

# SELECTION ON HERITABLE SEASONAL PHENOTYPIC PLASTICITY OF BODY MASS

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The ability to cope with environmental change is fundamental to a species' evolution. Organisms can respond to seasonal environmental variation through phenotypic plasticity. The substantial plasticity in body mass of temperate species has often been considered a simple consequence of change in environmental quality, but could also have evolved as an adaptation to seasonality. We investigated the genetic basis of, and selection acting on, seasonal plasticity in body mass for wild bighorn sheep ewes (*Ovis canadensis*) at Ram Mountain, Alberta, under two contrasting environmental conditions. Heritability of plasticity, estimated as mass-specific summer and winter mass changes, was low but significant. The additive genetic variance component of relative summer mass change was greater under good environmental conditions (characterized by a population increase and high juvenile survival) than under poor conditions (population decrease and low juvenile survival). Additive genetic variance of relative winter mass change appeared independent of environmental conditions. We found evidence of selection on summer (relative) and winter (relative and absolute) mass change. For a given mass, more plastic individuals (with greater seasonal mass changes) achieve greater fitness through reproduction in the following year. However, genetic correlations between mass parameters were positive. Our study supports the hypothesis that seasonal plasticity in body mass in vertebrates is an adaptation that evolved under natural selection to cope with environmental variation but genetic correlations with other traits might limit its evolutionary potential.

**KEY WORDS:** Adaptive phenotypic plasticity, body mass, genetic correlations, heritability, *Ovis canadensis*, temperate species.

Phenotypic plasticity, the ability of a genotype to change its phenotype in response to environmental conditions (Bradshaw 1965; Scheiner 1993), is an important adaptation to heterogeneous environments (Via and Lande 1985; Via et al. 1995). Laboratory experiments have clearly shown both genetic variation in plastic-

ity (Stinchcombe et al. 2004) and selection acting on it (Scheiner 1993). Little, however, is known about the genetics of and selection on plasticity in the wild. Laboratory studies have mostly focused on the plasticity of short-lived species, possibly because of the challenges inherent in studying the genetic basis of phenotypic

plasticity in wild long-lived organisms. The recent application of molecular pedigree reconstruction coupled with quantitative genetic models (Kruuk 2004) provides a powerful method to examine the contemporary evolution of quantitative traits in the wild. This methodology can also be applied to the study of phenotypic plasticity by using repeated measurements on individuals experiencing a variety of environmental conditions (Nussey et al. 2007).

A few recent studies that used long-term datasets from mammals and birds have shown that there could be substantial between-individual variation in the plastic response of a trait to environmental variation (Nussey et al. 2005a), and revealed that plasticity can be both heritable (Nussey et al. 2005b) and under directional selection (Brommer et al. 2005; Nussey et al. 2005a,b). Plasticity therefore may evolve in response to selection (but see also Reed et al. 2006). Assessments of the evolutionary potential of plasticity in wild populations, however, remain restricted to a few life-history and phenological traits in only a few species (red deer, *Cervus elaphus*: Nussey et al. 2005a; great tit, *Parus major*: Nussey et al. 2005b; collared flycatcher, *Ficedula albicollis*: Brommer et al. 2005; common guillemot, *Uria aalge*: Reed et al. 2006). Results of other plastic traits and species would further our understanding of the evolutionary dynamics of phenotypic plasticity and of its role in the response of natural populations to changes in their environment.

Seasonal mass changes are ubiquitous in vertebrates (e.g., rodents: Brown 1973; lagomorphs: Hodges et al. 2006; ungulates: Parker et al. 1993; Suttie and Webster 1995; Festa-Bianchet et al. 1996; birds: Meijer et al. 1996). Although there are no direct tests of seasonal mass change as an adaptive response, the ability of an animal to change its mass rapidly in response to drastic change in food availability is often considered an adaptation (e.g., Wikelski and Thom 2000; Hodges et al. 2006). In mammals, the general view is that individuals with greater mass (possibly achieved through a greater summer gain) at the onset of winter or before a period of resource shortage should be advantaged because then they have more resources to use (Suttie and Webster 1995; Parker et al. 1996; Hodges et al. 2006). The adaptive seasonal mass fluctuation hypothesis has received strong support from the discovery of an intrinsic biological basis for the seasonal fluctuation in body mass in temperate species, controlled by photoperiod (Suttie and Webster 1995; Mercer 1998). In this paper we analyze the genetic basis of, and selection on, the seasonal and interannual plasticity of body mass of wild bighorn sheep (*Ovis canadensis*).

In addition to testing whether seasonal plasticity is heritable and can be considered an adaptation, we also had the opportunity to examine how heritability and selective pressures varied over a major change in environmental quality (Charmanier and Garant 2005). Under harsh environmental conditions, a decrease in the genetic variance of a trait can reduce the evolutionary response of that trait despite strong selection acting on it (Wilson et al.

2006). In Soay sheep (*Ovis aries*), Wilson et al. (2006) suggested that environmental heterogeneity, mostly determined by changes in population density, might constrain the microevolution of birth weight through either a low heritable variation in poor environments or weakened selection under good conditions. To test the general validity of this phenomenon, one needs to investigate both selection upon and the genetic basis of a trait under a range of environmental conditions and species.

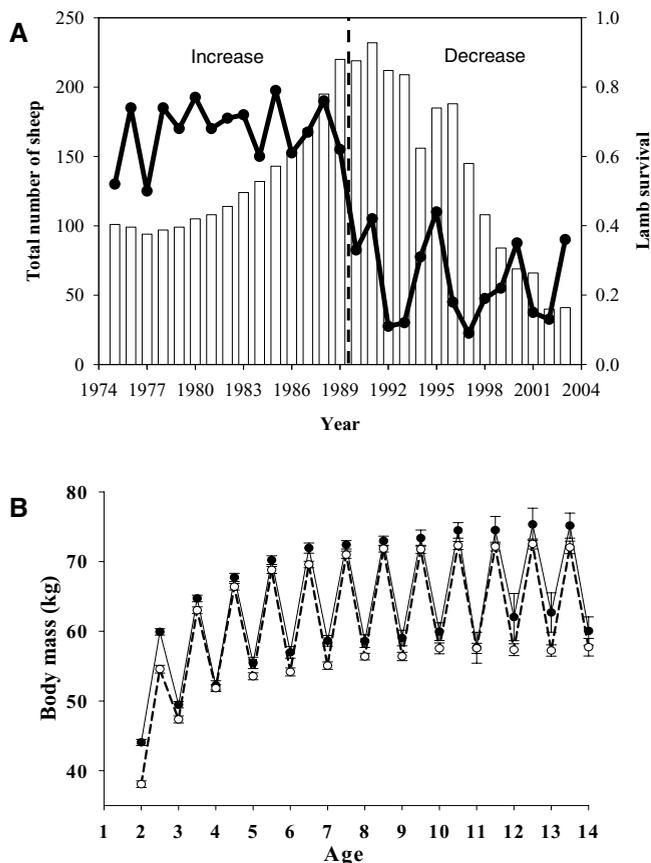
We used a longitudinal study of marked bighorn sheep (*O. canadensis*) to assess the genetic basis of phenotypic plasticity in seasonal and interannual mass change of ewes with known lifetime variation in body mass. We also investigate whether seasonal plasticity is the target of selection or is strictly a function of initial body mass, which is heritable in this population (Réale et al. 1999; Coltman et al. 2003; Coltman et al. 2005). We decomposed the seasonal phenotypic variance in mass into six parameters (spring and autumn mass, relative and absolute summer mass change, and relative and absolute winter mass change) over a 25-year period. We investigated three questions: (1) Is seasonal mass change (both absolute and relative) heritable, or is it strictly a consequence of environmental changes? (2) Is seasonal variation in mass under selection? (3) Do the selection regime and heritability of a trait change according to environmental conditions? Long-term monitoring of marked bighorn sheep at Ram Mountain includes repeated measurements of body mass each summer from individuals of known pedigree. The study therefore provides a unique opportunity to investigate the genetic basis and adaptive function of seasonal plasticity in body mass in the wild. To the best of our knowledge, despite the importance of seasonal plasticity to survive in most environments, no studies have investigated plasticity in morphological characters in mammals and there are no estimates of repeatability, heritability, and selection on seasonal mass change for vertebrates.

## Methods

### STUDY AREA AND BIGHORN POPULATION

We studied a marked population of bighorn sheep at Ram Mountain (elevation 1080 to 2170 m) in Alberta, Canada, about 30 km east of the main range of the Canadian Rockies (52°N, 115°W). More than 98% of the sheep are individually recognizable, marked at first capture using ear tags or visual collars. Since 1975, this population has been closely monitored: from late May to late September, sheep are captured between one and seven times. More than 90% of the ewes are captured at least twice each summer in a corral trap baited with salt and weighed to within 125 g using a Detecto spring scale (see Festa-Bianchet et al. 1996; Jorgenson et al. 1997 for more details). Lactation status of females is determined at each capture. Lamb-mother associations and lamb survival are noted during field observations from late May to the end of September.

We used data from ewes aged two years and older, because seasonal mass changes are complicated by the growth for lambs and yearlings. Although ewes still gain some mass until about six years of age, their curvilinear growth rate in summer is similar for all age classes (Festa-Bianchet et al. 1996). We only included ewes for which we had at least two mass measurements during one year from 1975 to 2003. In ungulates, individuals are most affected by poor environmental conditions in their first year of life (Gaillard et al. 2000). Consequently, we identified two periods of contrasting environmental conditions that differed in lamb survival and population trajectory (Fig. 1A): a population increase associated with good environmental conditions and high lamb survival, followed by a population decrease with low lamb survival and an



**Figure 1.** (A) Population density (total number of sheep) and lamb survival (from birth to one year old) of the Ram Mountain population. Mean lamb survival for the period of increase (1975–1989) and decrease (1990–2003) in density was respectively of 67% (SE = 0.023) and 24% (SE = 0.033), quasi-binomial model:  $t = -8.47$ ,  $P < 0.001$ . (B) Seasonal variation in body mass according to environmental conditions (phase of increasing or decreasing population density) for bighorn ewes between 2 to 14 years of age at Ram Mountain, Alberta (1975–2003,  $n = 1373$  weights from 243 individuals). Solid line with black symbols refers to the period of increase (1975–1989) and dotted line with open symbols refers to period of decrease in density (1990–2003).

apparent deterioration of environmental conditions—see Wilson et al. (2006) for a similar approach.

### MASS PARAMETERS

We described yearly mass fluctuations of individual ewes (Fig. 1B) using six mass parameters:

*Adjusted spring mass* and *autumn mass*: We obtained adjusted mass in spring and autumn using repeated mass measurements of the same individual during each summer. We used linear mixed models with a restricted maximum likelihood (REML) method to adjust mass by fitting a model in which mass at capture was the dependent variable and the square root of capture date (considering 25 May as day 1) was the independent variable. We included ewe identity (as an intercept) and the interaction between ewe identity and day of capture (as a slope representing individual growth rate) as random effects. We fitted separate regression models for each year of the study. The predicted values of individual intercepts (weight on day 0) and slopes (growth rates) were then obtained using the `ranef.lme` function (Pinheiro and Bates 2000) and used to adjust individual mass to June 5 (spring mass) and September 15 (autumn mass). The square root transformation linearized the relationship between mass and date. Because this method takes into account individual identity as well as the average ewe mass gain rate each year, it provides a more accurate estimate than simply fitting a regression model for each individual in each year, especially for individuals with few measurements. Mass on September 15 is likely very close to the yearly maximum, but by June 5 ewes have already gained some mass, as seasonal gain probably begins in May (Festa-Bianchet et al. 1996).

*Absolute summer mass change* was the difference between autumn and spring mass in the same year.

*Absolute winter mass change* was the difference between autumn mass in year  $x$  and spring mass in year  $x + 1$ .

*Relative summer and winter mass changes*: Absolute mass changes are a weak function of initial mass: heavy ewes generally gain less mass in summer and lose more mass in winter compared to light ewes (see Results). To measure individual mass change independent of initial mass, we calculated mass-specific changes (hereafter relative mass changes) by including in regression models adjusted mass in spring for summer mass changes and adjusted mass in autumn for winter mass changes. This procedure avoids the use of ratios or percentages and allows to estimate selection and heritability on relative mass changes.

### PEDIGREE RECONSTRUCTION AND QUANTITATIVE GENETIC ANALYSES

The known pedigree of the population consists of 717 maternities and 402 paternities, involving 936 marked sheep monitored since 1971. Paternity was determined using molecular techniques (Coltman et al. 2002, 2003, 2005). Genetic variance components

and heritabilities of the six mass parameters were estimated using an animal model (Kruuk 2004) with a REML approach, implemented in ASReml v1.1 (Gilmour et al. 2002). Age, reproductive status, and year were included as fixed effects in all models. Models of relative mass change included initial body mass as a covariate (spring mass for summer mass change and autumn mass for winter mass change). Total phenotypic variance ( $V_P$ ) of a trait was decomposed into its additive genetic ( $V_A$ ), permanent environmental ( $V_{PE}$ ), and residual ( $V_R$ ) components. Narrow sense heritability ( $h^2$ ) was calculated as  $V_A/V_P$  and the coefficient of additive genetic variance, in which the additive genetic variance is scaled by the trait mean value was calculated as:  $CV_A = 100 \cdot \sqrt{V_A}/\text{trait mean}$ . Environmental maternal effects were also assessed by including the mother's identity in the model as a random effect, but because this component of variance was very small and not significant, results are presented without it. Genetic maternal effects were not estimated because sample size was too small.

We first fitted univariate models for each mass parameter including all individuals and then reran the analyses for each population phase (increase and decrease: Fig. 1A) to assess the stability of variance components depending on the environment. Statistical significance of variance components and heritabilities, and of differences between pairs of additive variances and heritabilities were assessed by one-tailed and two-tailed  $t$ -tests, respectively, using standard errors provided by ASReml. We then estimated genetic correlations between pairs of traits with large additive variance (namely, mass in spring, mass in autumn, and relative summer and winter changes) using bivariate animal models and the whole dataset. We also estimated the cross-environment genetic covariances and correlations for a given trait by conducting a bivariate analysis in which the trait value in the increasing phase (i.e., environment 1) was considered a different trait from that measured in the decreasing population phase (i.e., environment 2). For the purposes of comparison, we also calculated phenotypic correlations using pairwise Pearson product moment correlations among traits. For these correlations, trait values were obtained from the residuals of a general linear model that included age, reproductive status, and year as fixed effects (Coltman et al. 2005). Phenotypic correlations and their significance were calculated with Statistica version 5.5 (Statsoft 1999).

#### SELECTION ANALYSES: INDIVIDUAL CONTRIBUTION TO POPULATION GROWTH

We quantified fitness by the individual contribution to population growth ( $p_{t(i)}$ ) from year  $t$  to year  $t + 1$  (Coulson et al. 2006). This new metric has two main advantages over traditional fitness estimates: it simultaneously accounts for both survival and fecundity components on the same scale, allowing the decomposition of the effects of selection via each path, and it is standardized

for change in population size. It estimates individual contribution to population growth using a three-step procedure. First, realized contribution of a focal individual from year  $t$  to year  $t + 1$  is calculated by summing the number of surviving offspring (multiplied by 0.5 because each parent contributes half the genes) produced over this time step that are alive at the end of the time step, plus one if the parent survives. Then, population growth without the focal individual is estimated by recalculating population growth after removing the individual's realized contribution. The fitness of an individual (i.e., its individual contribution to population growth) is the difference between population growth with and without the focal individual (see Coulson et al. 2006 for a detailed description).

Our selection analyses used a traditional regression approach (Lande and Arnold 1983). Trait values were standardized ( $\text{trait}_i - \text{mean}(\text{trait}_x)/\text{standard deviation}(\text{trait}_x)$ ) to allow comparison of the strength of selection among traits. Selection differentials ( $S_i$ ) were obtained by regressing each one of the six standardized mass parameters against relative fitness, as  $p_{t(i)}$  divided by the population growth rate (mean fitness). In each regression we controlled for age and reproductive status. We first investigated the form of the selection function using generalized additive models (Gams). As most functions showed linear or curvilinear relationships (see Results), selection differentials were estimated using linear and quadratic models. We did not detect any significant correlational selection between mass parameters in each quadratic model and therefore decided not to show these results. We compared selection differentials according to population phases with a log-likelihood ratio test of models with and without the interaction between density and each mass parameter. As our data included repeated measurements of the same ewe over time, we reported coefficients of selection from standard linear analyses but significance tests used linear mixed effects models. Analyses were performed with R version 2.2.1 ([www.r-project.org](http://www.r-project.org)).

## Results

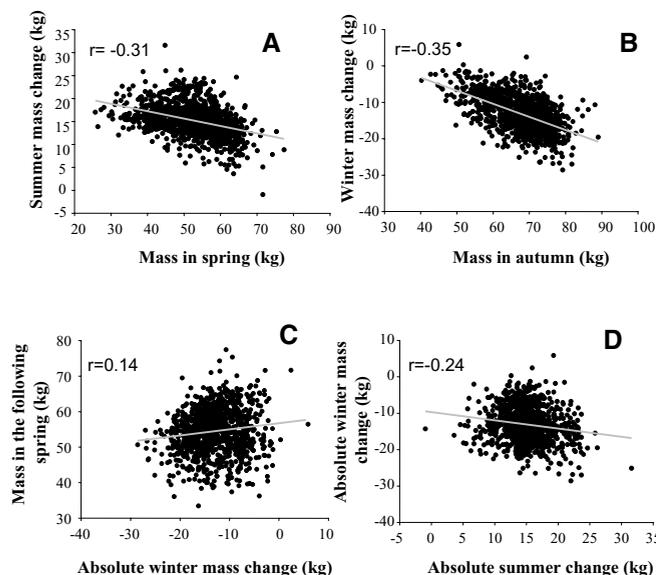
### QUANTITATIVE GENETICS

Bighorn ewes showed conspicuous seasonal variation in body mass (Fig. 1B). Heritability estimates for mass in spring and in autumn (Table 1) were similar to those previously reported for this population (Coltman et al. 2005). Relative mass changes in both summer ( $t = 3.23$ ,  $P < 0.001$ ) and winter ( $t = 2.51$ ,  $P = 0.006$ ) were moderately heritable (Table 1). Heritability was weak but significant for absolute summer mass change ( $t = 2.80$ ,  $P < 0.001$ ) and zero for absolute winter mass change. All phenotypic correlations among mass in spring, mass in autumn, summer, and winter mass changes were highly significant ( $P < 0.001$ , Fig. 2) and most were negative. We found a marginally nonsignificant positive genetic correlation between mass in June and relative summer mass change ( $0.467 \pm 0.255$ ,  $P = 0.068$ ). We also found

**Table 1.** Genetic components of mass parameters obtained from univariate animal models for all bighorn ewes. See text for details of models. Total phenotypic variance ( $V_P$ ) of a trait was decomposed into its additive ( $V_A$ ), permanent environmental ( $V_{PE}$ ), and residual ( $V_R$ ) components. Heritability ( $h^2$ ) was calculated as  $V_A/V_P$  and the coefficient of additive genetic variance was calculated as  $CV_A = 100 \cdot \sqrt{V_A} / \text{trait mean}$ .  $N = 243$  ewes in analyses.

Traits	Parameter Estimates						
	$N$	$h^2$ (SE)	$V_A$ (SE)	$V_{PE}$ (SE)	$V_R$ (SE)	$V_P$ (SE)	$CV_A$
Mass in spring	1373	0.283 (0.103)	5.92 (2.37)	7.55 (2.00)	7.45 (0.32)	20.92 (1.53)	4.64
Mass in autumn	1373	0.365 (0.112)	7.60 (2.66)	7.73 (2.13)	5.51 (0.24)	20.84 (1.69)	4.07
Absolute summer change	1373	0.056 (0.020)	0.27 (0.10)	0	4.55 (0.19)	4.82 (0.19)	3.43
Relative summer change	1373	0.210 (0.065)	1.00 (0.34)	0.32 (0.25)	3.45 (0.15)	4.77 (0.25)	6.55
Absolute winter change	1084	0	0	0	11.46 (0.50)	11.46 (0.50)	0
Relative winter change	1084	0.183 (0.073)	2.04 (0.87)	1.27 (0.71)	7.84 (0.39)	11.14 (0.67)	10.89

a strong positive genetic correlation between mass in June and in September ( $0.993 \pm 0.003$  SE,  $P < 0.001$ ) and a weaker marginally nonsignificant genetic correlation between mass in September and relative summer mass change ( $0.290 \pm 0.149$ ,  $P = 0.053$ ). However, to obtain convergence for these two bivariate models we had to remove the permanent environment effect and thus these results should be regarded with caution (see also Coltman et al. 2005). The genetic correlation between relative summer mass and winter mass change was positive ( $0.880 \pm 0.094$ ,  $P < 0.001$ ). Other models including relative winter mass change failed to converge.



**Figure 2.** Relation between (A) absolute summer mass gain and mass in spring, (B) absolute winter mass change and mass in autumn, (C) mass in the following spring and winter mass change, and (D) absolute winter change and summer change for bighorn sheep ewes, two years and older at Ram Mountain, Alberta (1975–2003). Note 1: Phenotypic correlations, from pairwise Pearson product moment. Note 2: the correlation between mass in spring and mass in fall was 0.88. All correlations  $P > 0.001$ .

### SELECTION ON MASS PARAMETERS

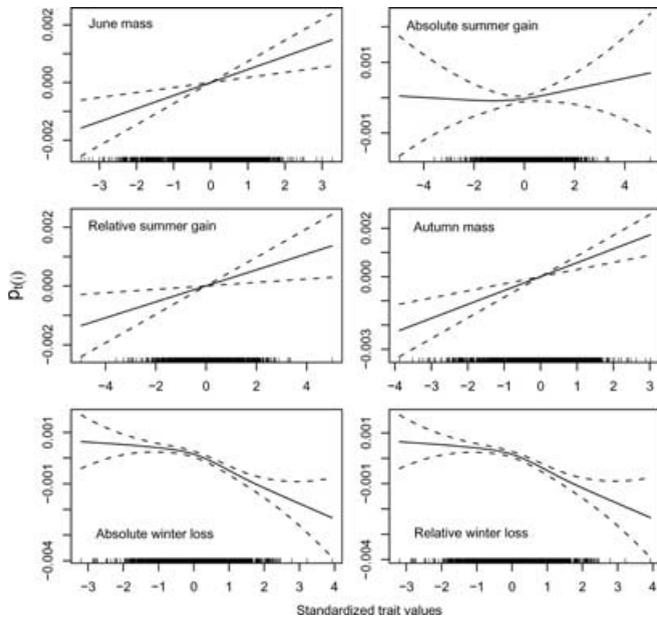
Linear selection differentials were significant for all but one (absolute summer change) mass parameter (Table 2). Spring mass, relative summer mass change, and autumn mass all had positive effects on fitness (Table 2). A negative linear selection on both relative and absolute winter mass loss suggested a selective advantage for ewes that lost more mass during winter. We also found significant negative quadratic selection (convex) for both absolute and relative winter mass change (Table 2 and Fig. 3).

We then decomposed selection on mass parameters through individual contributions to population growth rate via recruitment and survival. Natural selection affected mass parameters almost exclusively via recruitment (Fig. 4). Larger mass in spring and fall and greater relative summer change all led to higher recruitment in

**Table 2.** Directional ( $\beta_i$ ) and quadratic ( $\gamma_{ii}$ , concave/convex selection) standardized selection differentials measured between mass parameters of bighorn ewes and individual contribution to population growth ( $p_{t(i)}$ ) from year  $t$  to year  $t+1$ . Different models have been fitted for mass in spring and autumn because of their high phenotypic correlations (see text).

Traits	$\beta_i$ (SE) $\times 10^{-4}$ via $p_{t(i)}$	$\gamma_{ii}$ (SE) $\times 10^{-4}$ via $p_{t(i)}$
Mass in spring	4.52 (1.39)***	-0.51 (0.73)
Relative summer mass change	2.72 (1.07)*	0.33 (0.51)
Absolute summer change	0.87 (0.97)	0.66 (0.51)
Mass in autumn	5.74 (1.40)***	0.33 (0.73)
Winter relative mass change	-4.32 (0.72)***	-1.17 (0.43)*
Absolute winter mass change	-4.33 (0.67)***	-1.17 (0.43)*

Note: Coefficients and standard errors (SE) are from linear models but significance testing was made using linear mixed effects models controlling for repeated measurements, \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

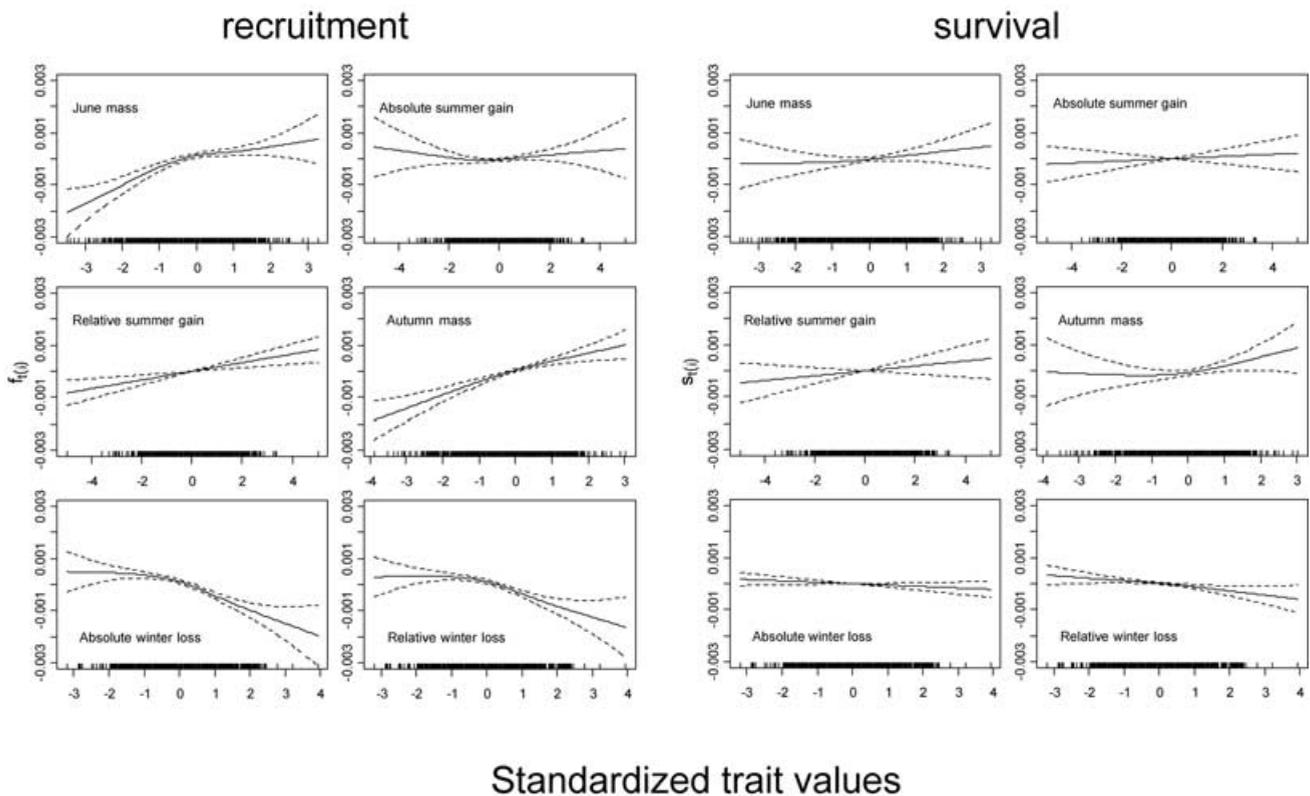


**Figure 3.** Relationships between fitness (measured as individual contribution to population growth) adjusted for age and the six standardized mass parameters as obtained from nonlinear generalized additive selection models. Tick marks show the locations of the observations. Dashed lines are 95% pointwise.

the following year (Table 3). Females with greater winter mass loss (both absolute and relative) were also selected through the fecundity component. There was a weak but significant quadratic convex selection on spring mass and quadratic concave selection on winter mass loss (both absolute and relative) for recruitment. For survival, the only significant relationship was a weak convex selection on fall mass (Table 3 and Fig. 4).

**ENVIRONMENTAL EFFECTS ON HERITABILITY**

Comparisons of heritabilities among population phases revealed no significant differences for any of the mass parameters (Table 4). The additive genetic variance component for summer mass change, however, was higher during the increasing than the decreasing phase ( $t = 1.97, P = 0.049$ , Table 4). During the decreasing phase the additive genetic component was not significant ( $t = 1.31, P = 0.096$ , Table 4). Also, the coefficient of additive genetic variance was almost twice as large in the increasing as in the decreasing phase (Table 4). Cross-environment genetic correlations for mass parameters were all significantly different from zero but not different from unity (mass in spring:  $0.926 \pm 0.165$ , mass in autumn:  $0.999 \pm 0.081$ , relative summer change:  $1.073 \pm 0.212$ , relative winter change:  $0.719 \pm 0.322$ ).



**Figure 4.** Association between individual contribution to population growth (adjusted for age) via recruitment and survival and six mass parameters as obtained from nonlinear generalized additive selection models. Tick marks show the locations of the observations. Dashed lines are 95% pointwise.

**Table 3.** Directional ( $\beta_i$ ) and quadratic ( $\gamma_{ii}$ , concave/convex selection) standardized selection differentials obtained from a regression between mass parameters and individual contribution to population growth via survival ( $s_{t(i)}$ ) and fecundity ( $f_{t(i)}$ ) from year  $t$  to year  $t+1$ , and depending on environmental conditions.

Traits	via $s_{t(i)}$	via $f_{t(i)}$
$\beta_i$ (SE) $\times 10^{-4}$		
Mass in spring	1.16 (1.01)	3.33 (0.63)***
Relative summer mass gain	0.93 (0.78)	1.67 (0.49)***
Absolute summer mass gain	0.42 (0.70)	0.37 (0.45)
Mass in autumn	1.62 (1.02)	4.02 (0.65)***
Relative winter mass change	-1.21 (0.41)	-3.09 (0.53)***
Absolute winter mass change	-0.55 (0.39)	-3.76 (0.50)***
$\gamma_{ii}$ (SE) $\times 10^{-4}$		
Mass in spring <sup>2</sup>	0.63 (0.53)	-1.05 (0.33)**
Relative summer mass gain <sup>2</sup>	0.23 (0.38)	0.15 (0.23)
Absolute summer mass gain <sup>2</sup>	0.32 (0.37)	0.39 (0.23)
Mass in autumn <sup>2</sup>	1.08 (0.53)*	-0.72 (0.33)
Relative winter mass change <sup>2</sup>	-0.26 (0.25)	-0.91 (0.32)**
Absolute winter mass change <sup>2</sup>	-0.20 (0.25)	-0.97 (0.32)**

Note: Coefficients and standard errors (SE) are from linear models but significance testing was made using linear mixed effects models controlling for repeated measurements, \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

**Table 4.** Genetic components of mass parameters from univariate animal models according to population phases. See text for details of models. Total phenotypic variance ( $V_P$ ) of a trait was decomposed into its additive ( $V_A$ ), permanent environmental ( $V_{PE}$ ), and residual ( $V_R$ ) components. Heritability ( $h^2$ ) was calculated as  $V_A/V_P$  and the coefficient of additive genetic variance was calculated as  $CV_A = 100 \times \sqrt{V_A}/\text{trait mean}$ .  $N = 243$  ewes in analyses.

Traits	Parameter Estimates						
	$N$	$h^2$ (SE)	$V_A$ (SE)	$V_{PE}$ (SE)	$V_R$ (SE)	$V_P$ (SE)	$CV_A$
Mass in spring							
Increase	563	0.317 (0.144)	6.54 (3.24)	6.17 (2.83)	7.94 (0.57)	20.64 (1.98)	4.87
Decrease	810	0.433 (0.141)	9.02 (3.48)	5.86 (2.58)	5.97 (0.34)	20.85 (2.11)	5.74
Mass in autumn							
Increase	563	0.468 (0.155)	9.59 (3.71)	4.53 (2.89)	6.38 (0.46)	20.50 (2.15)	4.58
Decrease	810	0.373 (0.144)	7.31 (3.20)	8.02 (2.59)	4.28 (0.24)	19.61 (2.03)	3.99
Relative summer change							
Increase	563	0.200 (0.053)	1.23 (0.37)	0	4.89 (0.34)	6.11 (0.42)	7.35
Decrease	810	0.098 (0.075)	0.34 (0.26)	0.68 (0.28)	2.45 (0.14)	3.47 (0.226)	3.79
Relative winter change							
Increase	459	0.128 (0.058)	1.62 (1.17)	0.86 (1.05)	10.22 (0.84)	12.71 (0.99)	9.71
Decrease	625	0.222 (0.100)	2.01 (0.98)	0	7.01 (0.47)	9.04 (0.65)	10.80

## ENVIRONMENTAL EFFECTS ON SELECTION

Selection differentials on all mass parameters differed significantly among population phases (all  $P < 0.001$ ), except for absolute summer gain ( $P = 0.160$ ) and mass in autumn ( $P = 0.100$ ). During the increase phase, linear selection differentials of mass in spring and mass in autumn were significantly positive. Absolute and relative winter mass changes were negatively related to fitness (linear selection, Table 5), suggesting a benefit for ewes that lost more mass. On the other hand, during the population decrease phase, the positive relationships between mass in spring and relative summer gain and fitness were no longer apparent but selection was greater for mass loss during winter (both absolute and relative, Table 5). When analyses were conducted for each of the population phases we found no evidence of disruptive selection for any mass parameter.

## Discussion

### SEASONAL MASS CHANGE: HERITABILITY AND SELECTION

Our analysis revealed that seasonal mass changes of bighorn ewes include both genetic and environmental components. Interestingly, we found that relative summer and winter mass changes had significant genetic variation and were heritable, suggesting a potential evolutionary response to selection in seasonal mass changes. Indeed, selection on relative winter and summer mass change favored more plastic individuals that had greater recruitment in the following year. Coltman et al. (2005) previously reported no selection on autumn mass for females in this population.

**Table 5.** Directional ( $\beta_i$ ) and quadratic ( $\gamma_{ii}$ , concave/convex selection) standardized selection differentials obtained from a regression between mass parameters and individual contribution to population growth ( $p_{t(i)}$ ) from year  $t$  to year  $t+1$ , and depending on environmental conditions.

Traits	Increase in population density	Decrease in population density
$\beta_i$ (SE) $\times 10^{-4}$ via $p_{t(i)}$		
Mass in spring	6.68 (1.71) ***	3.00 (2.33)
Relative summer mass gain	2.88 (1.41)	2.91 (1.59)
Absolute summer mass gain	-0.19 (1.24)	1.87 (1.49)
Mass in autumn	7.43 (1.74) ***	4.27 (2.32)
Relative winter mass change	-2.25 (0.67) ***	-5.99 (1.30) ***
Absolute winter mass change	-2.73 (0.65) ***	-4.93 (1.21) *
$\gamma_{ii}$ (SE) $\times 10^{-4}$ via $p_{t(i)}$		
Mass in spring <sup>2</sup>	-0.18 (0.91)	-0.26 (1.30)
Relative summer mass gain <sup>2</sup>	1.10 (0.72)	-0.48 (0.86)
Absolute summer mass gain <sup>2</sup>	1.65 (0.72)	-0.39 (0.86)
Mass in autumn <sup>2</sup>	0.84 (0.91)	0.60 (1.24)
Relative winter mass change <sup>2</sup>	-0.11 (0.39)	-2.19 (0.83)
Absolute winter mass change <sup>2</sup>	-0.07 (0.38)	-2.02 (0.83)

**Note:** Coefficients and standard errors (SE) are from linear models but significance testing was made using linear mixed effects models controlling for repeated measurements, \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

They, however, measured fitness as lifetime reproductive success, a generational measure that does not account for variation in population size. Here we used a novel estimate of fitness calculated on a yearly basis (Coulson et al. 2006) and should thus be more powerful in detecting selection of traits. This approach also allowed us to partition selection, on the same scale, among fitness components. Interestingly, we found that most of the selection on mass parameters acts via the fecundity components of fitness. Females appeared to trade current reproduction for survival when resources were limited, leading to very little variation in survival. This confirms that bighorn sheep ewes adopt a conservative reproductive strategy (Festa-Bianchet and Jorgenson 1998) by favoring survival over current reproduction.

In mammals, individuals with greater mass at the onset of winter (possibly achieved through a greater summer gain) are generally assumed to be advantaged over others because they have more resources to use during the seasonal resource shortage (Parker et al. 1993; Suttie and Webster 1995; Parker et al. 1996;

Hodges et al. 2006). The higher fitness for ewes with greater relative and absolute winter loss supports this view but should be interpreted cautiously because winter mass change of ewes that die over winter cannot be included in this analysis. The frequency distribution of winter mass change is therefore truncated on the right. If individuals that died during winter were those that had not accumulated enough body reserve, our estimates of selection on winter mass change would be conservative. Selection analysis reveals that ewes at the right tail of the trait frequency distribution (both for absolute and relative winter change) had lower fitness. Selection against individuals with small winter mass change may seem counterintuitive as it appears to imply an advantage of losing body reserves. We suggest that this result reflects a physiological constraint; ewes in poor condition at the onset of winter have a low mass change (relative and absolute) because they have little mass to lose. Because winter forage is insufficient to maintain body weight, a very limited mass loss during winter indicates poor body reserves and therefore an inability to reproduce successfully. For both relative and absolute winter changes, there appeared to be a threshold of mass loss. As long as ewes could lose a minimum amount of mass, their fitness was unaffected (Fig. 3). Beyond that threshold, however, the less mass they lost (suggesting poor body reserves), the worse they fared. Females who survived the winter despite losing little mass arrived in spring in poor condition and were less likely to wean a lamb the following autumn than females in better condition.

The shape of the selection function was the same for relative and absolute winter mass loss, in contrast to the result for summer mass changes. This likely arises because relative and absolute mass changes in winter and summer have different ecological relationships. A small gain in summer may mean inadequate nutrition, or that the ewe did not need to gain much mass to optimize body reserves, but a small loss in winter should always indicate inadequate fat reserves. Ewes appear more capable of controlling their summer mass gain than their winter mass loss, as suggested by a stronger correlation in mass in successive years for the same ewe in mid-September than in early June (Festa-Bianchet et al. 1996).

Absolute summer change heritability was very low, absolute winter change was not heritable and absolute summer changes were not selected, opposite to the results for relative changes. Absolute changes are a heterogeneous combination of individual states and may not detect individual variation in fitness components. For example, in a good year, a ewe in good condition in spring may only need to gain 5 kg over the summer. Alternatively, in a bad year, a ewe in poor condition may gain only 5 kg because of resource limitations. In these two cases, the absolute gain is the same but the biological consequences are very different. Those differences can only be detected when the variations in mass are observed on a relative scale, that is, when mass-specific changes

(gain or loss) are considered. This likely explains the contrasting results obtained for heritability and selection for relative and absolute mass parameters.

### ENVIRONMENTAL EFFECTS ON HERITABILITY, SELECTION, AND THE EVOLUTIONARY POTENTIAL OF PHENOTYPIC PLASTICITY

Heritabilities were similar during both population phases, although genetic variation for summer mass change was slightly lower under poor conditions. That result is consistent with a recent meta-analysis showing lower heritability for morphological traits under unfavorable conditions (Charmantier and Garant 2005). The overall small apparent effect of changing environmental conditions in our study might be associated with the larger standard error of period-specific estimates. The genetic correlations across population phases for the different mass traits were not different from one and were significantly different from zero. These strong correlations suggest that there was no genotype–environment interaction in the two population phases and that the same genes affected each mass parameter under both environmental conditions in the same way (Via and Lande 1985).

Although the population increased there was a positive selection of mass in spring, mass in autumn, and relative summer mass change (ewes with greater mass-specific gain had higher fitness), negative selection for both absolute and relative winter mass changes (ewe with greater winter loss had higher fitness). Under adverse conditions, however, the relationships between fitness and mass vanished, except for absolute and relative winter mass changes that remained negatively related to fitness. One possible explanation is that during periods of resource shortage selection during the juvenile stage may increase (Gaillard et al. 2000). If only the larger and more plastic individuals survive the juvenile period, ewes that survive to two years of age might be released from selection on mass during adulthood. This is supported indirectly by the observation that lamb mass affected survival only at high density (Festa-Bianchet et al. 1997). On the other hand, heritability of traits appeared to be similar in both environmental conditions considered in this study. Thus, our results contrast with the Wilson et al. (2006) study, which showed a microevolutionary constraint on birth weight in Soay sheep through low heritable variation in poor environments and weakened selection under good conditions. However, results may differ when considering selection for other demographic classes other than adult ewes (Coulson et al. 2003).

### POTENTIAL GENETIC CONSTRAINTS ON THE INDEPENDENT EVOLUTION OF MASS TRAITS

Selection favored greater plasticity in mass, and therefore one may expect plasticity to increase over time in the population. Genetic

covariance between two traits can reduce the evolutionary potential of each of these traits, at least in the short term (Lande 1982; Etterson and Shaw 2001; Sgrò and Hoffmann 2004). The strong phenotypic and genetic correlations between mass in spring and mass in autumn indicate a strong constraint on the independent evolution of each trait. However, selection pressures acted in the same direction on these traits and favored heavier individuals. The positive genetic correlations between mass parameters and especially the strong correlations within traits among phases suggest that the same genes affected each mass parameter under different conditions. Absolute phenotypic correlations between mass changes were weaker than those between absolute masses (Fig. 2), suggesting a weak constraint on the evolution of plasticity in mass. In contrast, absolute summer and winter mass change were negatively phenotypically correlated ( $r_P = -0.24$ ) but showed a strong positive genetic correlation ( $r_G = 0.88$ ). Strong genetic correlation coupled with antagonistic selection pressures acting on these two traits (Fig. 3) suggests that relative mass changes might not evolve independently. It is also possible that the apparent selection on seasonal mass plasticity is a byproduct of a correlation with other life-history traits at different developmental stages. Evolutionary models suggest a limit to phenotypic plasticity as more plastic individuals are likely to incur great fitness costs (De Witt et al. 1998). For example, plasticity might be correlated with slower growth or greater developmental instability. We did not find evidence of costs but the observational nature of our data limits our capacity to identify such costs.

## Conclusions

During periods of food shortages, organisms rely on their abilities to conserve energy and survive. A decrease in body mass under these conditions has been considered an adaptation (Wikelski and Thom 2000; Hodges et al. 2006). Marine iguanas, for example, reduce both body mass and length during periods of resource shortage (Wikelski and Thom 2000). The seasonal fluctuation in body mass in northern species is another example. The hypothesis that seasonal mass fluctuation is adaptive has received strong support with the discovery of an intrinsic biological basis for the seasonal fluctuation in body mass in temperate species, controlled by photoperiod (Suttie and Webster 1995; Mercer 1998). Our results suggest that relative seasonal mass changes are heritable and that selection on seasonal plasticity acts both directly on mass changes and indirectly by optimizing spring and autumn body mass, so that more plastic individuals are advantaged. Females with greater mass in autumn, achieved through a combination of large mass in spring and greater relative summer change, have more resources available to use during winter and are therefore more likely to reproduce successfully in the following year. Our results support the hypothesis that seasonal plasticity in body mass

is an adaptation that evolved under natural selection to cope with environmental variation (Hodges et al. 2006). However, genetic correlations among mass parameters suggest constraints on the independent evolution of seasonal plasticity.

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## REFERENCES

- Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv. Gen.* 13:115–155.
- Brommer, J. E., J. Merilä, B. C. Sheldon, and L. Gustafsson. 2005. Natural selection and genetic variation for reproductive reaction norms in a wild bird population. *Evolution* 59:1362–1371.
- Brown, J. 1973. Changes in patterns of seasonal growth of *Microtus pennsylvanicus*. *Ecology* 54:1103–1110.
- Charmantier, A., and D. Garant. 2005. Environmental quality and evolutionary potential: lessons from wild populations. *Proc. R. Soc. Lond. B* 272:1415–1425.
- Coltman, D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in bighorn rams. *Proc. R. Soc. Lond. B* 269:165–172.
- Coltman, D. W., P. O'Donoghue, J. T. Hogg, and M. Festa-Bianchet. 2005. Selection and genetic (co)variance in bighorn sheep. *Evolution* 59:1372–1382.
- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- Coulson, T., T. G. Benton, P. Lundberg, S. R. X. Dall, B. E. Kendall, and J. M. Gaillard. 2006. Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proc. R. Soc. Lond. B* 273:547–555.
- Coulson, T., L. E. B. Kruuk, G. Tavecchia, J. M. Pemberton, and T. H. Clutton-Brock. 2003. Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution* 57:2879–2892.
- De Witt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* 13:77–81.
- Etterson, J. R., and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. *Science* 294:151–154.
- Festa-Bianchet, M., and J. T. Jorgenson. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behav. Ecol.* 9:144–150.
- Festa-Bianchet, M., J. T. Jorgenson, C. H. Bérubé, C. Portier, and W. D. Wishart. 1997. Body mass and survival of bighorn sheep. *Can. J. Zool.* 75:1372–1379.
- Festa-Bianchet, M., J. T. Jorgenson, W. J. King, K. G. Smith, and W. D. Wishart. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. *Can. J. Zool.* 74:330–342.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31:367–393.
- Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, and R. Thompson. 2002. ASReml user guide. Release 1.0. VSN International, Hemel Hempstead, U.K.
- Hodges, K. E., R. Boonstra, and C. J. Krebs. 2006. Overwinter mass loss of snowshoe hares in the Yukon: starvation, stress, adaptation or artefact? *J. Anim. Ecol.* 75:1–13.
- Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology* 78:1019–1032.
- Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the 'animal model'. *Phil. Trans. R. Soc. Lond. B* 359:873–891.
- Lande, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* 63:607–615.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Meijer, T., M. Rozman, M. Schulte, and C. Stach-Dreesmann. 1996. New findings in body mass regulation in zebra finches (*Taeniopygia guttata*) in response to photoperiod and temperature. *J. Zool. Lond.* 240:717–734.
- Mercer, J. G. 1998. Regulation of appetite and body weight in seasonal mammals. *Comp. Biochem. Physiol. Part C* 119:295–303.
- Nussey, D. H., T. Clutton-Brock, D. A. Elston, S. Albon, and L. E. B. Kruuk. 2005a. Phenotypic plasticity in a maternal trait in red deer. *J. Anim. Ecol.* 74:387–396.
- Nussey, D. H., E. Postma, P. Gienapp, and M. E. Visser. 2005b. Selection on heritable phenotypic plasticity in a wild bird population. *Science* 310:304–306.
- Nussey, D. H., A. J. Wilson, and J. E. Brommer. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.* 20:831–844.
- Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1993. Seasonal patterns in body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer (*Odocoileus hemionus sitkensis*) in Alaska. *Can. J. Zool.* 71:1397–1404.
- . 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. *Can. J. Zool.* 74:442–450.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effects models in S and S-plus*. Springer-Verlag, New York.
- Réale, D., M. Festa-Bianchet, and J. T. Jorgenson. 1999. Heritability of body mass varies with age and season in wild bighorn sheep. *Heredity* 83:526–532.
- Reed, T. E., S. Wanless, M. P. Harris, M. Frederiksen, L. E. B. Kruuk, and E. J. A. Cunningham. 2006. Responding to environmental change: plastic responses vary little in a synchronous breeder. *Proc. R. Soc. Lond. B* 273:2713–2719.
- Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* 24:35–68.
- Sgrò, C. M., and A. A. Hoffmann. 2004. Genetic correlations, tradeoffs and environmental variation. *Heredity* 93:241–248.
- StatSoft. 1999. *Statistica β5 Windows*. Computer program manual. StatSoft, Inc., Tulsa, OK.
- Stinchcombe, J. R., L. A. Dorn, and J. Schmitt. 2004. Flowering time plasticity in *Arabidopsis thaliana*: a reanalysis of Westerman & Lawrence (1970). *J. Evol. Biol.* 17:197–207.
- Suttie, J. M., and J. R. Webster. 1995. Extreme seasonal growth in arctic deer: comparisons and control mechanisms. *Am. Zool.* 35:215–221.

- Via, S., R. Gomulkiewicz, G. De Jong, C. D. Schlichting, and P. H. Van Tien-  
deren. 1995. Adaptive phenotypic plasticity: consensus and controversy.  
*Trends Ecol. Evol.* 10:212–217.
- Via, S., and R. Lande. 1985. Genotype–environment interaction and the evo-  
lution of phenotypic plasticity. *Evolution* 39:505–522.
- Wikelski, M., and C. Thom. 2000. Marine iguanas shrink to survive El Nino.  
*Nature* 403:37–38.
- Wilson, A. J., J. M. Pemberton, J. Pilkington, D. W. Coltman, D. V. Mifsud,  
T. H. Clutton-Brock, and L. E. B. Kruuk. 2006. Environmental cou-  
pling of selection and heritability limits evolution. *Plos Biol.*: 1270–  
1275.

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