosis k^4). The change in the moments of these distributions over time is obtained by subtracting the moments estimated at time t from the moments estimated at time $t+1$: a change in the mean, for example, is simply $\Delta\bar{x}_t = \bar{x}_{t+1} - \bar{x}_t$. The trait value of each individual in the population in year t is then removed in turn and the moments of the distribution recalculated. The mean of a distribution with individual i 's trait value removed is termed $\bar{x}_{t(-i)}$ —a quantity we refer to as a reduced mean. The same process is repeated for year $t+1$. The difference in the reduced means for each individual between year t and year $t+1$ is then calculated $\Delta\bar{x}_{t(-i)} = \bar{x}_{t+1(-i)} - \bar{x}_{t(-i)}$. If an individual was not present in the population in year t its removal from the distribution has no effect on the population mean for year t , such that $\bar{x}_{t(-i)} = \bar{x}_t$. The mean of the values of $\Delta\bar{x}_{t(-i)}$ across all individuals within the population is equal to $\Delta\bar{x}_t$ (e.g. $(\sum_{i=1}^N \Delta\bar{x}_{t(-i)})/N = \Delta\bar{x}_t$). The final step in calculating an individual's contribution to a change in the moment of a distribution is to subtract the observed change in the means with individual i excluded from the observed change in the means ($c_i = \Delta\bar{x}_t - \Delta\bar{x}_{t(-i)}$). An individual with a positive c_i made a positive contribution to $\Delta\bar{x}_t$ while an individual with a negative c_i made a negative contribution. An individual, i , may have contributed to $\Delta\bar{x}_t$ by producing offspring that recruit to the population in year $t+1$ with their own trait values. Individual i may have survived or died between year t and year $t+1$. Consequently, in the same way that there are various routes via which an individual can contribute to the change in size of a distribution over a unit of time ($w_{t(-i)}$), there are also various ways in which an individual can contribute to the change in the moments of a phenotypic distribution over time. How can we combine the c values for a parent and any offspring? Imagine an individual has $c_i = 0.1$ and it produces two offspring with c_i values of 0.05 and -0.2 , the contribution of the focal individual to the change in the mean is simply the sum of these numbers (e.g. $0.1 + 0.05 - 0.2 = -0.05$). In the electronic supplementary material, we provide a mathematical proof that the de-lifed moments of a distribution average to the population moment.

So far we have been able to show how to calculate individual contributions to the population growth and individual contributions to changes in the moments of distributions of quantitative traits. However, one of our objectives is to link changes in allele distributions to changes in quantitative trait distributions and changes in population size and growth. Next, we demonstrate how we can calculate individual contributions to changes in allele frequencies.

5. INDIVIDUAL CONTRIBUTIONS TO TEMPORAL CHANGES IN THE DISTRIBUTIONS OF DISCRETE TRAITS (d_i)

Distributions of discrete traits like eye colour or alleles cannot be described with moments of the distribution. One way that the distributions of alleles or discrete traits can be characterized is with a vector describing the height of each bar of a histogram. To work out how a distribution of alleles has changed between time t and time $t+1$ ($\delta\mathbf{G}_{t:t+1}$), for instance, would involve calculating a vector for both time intervals (\mathbf{V}_t and \mathbf{V}_{t+1}) and subtracting the vector \mathbf{V}_t from \mathbf{V}_{t+1} . De-lifing is once again used to estimate an individual's contribution to changes in the distributions over time. For each individual in turn, its genotype in year t and year $t+1$ and the genotypes of its recruits in year $t+1$ are removed from the dataset and $\mathbf{V}_{t(-i)}$ and $\mathbf{V}_{t+1(-i)}$ are calculated. An individual's contribution to changes in the distribution are then described with a vector $\delta\mathbf{G}_{t:t+1(-i)} = \mathbf{V}_{t+1(-i)} - \mathbf{V}_{t(-i)}$. The sum of all $\delta\mathbf{G}_{t:t+1(-i)}$ across all individuals is $\delta\mathbf{G}_{t:t+1}$. As before, $\delta\mathbf{G}_{t:t+1}$ can be subtracted from each $\delta\mathbf{G}_{t:t+1(-i)}$ to provide vectors of individual contributions to changes in the frequency distributions of discrete traits (\mathbf{d}_i) that sum across individuals to produce a vector of zeros. Positive vector elements represent those individuals that increased the relative frequency of a trait value or allele, while negative elements represent those individual who have reduced relative frequencies.

As an example we consider a trait with three discrete values—alleles a, b and c. At time 1 there are 38, 42 and 18 copies of a, b and c, respectively, within the population (population size = $(38 + 42 + 18)/2 = 49$). At time 2 there are 30, 38 and 22 copies of alleles a, b and c (population size = 45). We focus on the contribution of individual X, which was alive at time 1, but was dead by time 2. She produced three offspring in year 1 that were all still alive at time 2. Individual X's genotype was ac, and her offspring's genotypes were aa, ab and ab. From this information we calculate

$$\delta\mathbf{G}_{1:2} = \begin{bmatrix} 30 \\ 38 \\ 22 \end{bmatrix} - \begin{bmatrix} 38 \\ 42 \\ 18 \end{bmatrix} = \begin{bmatrix} -8 \\ -4 \\ 4 \end{bmatrix},$$

and

$$\delta\mathbf{G}_{1:2(-x)} = \begin{bmatrix} 30-4 \\ 38-2 \\ 22 \end{bmatrix} - \begin{bmatrix} 38-1 \\ 42 \\ 18-1 \end{bmatrix} = \begin{bmatrix} -11 \\ -6 \\ 5 \end{bmatrix},$$

giving

$$\mathbf{d}_x = \begin{bmatrix} -11 \\ -6 \\ 5 \end{bmatrix} - \begin{bmatrix} -8 \\ -4 \\ 4 \end{bmatrix} = \begin{bmatrix} -3 \\ -2 \\ 1 \end{bmatrix}.$$

In other words, if individual X had not existed, the frequency of alleles a and b would have decreased more than they actually did, while the population-wide decrease in frequency of allele c would have been less.

There are various uses of $p_{t(i)}$, c_i and \mathbf{d}_i . Being able to decompose statistical descriptions of changes in distributions of traits and alleles into contributions from individuals at a specific point in time is a method that can provide insight into many aspects of population

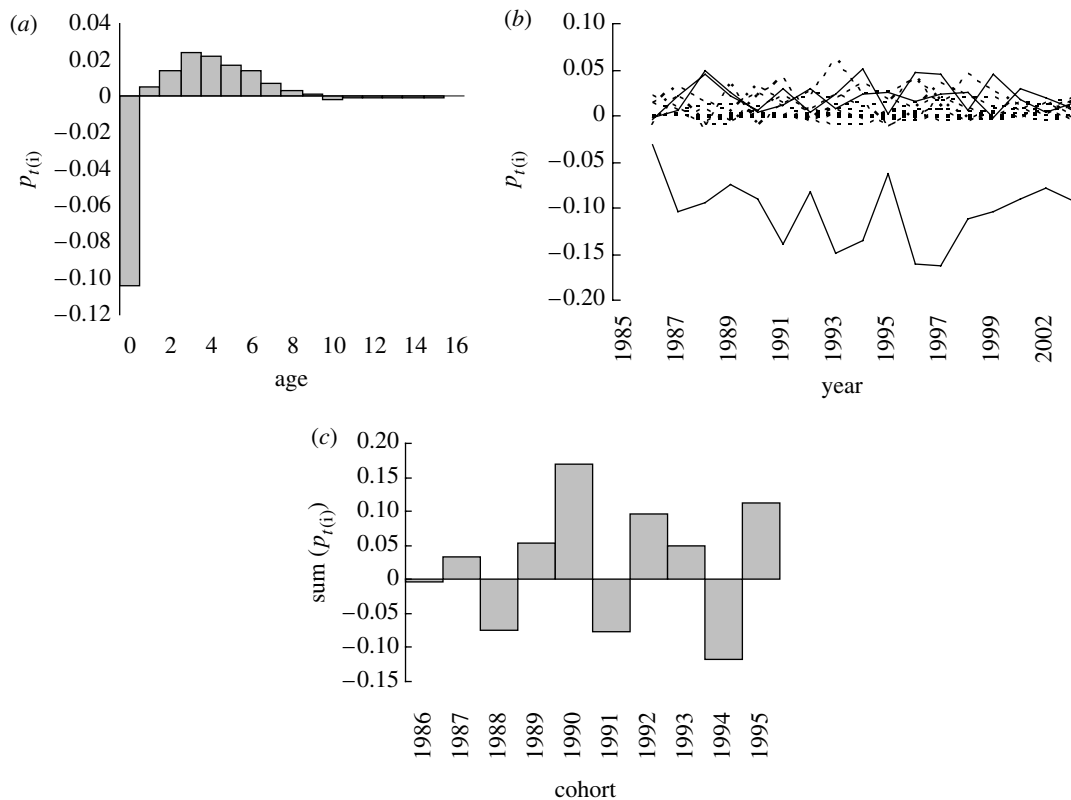


Figure 1. Individual contributions to population growth summed across individuals in the same phenotypic states for the Soay sheep. (a) Age-specific values of $p_{t(i)}$ for the Soay sheep averaged across years 1986–2003, (b) time series of age-specific contributions to population growth. The solid lines represent lambs (negative values of $p_{t(i)}$), and four and five year olds (positive values). There is substantial inter-annual variation in the contribution of different age-classes to population growth and (c) the contribution of different cohorts to population growth. Note that the foot and mouth outbreak means data are not available for 2001.

and evolutionary biology. Below we highlight several uses, giving worked examples for the first four uses. Future work will provide further worked examples of the other uses listed.

6. USES OF $p_{t(i)}$, c_i AND d_i : A WORKED EXAMPLE

For our worked examples we use data collected from marked Soay sheep (*Ovis aries*) living in the Village Bay catchment of Hirta in the St Kilda archipelago, Scotland, between 1986 and 2004. Individuals are uniquely marked within hours of birth and are followed throughout life with birth and death dates and breeding success data recorded. Genetic and morphometric data are also collected. In the examples provided below we use birth weight as an individual covariate as well as yearly values of $p_{t(i)}$ for each individual within the population. Total population size is calculated as the number of marked individuals (males and females of all ages) considered to be living in the study area in August each year. Full details of the study area, data collection protocols and previous research on the population can be found in Clutton-Brock & Pemberton (2004).

As many estimators of fitness that empiricists use are based on lifetime performance statistics like lifetime reproductive success (LRS) (Clutton-Brock 1988) we start by summing $p_{t(i)}$ values for each year an individual is alive to provide a measure of lifetime contribution to population growth for each individual. The correlation between LRS and the sum of the $p_{t(i)}$ for female sheep born between 1985 and 1995 is highly significant

($r^2 = 0.84$, $p < 0.001$). We do not consider males because estimates of their LRS are not as accurate as estimates for females (Clutton-Brock & Pemberton 2004), and we do not consider cohorts born later than 1995 as individuals from these cohorts are still alive and reproducing.

The main reason for developing the de-lifing approach, however, is to provide a measure of individual performance that is not per generation based but which incorporates both survival and recruitment in the environments which individuals experience. Once calculated the de-lifed statistics can be used in similar ways to per generation measures of fitness. The real advantage of the approach, however, is it permits time series of change to be generated in a way that is not possible using per generation measures. This allows variation in trait or allele performance to be correlated with temporally or spatially varying environmental covariates.

The $p_{t(i)}$ values can be summed across individuals in different states to estimate their contribution to population growth. For example, figure 1a is a histogram showing the average across years of the weighted sum of the age-specific $p_{t(i)}$ s between 1986 and 2003, and in figure 1b we provide time series of fluctuations in the sum of age-specific $p_{t(i)}$ s. It is clear that lambs contribute most to population growth, but because lambs successfully raise recruits less frequently than older individuals their contribution is negative. Within adults four and five year olds contribute most to population growth (a positive contribution), although there is substantial inter-annual variation. By using the survival and fecundity components

in equation (3.4) we could further decompose these age-specific contributions into age-specific contributions due to survival and fecundity.

A similar approach can be used to measure the contribution of different cohorts to population growth (figure 1c). To do this requires summing the $p_{t(i)}$ values for each individual within a cohort over all years they are alive. Cohort effects have previously been examined in the Soay sheep and the success of a cohort is determined to a large extent by variation in population density and climate in the years of conception and birth (Forchhammer *et al.* 2001). The pattern of successful and unsuccessful cohorts we report in figure 1c is similar to those reported by Forchhammer *et al.* (2001).

The de-lifing approach can be used to estimate selection on quantitative traits (Arnold & Wade 1984), and to examine how selection varies over time. The strength of selection is estimated by regressing a trait value against $p_{t(i)}$ —having transformed the data prior to analyses as is usual for estimation of standardized selection gradients (Arnold & Wade 1984). By estimating selection in each year, a time series of selection pressures can be generated. In figure 2a we plot $p_{t(i)}$ values against birth weight for 1993 to demonstrate how a standardized selection gradient can be calculated using the de-lifing approach, and in figure 2b we provide a plot of the time series of selection gradients between 1986 and 2003. Using the survival and fecundity components of equation (3.4) we could also estimate the strength of selection via survival and fecundity and, if desired, within specific age or size classes within a year. However, space precludes us from doing this here. Fluctuations in selection pressures on birth weight (Wilson *et al.* 2005a,b) and weight (Milner *et al.* 1999) have previously been examined in the Soay sheep. These analyses have reported selection for an increase in weight, which is consistent with our results. Temporal fluctuations in selection gradients have been calculated by estimating separate selection gradients using LRS for individuals within a cohort. The relationship between estimates of selection calculated using $p_{t(i)}$ and selection estimated using LRS calculated for each cohort born between 1986 and 1995 is weak, positive, but not significant (figure 2c).

The de-lifing approach can also be used to estimate a phenotypic response to selection. Significant associations between c_i or elements of \mathbf{d}_i and $p_{t(i)}$ for individuals in a particular phenotypic or genotypic state would inform whether individuals that positively or negatively contributed to changes in trait or allele distributions also tended to have a substantial impact on population growth. A significant association suggests a response to selection. With multiple years of data it is possible to identify whether the association between c_i , elements of \mathbf{d}_i and $p_{t(i)}$ are temporally variable and whether different phenotypes perform in contrasting ways in different environments.

Our method can be used with quantitative genetics approaches to infer changes in genetic structure (Falconer & Mackay 1996). If relatedness between individuals is known, heritabilities of $p_{t(i)}$ and c_i can be estimated using application of the animal model to pedigree data. Kruuk *et al.* (2000) provides an example of application of the animal model to detailed, long-term data on wild animals. A significant heritability of $p_{t(i)}$ would suggest that related individuals are more likely to contribute to population

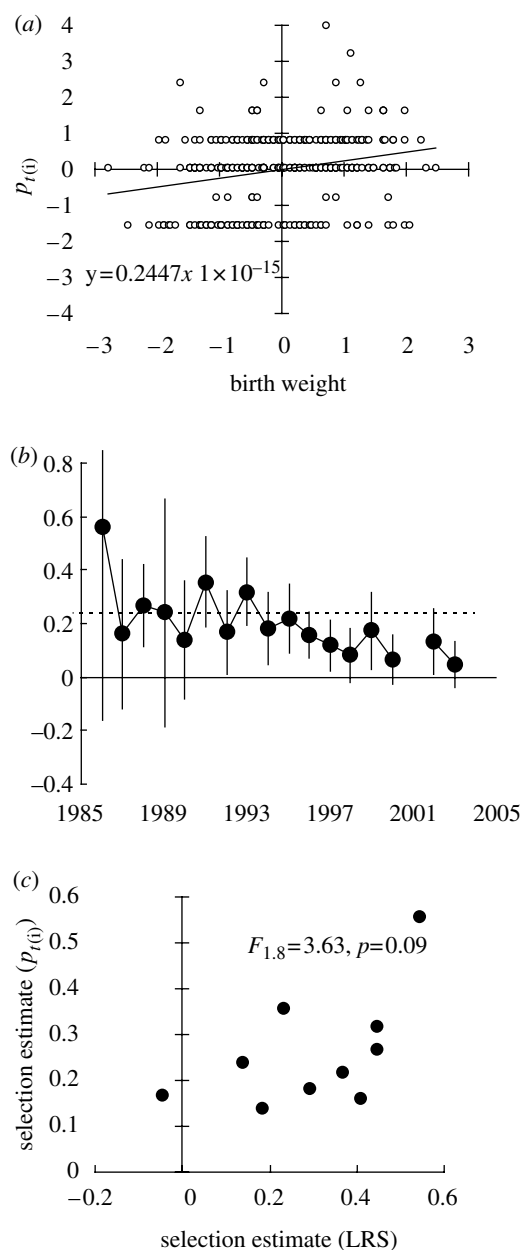


Figure 2. Using $p_{t(i)}$ to estimate selection in the Soay sheep. (a) An example of a selection gradient calculated using birth weights and $p_{t(i)}$ values for all Soay sheep (males and females) living in the population in 1993. Each dot represents an individual. Males and females of known ages are included in the plot. Data are transformed to have a mean of zero and a standard deviation of unity prior to analyses. (b) A time series of fluctuations in selection pressure on birth weight calculated using $p_{t(i)}$. There is evidence that the strength of selection on birth weight has declined during the course of the study. The horizontal dotted line shows the estimate of selection calculated using lifetime reproductive success. This is close to the mean of the estimates of fluctuating selection calculated using $p_{t(i)}$ (solid circles) (c) scatter plot showing the lack of correlation between annual estimates of selection calculated using $p_{t(i)}$ and cohort based estimates calculated using LRS.

growth in similar ways than unrelated individuals, and that a proportion of this association is due to additive genetic effects. Similarly, a significant heritability of c_i would suggest that related individuals are likely to contribute to observed changes in the moments of phenotypic trait distributions in similar ways. We would recommend using this approach in each year rather than with the lifetime

sum of the $p_{t(i)}$ s as this permits examination of whether heritabilities vary with environment. This, however, would require substantial pedigree data for a wild population. The animal model has been applied to the Soay sheep data to examine micro-evolution in birth weight and date (Wilson *et al.* 2005a,b).

As well as examining evolutionary changes in quantitative traits, the de-lifing approach allows the fitness of alleles and lineages to be explored. Correlation between aspects of an individual's genotype and $p_{t(i)}$ can be used to identify variations in fitness across genotypes. Similarly, correlations between elements of \mathbf{d}_i and $p_{t(i)}$ will identify how selection on an allele generates changes in the allele frequencies. The de-lifing method can be used to estimate the fitness of an allele by summing the $p_{t(i)}$ values of individuals within the population that carry a specific allele. If this is repeated over many time steps, the growth rate of the allele into the population can be explored. A similar approach can be used to examine the growth rates of lineages into populations. For example, the contribution of an individual's lineage to population growth at a specific point in time can be calculated as the sum of the $p_{t(i)}$ s of that individual's descendants alive in the population multiplied by the relatedness (r_i) of those descendants to the focal individual ($\sum_{i=1}^x p_{t(i)} r_i$, where x is the total number of descendants within the population at the time of interest). This quantity calculated over several years can be used to characterize the growth rates of a lineage into a population.

The de-lifing approach can also be used to examine spatial variation in individual performance. If data on the spatial position of individuals are available, the spatial distribution of $p_{t(i)}$, c_{is} and values of \mathbf{d}_i can be plotted, and spatial clustering of individual contributions to change can be explored. The consistency of these clusters can be compared over time, and any variation correlated with environmental variation. In different parts of the Soay sheep study area different demographic rates contribute to variation in population growth in contrasting ways (Coulson *et al.* 1999) so it is likely that c_{is} , $p_{t(i)}$ and elements of \mathbf{d}_i vary spatially.

7. DISCUSSION

We present a simple method that allows the decomposition of population growth, quantitative trait distributions and allele frequencies into contributions from individuals within the population over a time step. We demonstrate how to estimate useful de-lifed statistics and then discuss, with examples from a population of Soay sheep, how the statistics can be used to provide ecological and evolutionary insight.

Although there are multiple definitions of fitness in population biology, most widely used definitions are based on estimating a rate of growth. For example, in the fields of population genetics and adaptive dynamics fitness is the rate of spread of mutant alleles or strategies into populations of resident alleles or strategies (Metz *et al.* 1992; Benton & Grant 2000), and in population ecology mean fitness is the population growth rate (Coulson *et al.* 2003). Empirically it is usually difficult to estimate growth rates of alleles and strategies in the field, so proxies of fitness are often used, usually collected at the level of the individual (Clutton-Brock 1988; McGraw & Caswell

1996). These are typically per generation measures like LRS, and this is one reason for the current popularity of quantitative genetic approaches in field studies (Kruuk *et al.* 2000; Merila *et al.* 2001a). There are, however, various limitations with using per generation measures under some circumstances.

Per generation measures of individual fitness were developed for cases when generation time does not vary between individuals (Fisher 1930)—annual plants for example—where the population was at equilibrium. In this case the mean of LRS from one generation to the next gives the population growth rate over one time step, a quantity that is a short-term estimate of mean fitness. In cases where generations overlap and there is substantial inter-individual variation in generation length (most iteroparous species) or when the population fluctuates over time, the mean of per generation estimates of fitness do not give mean fitness. This can lead to selection and heritability being confounded, which in turn biases estimates of micro-evolutionary change (Falconer & Mackay 1996). One way around this problem is to estimate fitness as the relative performance of individuals over a period of time shorter than the generation. But what should the time period be? We suggest a functional time unit of the life cycle (e.g. time intervals between breeding seasons) would be most appropriate. In seasonal breeding species this is the year—the unit of time we have focused on in our examples.

The de-lifing approach we develop is a simple extension of a statistic with a long pedigree in population biology. Individual performance, defined as the number of recruits produced over a time period plus one if the parent survives, was first developed by Watson & Galton (1874) who used it to examine the spread of family names into populations. The quantity underpins much of branching theory. Recently, it has not been widely used in ecology; however, Lande *et al.* (2003) do use this individual performance measure in their decomposition of population growth. Our extension to the statistic is to correct for mean performance and to condition by population size. The logic of doing this is that the opportunity for an individual to contribute to population growth over a time step is a function of population size, and in stochastic and density-dependent environments the logical approach to measuring fitness is to assess how an individual performed relative to other individuals also experiencing that environment. Thus, estimating $p_{t(i)}$ gives a solution to assessing fitness in stochastic environments.

It is not surprising that there is a strong relationship between LRS and the sum of the $p_{t(i)}$ values across the lifespan in the Soay sheep. There are two reasons why the measures are strongly, but not perfectly correlated: first, LRS does not incorporate any information on survival, while individual performance (ξ) does. Individual performance summed across the lifespan equals LRS + longevity. In the Soay sheep not all females breed every year and some produce twins. Consequently, there is not a perfect correlation between LRS and longevity, and therefore, not a perfect correlation between individual performance and LRS. The second reason for the lack of a perfect correlation is that $p_{t(i)}$ values are relative and are conditioned on population size which fluctuates from year to year. In contrast, LRS is not a relative measure and is not corrected for population size. In general, we would

expect strong correlations between LRS and the sum of $p_{t(i)}$ values across the lifespan if there is a strong correlation between LRS and longevity and population size fluctuates little from year to year. The strength of the de-lifing approach is that it is related to LRS, but has the advantage in that it allows selection to be empirically estimated at time intervals shorter than the generation and decomposed into survival and fecundity contributions, while producing a statistic, $p_{t(i)}$, that is amenable to address problems frequently asked in population biology.

The strong correlation between LRS and the sum of the $p_{t(i)}$ values explains why the estimate of selection using LRS gives a value close to the mean value of the annual estimates of selection obtained using $p_{t(i)}$ (figure 2a). The real advantage of using $p_{t(i)}$ to estimate selection is it provides estimates of selection in each year. This is useful if one imagines selection happening repeatedly on phenotypes within the population on a time scale appropriate to the life history of the species; estimating selection using per generation measures of fitness does not permit this in iteroparous species (Grafen 1988). The advantage of gaining estimates of selection on the phenotypic distribution within a population at repeated points in time is that regression methods can be used to identify environmental processes that may be associated with fluctuations in selection pressures (Kingsolver *et al.* 2001; Coulson *et al.* 2003). The only way to approximate fluctuations in selection pressures using per generation measures is to estimate selection per cohort. When comparing estimates of fluctuating selection using this approach with estimates gained using $p_{t(i)}$ we find, unsurprisingly, that the estimates of fluctuating selection are not correlated (figure 2). The de-lifing approach estimates selection across all individuals that are in the population at a point in time. In iteroparous species with overlapping generations a population is made up of individuals from multiple cohorts. Estimating selection on a per cohort basis using LRS estimates selection across a different set of individuals than those alive in a population at a point in time; it estimates the strength of selection on a specific cohort. There is no reason why selection on one cohort should correlate with selection across cohorts estimated at a point in time unless selection is temporally constant. Previous research has suggested that selection fluctuates substantially over time in Soay sheep (Clutton-Brock & Pemberton 2004).

We found strong evidence of senescence in $p_{t(i)}$ values in the Soay sheep (figure 1a). This is consistent with previous research that has reported senescence in reproductive and survival rates (Catchpole *et al.* 2000; Coulson *et al.* 2001). It is also unsurprising that lambs tend to contribute to population growth more than other ages as there are more of them. Their contribution is negative as they have lower survival and fecundity rates compared to older animals (Clutton-Brock & Pemberton 2004). We also report considerable variation in the contribution of different ages to population growth in each year (figure 1b). This too is consistent with previous research that identified a substantial contribution of fluctuations in age structure to the population dynamics in the Soay sheep (Coulson *et al.* 2001) and in age-structured population in general (Clutton-Brock & Coulson 2002; Lande *et al.* submitted).

Although complete population coverage is required to completely decompose population-level changes in population size, trait and allele frequencies, this does not preclude the approach from being used for less detailed datasets. Because $p_{t(i)}$ and d_i can only take a limited number of values determined by maximum clutch size, individuals can be classified by their performance if their reproductive success and survival status are known for a year, and an estimate of total population size exists. For example, individual performance over a time step may only be accurately characterized for a fraction of a population, however, an estimate of population size may be available. Equation (3.3) can still be used to estimate $p_{t(i)}$ for those individuals with performance records, and these data used to estimate selection and responses to selection. This means individual fitness estimates over a time step can be calculated, even for individuals for which lifetime fitness metrics do not exist. Many vertebrate studies collect these types of data. Work is required to determine what number of individual performance records would be needed to provide accurate estimates of ecological and evolutionary processes.

We present methods of estimate individual contributions to population growth and changes in allele and phenotypic trait distributions over a time period shorter than a generation—a year is a suitable time step for seasonal breeders. The estimates of individual fitness average to give mean fitness. Because selection can only operate on the distribution of phenotypes within a population at a specific point in time, the measure should prove useful in measuring ecological and evolutionary change in the field.

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REFERENCES

- Arnold, S. J. & Wade, M. J. 1984 On the measurement of natural and sexual selection: theory. *Evolution* **38**, 709–719.
- Benton, T. G. & Grant, A. 2000 Evolutionary fitness in ecology: comparing measures of fitness in stochastic, density-dependent environments. *Evol. Ecol. Res.* **2**, 769–789.
- Caswell, H. 2001 *Matrix population models: construction, analysis and interpretation*. Sunderland, MA: Sinauer Associates Inc.
- Catchpole, E. A., Morgan, B. J. T., Coulson, T. N., Freeman, S. N. & Albon, S. D. 2000 Factors influencing Soay sheep survival. *Appl. Stat.* **49**, 453–472.
- Charlesworth, B. 1994 *Evolution in age structured populations*. Cambridge, UK: Cambridge University Press.
- Clutton-Brock, T. H. 1988 *Reproductive success: studies of individual variation in contrasting breeding systems*. Chicago, IL: University of Chicago Press.

- Clutton-Brock, T. H. & Coulson, T. N. 2002 Ungulate population dynamics: the devil is in the detail. *Phil. Trans. R. Soc.* **357**, 1299–1306. (doi:10.1098/rstb.2002.1129)
- Clutton-Brock, T. H. & Pemberton, J. M. 2004 *Soay sheep: dynamics and selection in an island population*. Cambridge, UK: Cambridge University Press.
- Coulson, T., Albon, S., Pilkington, J. & Clutton-Brock, T. 1999 Small-scale spatial dynamics in a fluctuating ungulate population. *J. Anim. Ecol.* **68**, 658–671. (doi:10.1046/j.1365-2656.1999.00298.x)
- Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. & Grenfell, B. T. 2001 Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**, 1528–1531. (doi:10.1126/science.292.5521.1528)
- Coulson, T., Kruuk, L. E. B., Tavecchia, G., Pemberton, J. M. & Clutton-Brock, T. H. 2003 Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution* **57**, 2879–2892.
- Dawkins, R. 1982 *The extended phenotype*. Oxford, UK: Oxford University Press.
- Engen, S., Lande, R. & Saether, B.-E. In press Effective size of a fluctuating age structured population. *Genetics*.
- Falconer, D. S. 1960 *Introduction to quantitative genetics*. London: Longman.
- Falconer, D. S. & Mackay, T. F. C. 1996 *Introduction to quantitative genetics*. Essex, UK: Longman Group Ltd.
- Fisher 1930 *The genetical theory of natural selection*. Oxford, UK: Clarendon Press.
- Forchhammer, M. C., Clutton-Brock, T. H., Lindstrom, J. & Albon, S. D. 2001 Climate and population density induce long-term cohort variation in a northern ungulate. *J. Anim. Ecol.* **70**, 721–729. (doi:10.1046/j.0021-8790.2001.00532.x)
- Grafen, A. 1988 On the uses of data on lifetime reproductive success. In *Reproductive Success: studies of individual variation in contrasting breeding systems* (ed. T. H. Clutton-Brock), pp. 454–471. Chicago, IL: University of Chicago Press.
- Hamilton, W. D. 1964 The genetic evolution of social behaviour. *J. Theor. Biol.* **7**, 1–52. (doi:10.1016/0022-5193(64)90038-4)
- Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang, A., Gibert, P. & Beerli, P. 2001 The strength of phenotypic selection in natural populations. *Am. Nat.* **157**, 245–261. (doi:10.1086/319193)
- Krebs, J. R. & Davies, N. B. 1997 *Behavioural ecology: an evolutionary approach*. Oxford, UK: Blackwell Science.
- Kruuk, L. E. B., Clutton-Brock, T. H., Rose, K. E. & Guinness, F. E. 1999 Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proc. R. Soc. B* **266**, 1655–1661. (doi:10.1098/rspb.1999.0828)
- Kruuk, L. E. B., Clutton-Brock, T. H., Slate, J., Pemberton, J. M., Brotherstone, S. & Guinness, F. E. 2000 Heritability of fitness in a wild mammal population. *Proc. Natl Acad. Sci. USA* **97**, 698–703. (doi:10.1073/pnas.97.2.698)
- Lande, R. 1982 A quantitative theory of life history evolution. *Ecology* **63**, 607–615.
- Lande, R., Engen, S. & Saether, B.-E. 2003 *Stochastic population dynamics in ecology and conservation*. Oxford series in ecology and evolution. Oxford, UK: Oxford University Press.
- Lande, R., Engen, S., Saether, B. -E. & Coulson, T. Submitted Using reproductive value to estimate key parameters in age-structured populations. *Ecology*.
- Lewontin, R. C. 1974 *The genetic basis of evolutionary change*. New York: University of Columbia Press.
- Maynard-Smith, J. 1982 *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.
- McGraw, J. B. & Caswell, H. 1996 Estimation of individual fitness from life-history data. *Am. Nat.* **147**, 47–64. (doi:10.1086/285839)
- Merila, J., Kruuk, L. E. B. & Sheldon, B. C. 2001a Cryptic evolution in a wild bird population. *Nature* **412**, 76–79.
- Merila, J., Sheldon, B. C. & Kruuk, L. E. B. 2001b Explaining stasis: microevolutionary studies in natural populations. *Genetica* **112**, 199–222.
- Metz, J. A. J., Nisbet, R. M. & Geritz, S. A. H. 1992 How should we define 'fitness' for general ecological scenarios. *Trends Ecol. Evol.* **7**, 198–202. (doi:10.1016/0169-5347(92)90073-K)
- Milner, J. M., Albon, S. D., Illius, A. W., Pemberton, J. M. & Clutton-Brock, T. H. 1999 Repeated selection of morphometric traits in the Soay sheep on St Kilda. *J. Anim. Ecol.* **68**, 472–488. (doi:10.1046/j.1365-2656.1999.00299.x)
- Roff, D. A. 2002 *Life history evolution*. Sunderland, MA: Sinauer Associates.
- Shertzer, K. W. & Ellner, S. P. 2002 Energy storage and the evolution of population dynamics. *J. Theor. Biol.* **215**, 183–200. (doi:10.1006/jtbi.2001.2507)
- van Tienderen, P. H. 2000 Elasticities and the link between demographic and evolutionary dynamics. *Ecology* **81**, 666–679.
- Watson, H. W. & Galton, F. 1874 On the probability of the extinction of families. *J. Anthropol. Inst. Great Britain Ireland* **6**, 138–144.
- Wilson, A. J., Coltman, D. W., Pemberton, J. M., Overall, A. D. J., Byrne, K. A. & Kruuk, L. E. B. 2005a Maternal genetic effects set the potential for evolution in a free-living vertebrate population. *J. Evol. Biol.* **18**, 405–414. (doi:10.1111/j.1420-9101.2004.00824.x)
- Wilson, A. J., Pilkington, J. G., Pemberton, J. M., Coltman, D. W., Overall, A. D. J., Byrne, K. A. & Kruuk, L. E. B. 2005b Selection on mothers and offspring: whose phenotype is it and does it matter? *Evolution* **59**, 451–463.