



The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda Arpat Ozgul, et al. Science **325**, 464 (2009); DOI: 10.1126/science.1173668

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result from warmer SST and a weakening of the large-scale atmospheric circulation in the Pacific in this model.

The question of whether low-level clouds act as a positive or negative feedback to climate change has been an issue for decades. The analysis presented here provides observational evidence that this feedback is positive in the NE Pacific on decadal time scales. The only model in the CMIP3 archive that properly simulates clouds in the NE Pacific and exhibits $2 \times CO_2$ circulation changes that are consistent with multimodel mean produces a reduction in cloud throughout much of the Pacific in response to greenhouse gas forcing (i.e., a positive feedback). Evaluating cloud feedback with one model is, however, far from ideal. This presents a clear challenge to develop a larger number of climate models that can pass these and other tests so that we may have greater confidence in the sign of the low-cloud feedback under future changes in greenhouse gas concentrations.

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

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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 decomposed the change in mean body weight in a free-living population of Soay sheep into all the 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 has so little effect even though weight is heritable, and why environmental change has caused a decline in the body size of Soay sheep.

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 on ecological time scales (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 the quantification of different sources of change. For example, evolutionary models of phenotypic change (5, 6) focus on selection and the 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.

In 1970, Price developed an equation that describes change in the mean value of a phenotypic

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Fig. 1. Mean annual August weights for (A) lambs, (B) yearlings, (C) adults, and (D) senescent female Soay sheep. The solid lines show the observed fluctuations in $\Delta \overline{Z}$, and the dashed lines show those obtained from the application of the age-structured Price equation. Lambs declined on average (±SE) by 90 \pm 30 g/year, yearlings by 170 \pm 30 g/year, adults by 120 \pm 30 g/year, and senescent sheep by 80 \pm 60 g/year. This pattern of decline suggests some compensatory growth at 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 estimating observed mean body weight.

trait, $\Delta \overline{Z}$, 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 $\Delta \overline{Z}$ into contributions from selection and other processes in a variable environment. Survival-related terms are (i) changes in demographic structure (DCs) caused by age-specific survival rates (14); (ii) age-specific viability selection (VS) differentials, which describe change resulting from differential survival associated with the trait (15); and (iii) age-specific trait development, which describes how the average trait value changes among surviving individuals as they age [growth rate (GR)]. Reproduction-related terms are (i) changes in demographic structure caused by age-specific reproduction (DCr) (14); (ii) age-specific fertility selection (FS) differentials, which describe the difference in mean trait value between selected parents and the unselected population (16); (iii) the mean age-specific difference between offspring and parental trait values [offspringmother difference (OMD)] (12); and (iv) the covariation between litter size and the difference between offspring and parental trait values [offspring difference covariance (ODC)] (13).

Using the age-structured Price equation and data from an ungulate population, we decomposed 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 focused on this heritable trait





Fig. 2. Decomposing (**A**) the mean and (**B**) the variance of $\Delta \overline{Z}$ calculated across the time series. (A) Time series of the contributions of different terms to $\Delta \overline{Z}$ summed across age classes. (B) The percentage contribution of each term to the observed total variation in $\Delta \overline{Z}$.



Fig. 3. Distributions of age-specific contributions to $\Delta \overline{Z}$ from (A) growth or reversion (GR) and (B) VS over time. Box plots show the median contribution (heavy horizontal lines), interquartile 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 4 years old are unable to





ing trend despite positive selection for larger body size; it has been speculated that these counterintuitive findings 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% (senescents) and ~0.8% (yearlings) of mean body weight/year. This decline is mirrored by a decrease in hindleg length (7), suggesting that the body weight decline reflects sheep getting smaller rather than a decline in body condition.

We decomposed $\Delta \overline{Z}$ for body weight to generate a time series of each term of the agestructured Price equation (Fig. 2A). These terms sum to produce $\Delta \overline{Z}$. On average, the growth of surviving individuals contributed positively to $\Delta \overline{Z}$ [GR (mean ± SE), 1056 ± 105 g/year), followed by change in the demographic struc-

produce female offspring with birth weights 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 birth weight with the mother's age.

Α 0.1

(kg)

ß

Contributions to

0.8

0.6

0.4

0.2

0.0

-0.2



Fig. 4. Temporal trend in the contributions of GRs to $\Delta \overline{Z}$ from the first to the second (circles) and the second to the third (triangles) August of life. Trends in these contributions occur because of a decrease in the GRs of individuals in the first year of life $[\overline{G}_+(1,t)]$ rather than 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 = 0.02) is partly compensated for by a nonsignificant increase in the contribution from growth in the second year of life (dashed line, $F_{1.19} = 1.29$, P = 0.27). Shaded regions indicate the 95% confidence limits.

ture due to reproduction (DCr, 659 ± 39 g/year) and survival (DCs, 251 ± 161 g/year). Viability and fertility selection contributed less (VS, $153 \pm$ 36; FS, 32 ± 15 g/year). These positive contributions were offset by the negative contribution from the difference between offspring and parental weights (OMD, -2220 ± 51 g/year). The positive terms increased mean body weight by +2151 g/year; the negative terms decreased it by -2232 g/year, giving an average decrease in weight of 81 g/year.

The above analysis pools contributions across age classes. We next investigated age-related variation in $\Delta \overline{Z}$. On average, the positive contributions of VS and GR (Fig. 3) occurred in the first 2 years of life, dropping to 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 $\Delta \overline{Z}$. Examination of this term showed that, on average, younger females produce lambs that are smaller than they themselves 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 collected weight data, daughters weigh, on average, ~150 g less than their mothers did at the same age. Given that the mean contribution of selection was +185 g, this suggests an upper limit for the contribution of a response to selection (22) of 35 g/year, corresponding to ~100 g per generation, or <0.8% of August lamb 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 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/year). The contribution of slower growth between the first and second year of life has partly been compensated for by an increase in the contribution of GRs 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 GRs 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 (NAO) index (23). Lambs grew more slowly in years of high density after a bad winter: Over the course of the study, the NAO has steadily decreased, meaning that long harsh winters occur less frequently than they used to. Changing winter conditions have extended the season of grass growth while reducing the length of time that individuals depend on stored fat reserves. A consequence of this is that an increasing proportion of small slow-growing individuals are surviving through the winter than used to be the case. The survival of these individuals has acted to reduce average growth rates and to increase population size (24). 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 analyzing temporal variation in $\Delta \overline{Z}$ (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. VS and FS accounted for 5.8%, and 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, which in turn suggests 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 determined that positive viability selection on size early in life is countered by young mothers being unable to produce offspring that are as heavy as they themselves were at birth. Finally, we report that environmental change has resulted in a reduction in lamb growth rates, and 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 of 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.

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