



Published in final edited form as:

Science. 2009 July 24; 325(5939): 464–467. doi:10.1126/science.1173668.

The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda

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Abstract

Environmental change, including climate change, can cause rapid phenotypic change via both ecological and evolutionary processes. Because ecological and evolutionary dynamics are intimately linked, a major challenge is to identify their relative roles. We exactly decompose change in mean body weight in a free-living population of Soay sheep into all processes that contribute to change. Ecological processes contribute most, with selection – the underpinning of adaptive evolution – explaining little of the observed phenotypic trend. Our results enable us to explain why selection is not realized even though weight is heritable and why environmental change has caused a decline in Soay sheep body size.

A major goal of population biology is to understand how environmental change generates a rapid phenotypic response (1, 2). Recently it has been recognized that evolution can occur at ecological timescales (2), and the new challenge is to differentiate trait dynamics driven by evolution from those driven by ecological responses to environmental change (3). This is difficult because ecological and evolutionary effects are intimately intertwined (2, 4), and available analytical methods do not allow quantification of different sources of change. For example, evolutionary models of phenotypic change (5, 6) focus on selection and genetic response to it (7). However, when applied in well-studied, pedigreed wild animal populations, they often fail to explain phenotypic outcome, leading many authors to speculate that plastic responses to environmental variation play a large role in phenotypic dynamics (1, 8–11). Conversely, some phenotypic trends are interpreted as evolutionary change without any evolutionary analysis. An exact method to decompose phenotypic change into contributing processes would aid in identifying the roles of selection (the underpinning of adaptive evolution) and ecology in generating phenotypic trends.

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In 1970 Price developed an equation that describes change in the mean value of a phenotypic trait, \bar{Z} , with time (12). Coulson and Tuljapurkar (13) derived an age-structured version of this equation which separates fitness into its survival and fertility components. This equation permits an exact retrospective decomposition of \bar{Z} into contributions from selection and other processes in a variable environment. Survival-related terms are (i) changes in demographic structure caused by age-specific survival rates (termed DCs) (14), (ii) age-specific viability selection differentials, which describe change resulting from differential survival associated with the trait (VS) (15), and (iii) age-specific trait development, which describes how the average trait value changes among surviving individuals as they age (GR). Reproduction-related terms are (i) changes in demographic structure caused by age-specific reproduction (DCr) (14), (ii) age-specific fertility selection differentials which describe the difference in mean trait value between selected parents and the unselected population (FS) (16), (iii) the mean age-specific difference between offspring and parental trait values (OMD) (12), and (iv) the covariation between litter size and the difference between offspring and parental trait values (ODC) (13).

Using the age-structured Price equation and data from an ungulate population, we decompose the observed change in a heritable phenotypic trait into the different contributing processes. We used detailed individual-based life history data and August body weights from the female component of a population of Soay sheep living on the island of Hirta in the St. Kilda archipelago, Scotland (7). We focus on this heritable trait because mean body weight has fluctuated substantially around a declining trend over 20 years (17). Previous research has reported this declining trend despite positive selection for larger body size with these counterintuitive findings speculated to result from environmental deterioration obscuring evolutionary change (18).

We grouped individuals into four age classes (19): lambs (<1 year), yearlings, prime-aged adults (2 to 6 years), and senescent individuals (>6 years). Mean weights fluctuated around a declining trend in all age classes (Fig. 1) with declines representing a loss of between ~0.3% (senescent) and ~0.8% (yearlings) of mean body weight/year. This decline is mirrored by a decrease in hind-leg length (7), suggesting that the body weight decline reflects sheep getting smaller rather than a decline in body condition.

We decomposed \bar{Z} for body weight to generate a time series of each term of the age-structured Price equation (Fig. 2A). These terms sum to produce \bar{Z} . On average, the growth of surviving individuals contributed positively to \bar{Z} (GR: mean±SE: 1056±105g/yr), followed by change in the demographic structure due to reproduction (DCr: 659±39g/yr) and survival (DCs: 251±161g/yr). Viability and fertility selection contributed less (VS: 153±36; FS: 32±15g/yr). These positive contributions were offset by the negative contribution from the difference between offspring and parental weights (OMD: -2220±51g/yr). The positive terms increased mean body weight by 2151g/yr; the negative terms decreased it by -2232g/yr, giving an average decrease in weight of 81g/yr.

The above analysis pools contributions across age classes. We next investigated age-related variation in \bar{Z} . On average, the positive contributions of VS and GR (Fig. 3) occurred in the first two years of life, dropping close to zero by the time individuals reached adult body size;

heavy individuals were more likely to survive than light individuals when young (20). These results raise an intriguing question: given positive viability selection on size (Fig. 2A), and the heritable nature of the trait (20), why have sheep not increased in size? The answer must be found in the OMD term, which is the only term that contributes negatively to \bar{Z} . Examination of this term showed that, on average, younger females produce lambs that are smaller than they were at birth probably because of physiological or morphological constraints caused by not having reached full adult body size (Fig. 3C) (21). Consequently the mean birth weight of parents is greater than that of their offspring counteracting much of the effect of selection. By the first August of life, when we collect weight data, daughters weigh, on average, ~150g less than their mothers were at the same age. Given the mean contribution of selection was +185g, this suggests an upper limit for the contribution of a response to selection (22) of 35g/year corresponding to ~100g/generation, or <0.8% of lamb August weight.

The difference between parental and offspring birth weights cannot alone explain the decline in body weight. We next examined trends in each component of the age-structured Price equation. The contribution of the growth rate (GR) between the first and second August of life has declined over the course of the study (Fig. 4). During this period sheep are growing more slowly than they used to (on average by 93 ± 36 g/yr). The contribution of slower growth between the first and second year of life has partly been compensated by an increase in the contribution of growth rates in the second year of life, but not sufficiently to prevent the observed decline in adult body mass (Fig. 1).

Why are sheep growing more slowly than they used to? We next analyzed individual growth rates within each age class (7). The growth of lambs was significantly negatively influenced by August body weight and population density operating additively and via an interaction with the preceding winter's North Atlantic Oscillation index (23) – lambs grew more slowly in years of high density following a bad winter: growth slows as competition for food increases and the amount of stored reserves required to stay alive also increases. This interpretation is complicated by a concordant increase in population size, resulting from increased survival rates in the first year of life, as winters have warmed and shortened (24). Changing winter conditions have extended the season of grass growth while reducing the length of time individuals depend upon stored fat reserves. This suggests that the form of density-dependence has changed with the climate (24), and that this has had phenotypic consequences. These results suggest that climate change has the potential to generate rapid change in phenotypic traits, providing contemporary support for observations from the fossil record of phenotypic change accompanying climate change (25).

We next identified how each term contributed to the temporal dynamics of mean body size by analysing temporal variation in \bar{Z} (7). Fluctuations in the population structure (DCs and DCr) caused by density-dependence and climatic variation (24), followed by the growth terms (GR), contributed most. These terms accounted for 88% of the observed variance. Viability (VS) and fertility selection (FS) accounted for 5.8%, and the OMD and ODC explained 4% (Fig. 2B). An individual-based analysis of annual growth rates suggests that climate and population density explain substantial amounts of variation, particularly for lambs (7). Although the OMD and ODC terms contribute little to the dynamics, we also

conducted an individual-based analysis of the difference between offspring and maternal weights. Population density and maternal body weight (which is determined by the birth weight of the mother and her growth since birth) explain significant amounts of variation suggesting that any response to selection contributes substantially less than 4% to the phenotypic dynamics, suggesting that the recent dynamics of body weight have not been strongly influenced by selection and adaptive evolution.

Our approach has provided several insights. First, the dynamics of body size – both the trend and variation around the trend – are primarily a consequence of environmental variation and not evolution. Second, we identified that positive viability selection on size early in life is countered by young mothers being unable to produce offspring that were as heavy as they were at birth. Finally, we report that environmental change has resulted in a reduction in lamb growth rates and that this explains why sheep are smaller than they used to be. There are two general conclusions from this analysis. First, the recent focus on evolutionary explanations for changes in heritable phenotypic traits (26, 27) could fruitfully be complemented with research identifying the role of environmental variation. Second, individuals and populations respond to environmental change in complex ways, and there should be no expectation for simple linear associations between environment, phenotype, genotype and population dynamics. These results reinforce the need for a theory linking genetic, phenotypic and population dynamics in age-structured populations in variable environments.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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28. Thanks to the NTS and SNH for permission to work on St. Kilda and the MOD, QinetiQ, Amey and ESS staff on St. Kilda and Benbecula for logistical support. J. Pilkington, previous field assistants and many volunteers collected the data. L-M. Chevin, M. Crawley, T. Ezard, J. Hostetler, O. Jones, L. Kruuk, R. Lande, A. Malo, F. Pelletier, M. Oli, J. Slate, I. Smallegange and A. Wilson provided comments. This work was funded by NERC NE/E015921/1 and NIA P01/AG/22500

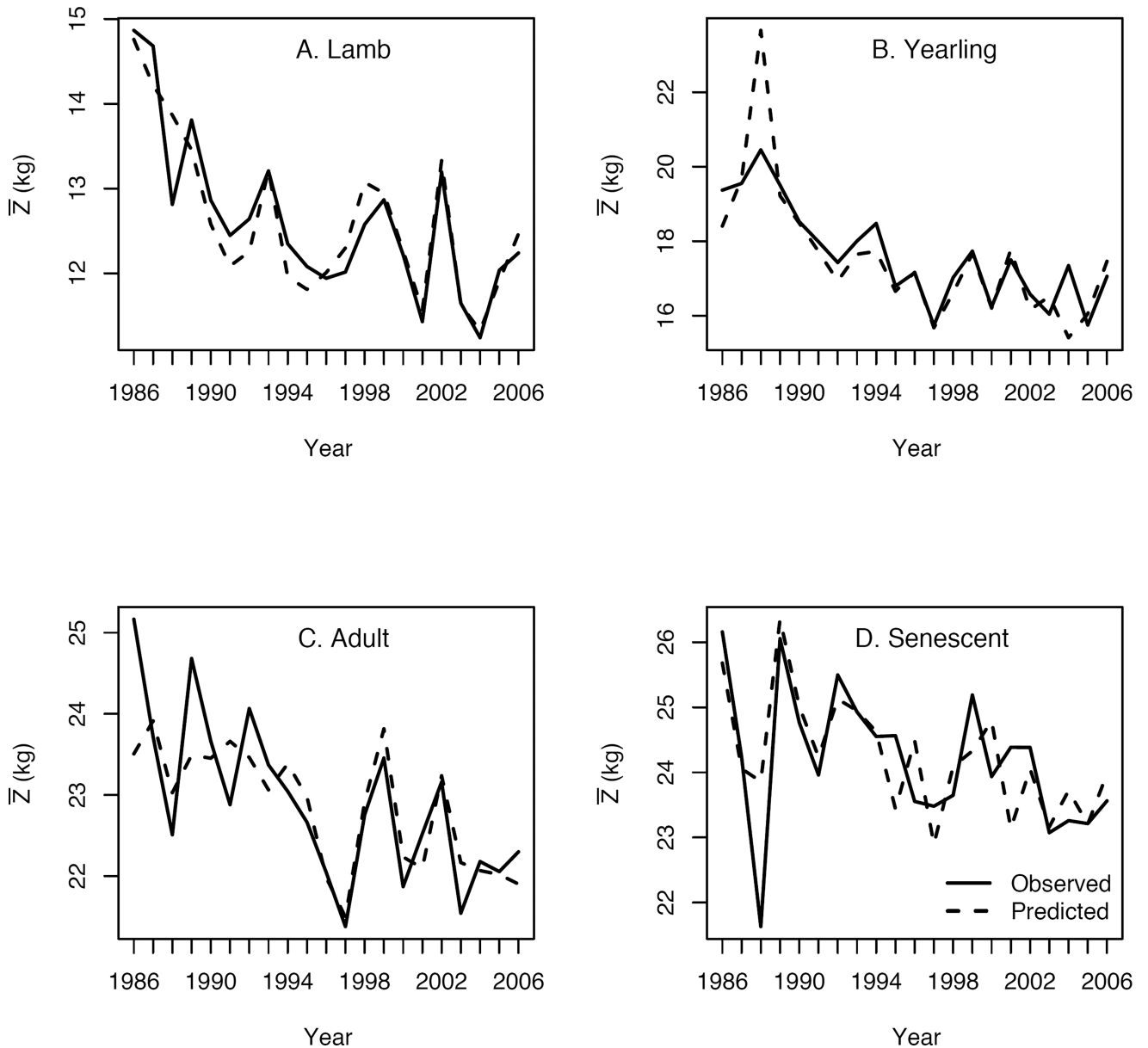


Figure 1.

Mean annual August weights (kg) for (A) lambs, (B) yearlings, (C) adults and (D) senescent female Soay sheep. The solid lines show the observed fluctuations in \bar{Z} and the dashed lines show those obtained from the application of the age-structured Price equation. Lambs declined on average (\pm SE) by 90 ± 30 g/yr, yearlings by 170 ± 30 g/yr, adults by 120 ± 30 g/yr, and senescent sheep by 80 ± 60 g/yr. This pattern of decline suggests some compensatory growth in later ages. The majority of the decline in body size occurred in the first decade of the study when population size increased and the North Atlantic Oscillation was predominantly positive. The solid and dashed lines do not match perfectly because several of the terms require information on animals caught in successive catches – a constraint that is not required when estimated observed mean body weight.

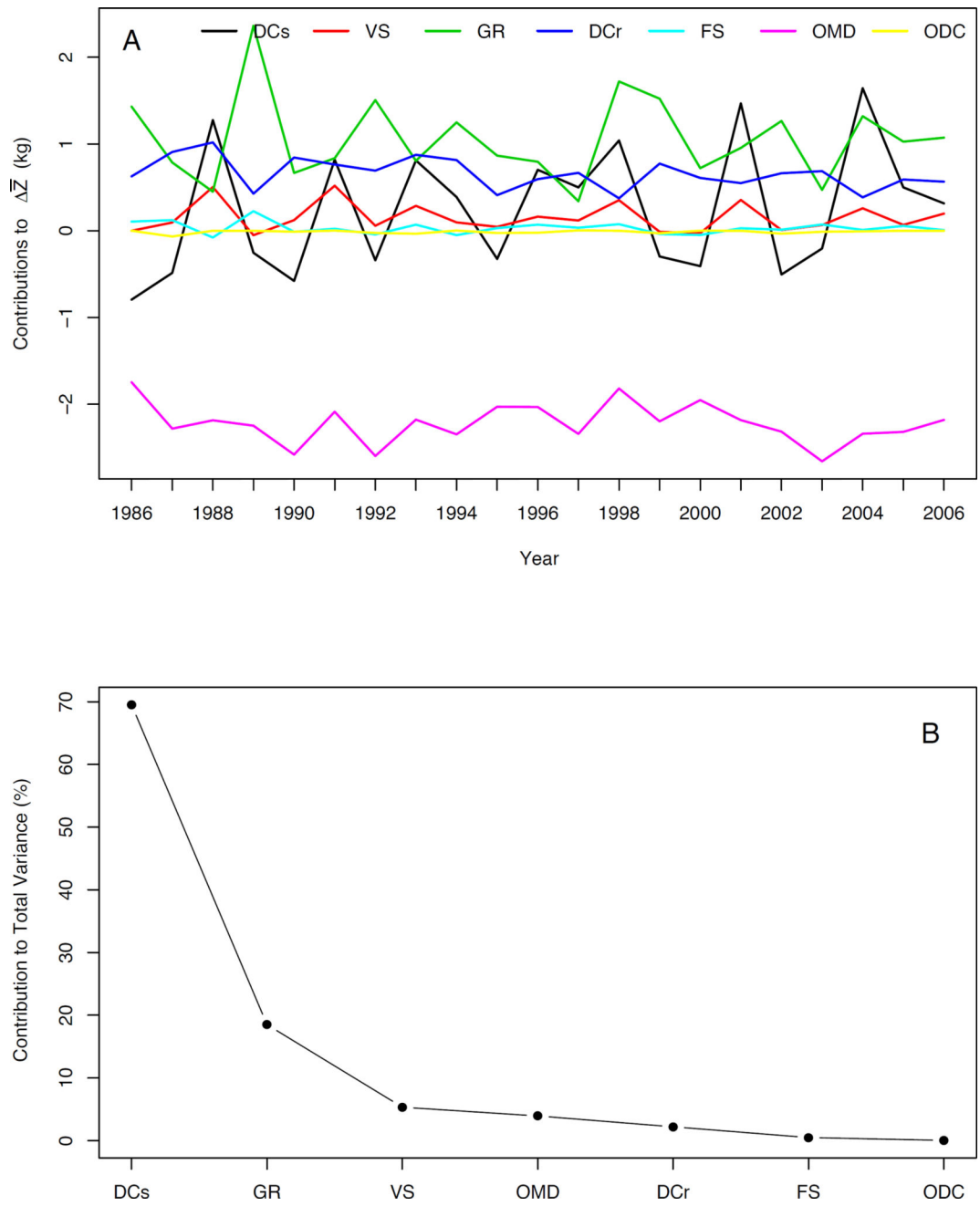


Figure 2. Decomposing (A) the mean and (B) the variance of \bar{Z} calculated across the time series. (A) Time-series of the contributions of different terms to \bar{Z} summed across age classes: see main text for definition of abbreviations. (B) The percentage contribution of each term to the observed total variation in \bar{Z} .

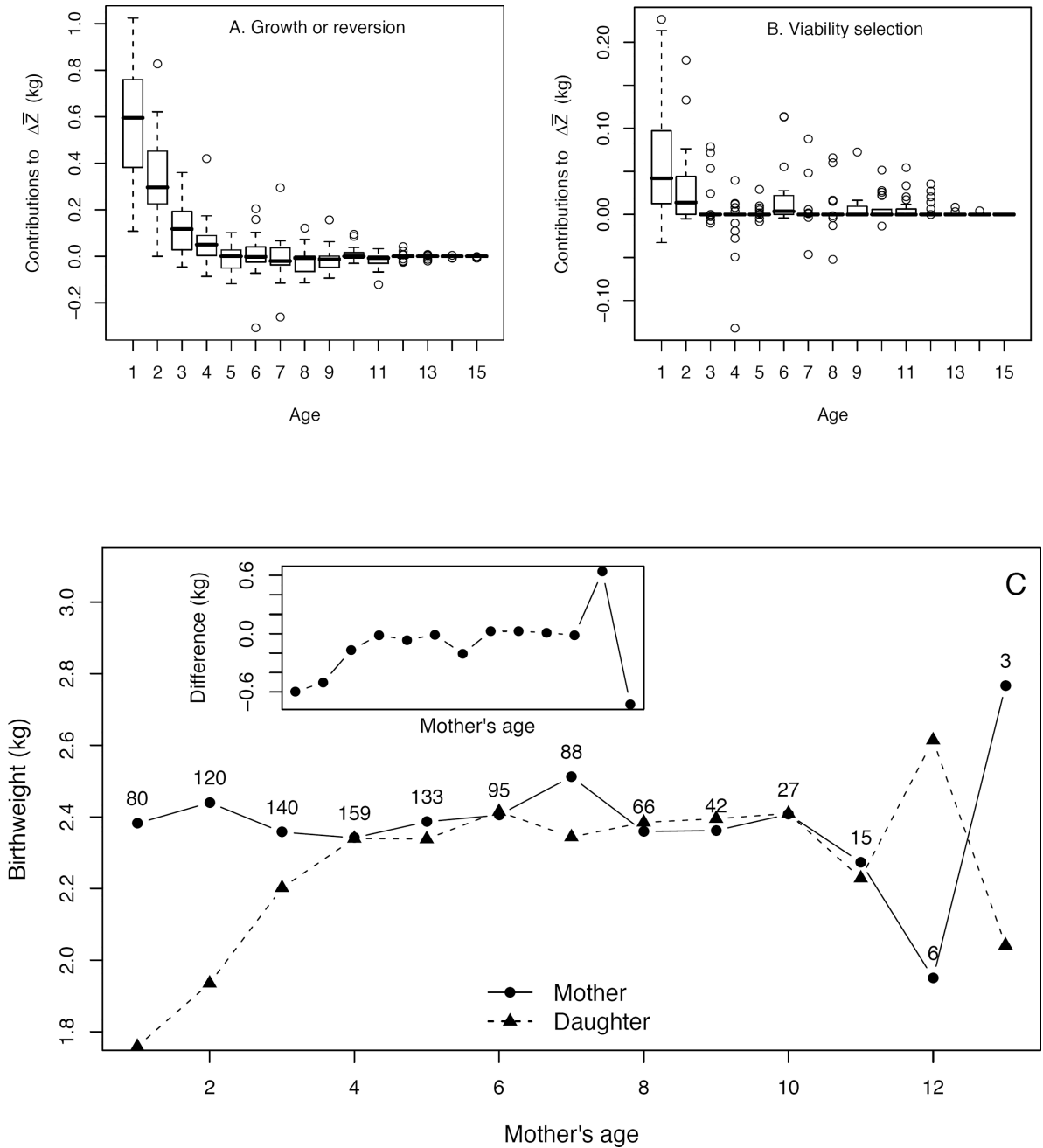


Figure 3. Distributions of age-specific contributions to \bar{Z} from (A) growth or reversion (GR) and (B) viability selection (VS) over time. Box plots show the median contribution (straight lines), inter-quartile range (bars), non-outlier limits (dotted lines) and outliers (circles) for each age group. (C) Mean maternal and female offspring birth weights as a function of maternal age. On average, mothers less than four years old are unable to produce female offspring with birth weights that were as large as their own. The numbers represent the sample size of mothers at each age; the inset graph shows the association between the average difference between offspring and maternal birthweight with mother's age.

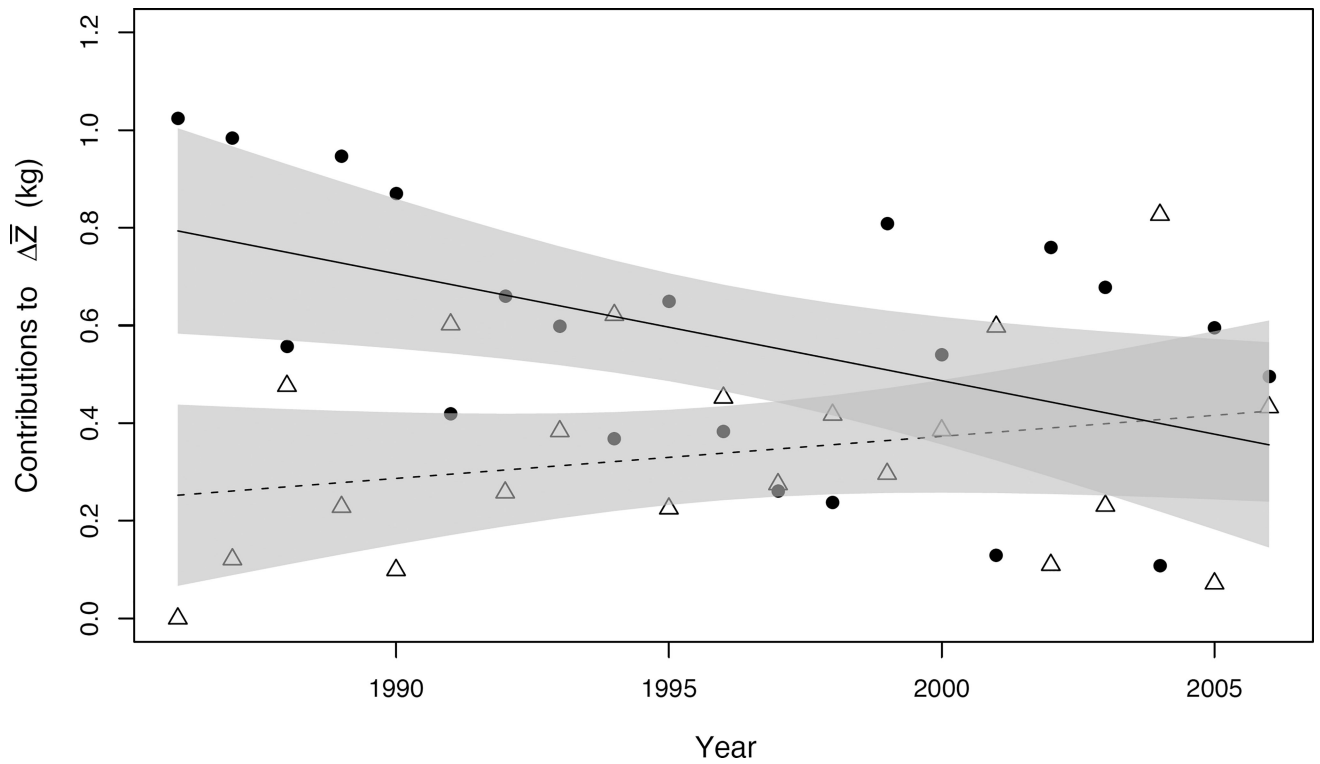


Figure 4.

Temporal trend in the contributions of growth rates from first-to-second (circles), and second-to-third (triangles) August of life (GR) to \bar{Z} . Trends in these contributions occur because of a decrease in growth rates of individuals in the first year of life ($\bar{G}_+(1,t)$) rather than due to a change in the proportion of lambs within the population. The significant decline in the contribution of growth in the first year of life (solid line, $F_{1,19}=6.50$, p -value: 0.02) is partly compensated for by a non-significant increase in the contribution from growth in the second year of life (dashed line, $F_{1,19}=1.29$, p -value: 0.27). Shaded regions indicate the 95% confidence limits.