SELECTION AND GENETIC (CO)VARIANCE IN BIGHORN SHEEP

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Abstract.—Genetic theory predicts that directional selection should deplete additive genetic variance for traits closely related to fitness, and may favor the maintenance of alleles with antagonistically pleiotropic effects on fitness-related traits. Trait heritability is therefore expected to decline with the degree of association with fitness, and some genetic correlations between selected traits are expected to be negative. Here we demonstrate a negative relationship between trait heritability and association with lifetime reproductive success in a wild population of bighorn sheep (*Ovis canadensis*) at Ram Mountain, Alberta, Canada. Lower heritability for fitness-related traits, however, was not wholly a consequence of declining genetic variance, because those traits showed high levels of residual variance. Genetic correlations estimated between pairs of traits with significant heritability were positive. Principal component analyses suggest that positive relationships between morphometric traits constitute the main axis of genetic variation. Trade-offs in the form of negative genetic or phenotypic correlations among the traits we have measured do not appear to constrain the potential for evolution in this population.

Key words.—Condition, genetic correlation, heritability, life history, *Ovis canadensis*.

Fisher's fundamental theorem predicts that the rate of change in mean fitness due to natural selection in a population should be equal to the additive genetic variance for fitness (Fisher 1930). As a result, selection will have a greater effect on the additive genetic variance for traits that are closely associated with fitness than for those that are not. It has therefore been hypothesized that fitness-related traits should have low heritability (Charlesworth 1987; Mousseau and Roff 1987; Roff and Mousseau 1987). Early literature reviews supported this hypothesis, as life-history traits, which are by definition closely associated with fitness and therefore subject to strong directional selection, were shown to have lower heritability than either morphometric or physiological traits that are typically subject to weak stabilizing selection (Mousseau and Roff 1987; Roff and Mousseau 1987). However, because the heritability of a trait is defined as the proportion of total phenotypic variance attributed to additive genetic effects, heritability will also be determined by other components of variance. Price and Schluter (1991) suggested that the low heritability of life-history traits may be due to high levels of residual variance. Their prediction was soon supported by a comparison of life-history and morphological traits using the additive genetic variance scaled by the mean instead of the phenotypic variance (Houle 1992). Two recent empirical studies from wild populations have also shown that the low heritability of traits closely associated with fitness, primarily life-history characters, is more a consequence of their high levels of residual variation than depletion of additive genetic variation (Kruuk et al. 2000; Merilä and Sheldon 2000). Furthermore, sexually selected traits typically show surprisingly high levels of additive genetic variance despite being subject to strong selection (Pomiankowski and Møller 1995; Rowe and Houle 1996). These recent findings have suggested a central question in evolutionary biology: how can genetic variation be maintained for traits under selection?

Additive genetic variation for a selected trait may be maintained if many of the genes underlying its variation have antagonistically pleiotropic effects on other fitness-related traits, or if linkage disequilibrium arises between alleles whose effects are negative on one trait and positive on another (Roff 1996, 1997). Alternatively, one can view the covariance structure of fitness-related traits from an energetic standpoint of a major axis of genetic variation for resource acquisition or allocation (van Noordwijk and de Jong 1986; Houle 1991; Reznick et al. 2000; Worley et al. 2003). Positive genetic correlations among characters are expected if there is genetic variation for the ability to acquire resources or in condition (Rowe and Houle 1996), allowing some individuals to invest more in all traits. In this case genetic variation in the population can be maintained despite selection by the constant input of deleterious mutations to the large pool of loci that affect resource acquisition (Houle et al. 1996).

Here we studied the genetic variance-covariance or **G** matrix and estimates of selection on a range of phenotypic traits using lifetime data from a wild population. Our aim was to assess whether the potential for evolution is generally constrained by trade-offs or negative genetic correlations. However, it is difficult to assess evolutionary constraint though the simple examination of pair-wise comparisons. Trade-offs may involve more than two traits, and if the traits involved in higher order trade-offs have not been measured the trade-off may not be detectable (Pease and Bull 1988; Charlesworth 1990). Therefore, the dominant multivariate genetic relationships between traits may be poorly reflected in bivariate coefficients. We therefore also took a multivariate approach by examining the eigenstructure of the **G** matrix (Schluter 1996) in the context of multivariate selection (Blows et al. 2004). More specifically, we examined how the major axes of genetic variation in this population are oriented with respect to the vector of selection gradients.

Here we use data from a long-term study of a natural pop-

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ulation of wild bighorn sheep (*Ovis canadensis*) at Ram Mountain, Canada, in which previous studies using only matrilineal pedigree information demonstrated heritable variation for morphometric (Réale et al. 1999; Réale and Festa-Bianchet 2000a) and life-history traits (Réale and Festa-Bianchet 2000b). We extend these analyses using three more years of data, a genetically reconstructed pedigree with paternal links (Coltman et al. 2002, 2003), and data on lifetime reproductive success from both sexes. We use powerful multivariate animal models that are well suited for estimating genetic (co)variance components in wild populations with unbalanced pedigrees (Milner et al. 2000; Coltman et al. 2001; Kruuk et al. 2001; Merilä et al. 2001a, b; Jensen et al. 2003).

METHODS

Population and Study Site

The study population inhabits Ram Mountain, Alberta, Canada (52°N, 115°W, elevation 1080 to 2170 m), an isolated mountainous outcrop approximately 30 km east of the main range of the Rocky Mountains. Ram Mountain includes approximately 38 km^2 of alpine and subalpine habitat, surrounded on three sides by coniferous forest and on the fourth side by the North Saskatchewan River. This bighorn sheep population has been monitored intensively since 1971, during which time it ranged from 20 to 103 adult ewes. Each year, sheep were captured in a corral trap baited with salt from late May to early October, and marked with colored plastic ear tags or collars for individual identification. The study area was regularly censused by foot during the trapping period. At each capture, sheep were weighed to the nearest 250 g with a Detecto spring scale. Horn length along the outside curvature was measured using tape. Ewes of all ages and rams up to age three are typically caught between four and six times each summer; we therefore use mass and horn length measurements for these classes adjusted to 5 June and 15 September using each individual's own rate of mass gain for that year determined through repeated captures. Adult rams were typically captured once or twice in most summers, mostly from early June to mid-July. Therefore, for adult rams and for a few other individuals for whom there were insufficient data to estimate the specific rate of mass gain, we used age-specific linear regressions of mass on capture date for all individuals of the same age and sex class combined. For further details on field methods see (Jorgenson et al. 1993, 1998; Festa-Bianchet et al. 1996).

Traits Studied

We estimated variance components for the following fifteen traits:

(1) Horn length.—In rams only, the length of the longest horn corrected for capture date (Jorgenson et al. 1998).

(2) Horn base.—In rams only, the average circumference of the base of the horn corrected for capture date (Jorgenson et al. 1998).

(3 & 4) Spring body weights.—For rams and ewes, body weight adjusted to June 5 (Festa-Bianchet et al. 1996, 1997).

(5) Autumn body weight.—For ewes only, body weight adjusted to September 15th.

(6) Spring offspring weight.—For ewes, the weight of their lamb adjusted to June 15 using linear regressions of lamb weight on date (Festa-Bianchet et al. 2000). This corresponds to the weight of the lamb at about three weeks of age, and thus represents mostly prenatal maternal effort. We used June 15 rather than June 5 because a few lambs were not yet born by June 5.

(7) Autumn offspring weight.—For ewes, the weight of their lamb adjusted to September 15 using linear regressions of lamb weight on date (Festa-Bianchet et al. 2000). This corresponds to the weight of the lamb near the time of weaning, thereby reflecting a composite measure of maternal effort.

(8) Fecundity.—Indicated as ''1'' for each season following the age at primiparity in which a ewe was lactating or pregnant (secreting colostrum) at first capture, or was seen nursing a lamb.

(9) Weaning success.—For each fecund ewe this was indicated as ''1'' for each season in which her lamb survived until September, and ''0'' if her lamb did not survive until September.

(10) Age at primiparity.—The age at which ewes were first lactating, pregnant or with a lamb.

(11 and 12) Longevity.—The age at death for males and females that survived to at least one year of age. Individuals that were artificially removed or were still alive in 2003 were not considered.

(13) Mating success.—For rams, the number of paternities assigned in a season.

(14 and 15) Lifetime reproductive success.—For rams and ewes, the total number of offspring produced that survived to age one. Females born after 1994 and males born after 1997 were not considered, nor were other individuals that were artificially removed to control population density or were still alive in 2003.

We categorized traits based on morphological measurements (1–7) as ''morphometric.'' The remaining traits are related to reproduction (8–15). We categorized these traits as ''life history'' (Mousseau and Roff 1987; Roff and Mousseau 1987).

Pedigree Reconstruction

Maternity was known from field observations for 717 of the 936 (76.6%) marked sheep followed since 1971. Tissue sampling for DNA analyses started in 1988. Blood samples were taken from all captured sheep until 1993 and stored in preservative at −20°C. Sampling was discontinued from 1994 to 1996. Sampling resumed in 1997, when hair samples were taken from all captured sheep by plucking 50 to 100 hairs including roots from the back or flank. Hairs were kept either in paper envelopes or plastic bags containing approximately 5 g of silica at room temperature. From 1998 to 2002, a tissue sample from each captured sheep was taken from the ear using an 8 mm punch. Ear tissue was kept in a solution of 20% dimethylsulphoxide/saturated NaCl at −20°C. We collected samples from 440 marked individuals over the course of the study.

DNA was extracted from blood using a standard phenol-

chloroform method, and from either 20–30 hairs including follicles or approximately 5 mg of ear tissue, using the QIAamp tissue extraction kit (QIAGEN Inc., Mississauga, Ontario). Polymerase chain reaction (PCR) amplification at 32 ungulate derived loci, 15 as described previously (Coltman et al. 2002) plus BL25, BM4025, BM4630, BMS772, HEL10, HUJ1177, MCM527, MAF64, OarFCB11, OarFCB193, OarHH35, OarHH62, OarJMP29, OarJMP58, MAF92, RT27, and URB037 (Crawford et al. 1995; Slate et al. 1998), and fragment analysis were performed as described elsewhere (Coltman et al. 2002). After correction for multiple comparisons, we found no evidence for allelic disequilibria at these loci using exacts tests as implemented in GENEPOP (Raymond and Rousset 1995).

Paternity of 235 individuals was assigned using the likelihood-based approach described in CERVUS (Marshall et al. 1998) at a confidence level of >95% using input parameters as given in Coltman et al. (2002). Following paternity analysis, we used COLONY (Wang 2004) to identify 38 clusters of 167 paternal half-sibling among the unassigned offspring. Members of paternal half-sibships were assigned a common paternal identity for the animal model analyses. Paternal identity links in the pedigree were therefore defined for 402 of 936 marked individuals (42.9%).

Animal Model Analyses

Breeding values, genetic variance components, and heritabilities were estimated using multiple trait restricted estimate maximum likelihood (REML) models (Meyer 1991) implemented by the programs PEST (Groeneveld et al. 1992) and VCE (Groeneveld 1995). An animal model was fitted in which the phenotype of each animal was partitioned into components of additive genetic value and other random and fixed effects: $\mathbf{y} = X\mathbf{b} + Z\mathbf{a} + P\mathbf{c} + e$, where $\mathbf{y}$ was a vector of phenotypic values, $\mathbf{b}$ was a vector of fixed effects, and $\mathbf{a}$ and $\mathbf{c}$ were vectors of additive genetic and permanent environmental effects, e was a vector of residual values, and X, Z, and P were the corresponding design matrices relating records to the appropriate fixed or random effects (Lynch and Walsh 1998). The permanent environmental effect grouped repeated observations on the same individual to quantify any remaining between-individual variance over and above that due to additive genetic effects; which would be due to maternal, cohort, or other long-term environmental and non-additive genetic effects including dominance variance. The permanent environmental effect was fitted for traits that have repeated measures on individuals in different years. The total phenotypic variance (V_P) was therefore partitioned into two or three components: the additive genetic variance (V_A), the residual variance (V_R), and where appropriate, the permanent environmental variance (V_E), thus $V_P = V_A + V_E + V_R$. Heritability was calculated as $h^2 = V_A/V_P$ and the permanent environmental effect as $c^2 = V_E/V_P$. Coefficients of additive genetic, permanent environmental, and residual variance were calculated as $CV_A = 100 \cdot \sqrt{V_A}/\bar{x}$, as $CV_E = 100 \cdot \sqrt{V_E}/\bar{x}$ and $CV_R = 100 \cdot \sqrt{V_R}/\bar{x}$, respectively (Houle 1992). The VCE program (Groeneveld 1995) returns standard errors for h^2 and c^2. Fixed effects were fitted as factors, and included age, year of measurement, and offspring sex. Age and year

of measurement were fitted for all traits with repeated measurements. Rams aged 10+ and ewes aged 15+ were pooled to ensure reasonable sample sizes (20+ observations) for morphometric and reproductive status measurements. Ewes age 13+ were pooled for offspring weights. Offspring sex was fitted for lamb weights because males are heavier than females from birth (Festa-Bianchet et al. 1996).

Initially, variance components were estimated for each trait with repeated measures separately in single-trait animal models to assess the significance of the permanent environmental effect term by t-tests (i.e., by comparing the c^2 estimate against 0). If the permanent environmental effect was not significant at $P < 0.05$, or if the data did not consist of repeated measures (e.g., longevity, lifetime reproductive success, and age at primiparity), then we estimated the additive genetic variance and heritability in a final model that did not include a permanent environmental effect. The significance of heritability estimates from the final models was also assessed using t-tests.

We estimated genetic correlations in a pair-wise fashion using two-trait animal models for traits that were observed to have significant additive genetic variance. In theory, any estimate of the genetic correlation r_A including a trait x and/or y with $h^2 = 0$ is undefined because the genetic correlation is estimated by

$$r_{A(xy)} = \frac{\text{Cov}_{A(xy)}}{\sqrt{V_{A(x)} V_{A(y)}}}. \tag{1}$$

where Cov_A gives the genetic covariance (Lynch and Walsh 1998). Estimates of genetic covariances between traits with heritability estimates not significantly greater than zero often failed to converge in VCE and frequently yielded genetic correlation estimates of +1.0 or −1.0 (data not shown). We therefore restricted our analyses to genetic correlations between the subset of traits with significant h^2 estimates. The statistical significance of genetic correlation estimates was assessed by t-test using standard errors returned by the VCE software. Phenotypic correlations were estimated for each trait pair as the Pearson product moment correlation coefficient using the mean of the response residuals from a general linear model including the fixed effects for that trait. Standard errors for phenotypic correlation coefficients were obtained as described in (Sokal and Rohlf 1995).

The additive genetic variance for a character does not reflect the potential for that character to evolve when selection acts on genetically correlated characters. Hansen et al (2003) proposed the use of estimates of ''conditional'' genetic variance to better reflect the evolutionary potential of genetically correlated traits. This method assesses the ability of a trait to evolve without perturbing a genetically correlated trait which is presumed to be constrained by strong stabilizing selection. We also estimated the conditional additive genetic variance ($V_{A(y|x)}$) for each trait y that would be available for selection to act upon assuming stabilizing selection on each other measured trait x as

$$V_{A(y|x)} = V_{A(y)} - \frac{[\text{Cov}_{A(xy)}]^2}{V_{A(x)}} \tag{2}$$

where $V_{A(y)}$ denotes the additive genetic variance in y, $V_{A(x)}$

denotes the additive genetic variance in x, and $Cov_{A(xy)}$ is the additive genetic covariance between trait x and y (Hansen et al. 2003; Jensen et al. 2003). We expressed the conditional heritability of trait y on trait x as $V_{A(y|x)}/V_{P(x)}$. This approach provides another way of quantifying the independent evolvability and modularity or integration of a number of characteristics measured simultaneously (Hansen et al. 2003).

Selection Analyses

We quantified univariate selection differentials using least-squares regressions of relative fitness on trait values (Arnold and Wade 1984). Throughout the manuscript we present variance-standardized estimates of selection parameters using trait values set to zero mean and unit variance. For relative fitness we used the lifetime reproductive success (LRS) divided by mean (LRS) of other individuals in the same cohort. To ensure adequate sample sizes within cohorts we restricted the selection analyses to rams born from 1985 to 1991 (inclusive) and ewes born in 1991 or earlier. Standardized directional (S) and nonlinear (c) differentials were estimated using linear and second order polynomial regressions, respectively. We quantified total relative association of a trait with fitness due both to directional and stabilizing selection as the total variance in fitness explained (R^2) by the model including both linear and polynomial terms. We also quantified standardized multivariate selection gradients (β) using multiple regression to provide an estimate of the directional selection acting on each trait while correcting for selection on other measured traits (Lande and Arnold 1983). We calculated the expected correlated response R to selection using a form of the multivariate breeder's equation appropriate for variance-standardized selection data (Roff 1997) for each trait i as

$$R_i = \beta_i h_i^2 + \sum_{i \neq j} \beta_j h_i h_j r_{A(ij)}. \tag{3}$$

Orientation of the **G** Matrix

We used principal component analysis to determine the major independent axes of variation in the **G** matrix (Blows et al. 2004; Schluter 1996). Each principal component or eigenvector **g** consists of a vector of elements that measure the contribution of each trait to the direction of variation. We calculated that angle θ between each of the first three principal components and the vector of multivariate selection gradients (β). An angle of 0° indicates that selection and the main axis of genetic variation are collinear, whereas an angle of 90° indicates that they are orthogonal.

RESULTS

Genetic Variances from Single Trait Animal Models

Six of ten traits that were estimated from repeated measures were observed to have significant permanent environmental effects (Table 1). Five of these were morphometric traits, and the permanent environmental effects were of similar magnitude as the heritability estimates for the same traits. Significant heritability estimates were found for all morphometric traits in both sexes, ranging from 0.16 to 0.43 (Table

1) with a mean of 0.28 (Table 2). Horn base circumference had the highest heritability (0.43 ± 0.12).

Of the eight life-history traits, only female fecundity showed a statistically significant heritability estimate. The mean heritability of life-history traits was less than that of morphometric traits (Table 2, Wilcoxon rank-sum test $z = 3.16$, $P < 0.005$). However, mean coefficients of additive genetic variation were not significantly different (Table 2, Wilcoxon rank-sum test $z = 0.06$, $P > 0.05$). The trend towards lower heritability of life-history traits is partly due to their high levels of residual variance. The average CV_R (Table 2) for life-history traits was more than ten-fold greater than that for morphometric traits (Table 2, Wilcoxon rank-sum test $z = 3.18$, $P < 0.005$).

Phenotypic and Genetic Correlations

Phenotypic correlations between morphometric traits measured at the individual level tended to be strong and positive in both sexes, ranging from +0.61 to +0.76 (Table 3). Offspring weights were more weakly correlated with each other and with individual weight (Table 3). Phenotypic correlations between life-history traits and between morphometric/life-history trait pairs tended to be weaker and more variable in sign than correlations among morphometric traits (Table 3). Of the negative correlations, only those between horn length and longevity in rams and age of primiparity and longevity in ewes were statistically significant.

Genetic correlations between morphometric traits were all significantly greater than zero (Table 4). The genetic correlation between ewe weights in June and September was high (0.90), however a standard error estimate was not obtained for the correlation coefficient because the model including these two traits did not converge. Fecundity was significantly correlated with ewe weights and offspring weight in September. Genetic correlations between the sexes were high and positive for morphometric traits and more variable for pairs including life-history traits (Table 4). Between-sex estimates were generally subject to larger standard errors (ranging from 0.13 to 0.33) than within-sex estimates (ranging from 0.10 to 0.20, Table 4). Genetic correlation coefficients (Table 4) were positively correlated with their corresponding phenotypic correlation coefficients (Pearson $r = +0.75$, $n = 13$, $P < 0.01$) and were always of the same sign. However, genetic correlation coefficients were of greater magnitude than their comparable phenotypic correlations (mean $r_A = +0.55 \pm 0.06$ versus mean $r_P = +0.33 \pm 0.08$; Wilcoxon signed-rank test $z = 2.80$, $P < 0.01$).

Conditional Genetic Variances

The amount of genetic variance in most traits was considerably reduced when conditioned by the amount of genetic variance in other traits (Table 5). Morphometric traits retained from 48 to 76% of their genetic variance on average after conditioning on one other trait. Ewe and ram weights were particularly strongly influenced by their high genetic covariances with other traits. Less than 50% of the additive genetic variance for ram weights was available for selection independent of ewe weight.

TABLE 1. Genetic variance estimates from single trait animal models. Estimates of ratios (indicated ± standard error) that are significantly greater than zero are shown in bold.

Trait	Fixed effects (levels)	N observations (individuals)	Mean	SD	V_A	h^2	V_E	c^2	V_R	CV_A	CV_E	CV_R
Males												
Morphometric traits												
Horn base circumference [HB] (cm)	Age (10) Year (30)	727 (215)	31.15	7.16	2.94	**0.43 ± 0.12**	2.35	**0.35 ± 0.11**	1.48	5.5	4.9	3.9
Horn length [HL] (cm)	Age (10) Year (30)	727 (215)	54.47	19.02	11.95	**0.39 ± 0.13**	12.70	**0.42 ± 0.13**	5.90	6.4	6.5	4.5
Weight [MWT] (kg)	Age (10) Year (32)	998 (274)	60.62	21.12	10.01	**0.23 ± 0.09**	15.92	**0.37 ± 0.09**	16.76	5.2	6.6	6.8
Life-history traits												
Mating success [MS] (paternity y^{-1})	Age (10) Year (17)	499 (107)	0.47	1.09	0.049	0.06 ± 0.03	0.15	**0.17 ± 0.04**	0.68	47.0	83.0	175.5
Longevity [MLG] (y)	None	266	4.85	2.78	0	0			7.74	0		57.4
Lifetime reproductive success [MLRS]	None	148	1.01	2.88	0	0			8.31	0		284.5
Females												
Morphometric traits												
Lamb weight in June [LWJ] (kg)	Age (12) Year (29) Sex (2)	412 (174)	8.81	2.57	0.72	**0.16 ± 0.04**			3.83	9.7		22.1
Lamb weight in Sept [LWS] (kg)	Age (12) Year (29) Sex (2)	494 (180)	26.46	4.93	4.08	**0.25 ± 0.04**			12.51	7.6		13.4
Weight in June [FWJ] (kg)	Age (15) Year (30)	1677 (287)	49.19	11.28	4.47	**0.20 ± 0.05**	5.12	**0.23 ± 0.04**	12.50	4.3	4.6	7.2
Weight in Sept [FWS] (kg)	Age (15) Year (30) RS (9)	1518 (276)	64.77	10.68	8.59	**0.32 ± 0.07**	8.32	**0.31 ± 0.06**	10.36	4.5	4.5	5.0
Life-history traits												
Age at primiparity [AP]	None	199	3.34	0.99	0.15	0.16 ± 0.15			0.83	11.7		27.2
Fecundity [FEC] (births y^{-1})	Age (14) Year (31)	1234 (240)	0.91	0.28	0.005	**0.07 ± 0.02**			0.067	7.8		28.4
Weaning success [WS] (offspring y^{-1})	Age (14) Year (31)	1123 (240)	0.71	0.45	0	0			0.18	0		58.4
Longevity [FLG] (y)	None	210	7.18	4.70	1.60	0.07 ± 0.14			20.50	17.6		63.1
Lifetime reproductive success [FLRS]	None	184	1.79	2.12	0	0			4.50	0		118.2

TABLE 2. Mean ratios of genetic variance components (± standard error) and strength of association with lifetime reproductive success for traits categorized as morphometric and life-history (excluding LRS).

Trait type	h^2	CV_A	CV_R
Morphometric ($n = 7$)	0.28 ± 0.04	5.9 ± 0.7	9.0 ± 2.5
Life-history ($n = 8$)	0.04 ± 0.02	14.0 ± 6.6	68.3 ± 20.7

Genetic Variance and the Strength of Selection

Significant linear selection differentials were observed for mating success and longevity in rams, and for June weight, fecundity, weaning success, and longevity in ewes (Table 6). A significant nonlinear differential for ewe longevity was a consequence of an asymptotic relationship between lifetime reproductive success and age after about 14 years, as ewes have very low reproductive success subsequent to this age (Bérubé et al. 1999). Due to multicollinearity we estimated linear selection gradients on a subset of the measured traits. We dropped horn base (highly correlated with horn length and weight) in males and weight in September (highly correlated with weight in June) from the multiple regression analysis. Linear selection gradients on male mating success, female weaning success and longevity in both sexes were positive and statistically significant. We did not estimate nonlinear gradients due to limited sample sizes (73 rams and 103 ewes with complete data). We used the variance-standardized multivariate linear selection gradients presented in Table 6 to calculate the response to selection. The predicted multivariate response to selection on heritable traits (measured in standard deviations per generation) ranged from -0.113 (horn length) to $+0.008$ (fecundity).

Life-history and morphometric traits exhibited variable degrees of association with lifetime reproductive success, indexed by the amount of variation explained by that trait in a univariate regression on relative fitness (Table 6). Life-history traits were more closely associated with relative fitness than were morphometric traits, accounting for from 2 to 33% of the total variance in fitness compared to a maximum of 4% in total fitness for morphometric traits in univariate regression models. Trait heritability was strongly negatively correlated to the association with fitness ($\rho = -0.79$, $P < 0.005$; Fig. 1A). However, genetic variance measured as the CV_A was very weakly correlated to the association with fitness ($\rho = +0.11$, $P > 0.05$; Fig. 2B). Residual variance expressed as the CV_R was strongly positively correlated with r_{LRS} ($\rho = +0.76$, $P < 0.005$; Fig. 2C).

Orientation of the **G** Matrix

Principal component analysis indicated that the first three eigenvectors explained 98.3% of the total genetic variance in the eight heritable traits (Table 7). The first eigenvector explained most of the variance (67.3%), and showed positive coefficients for five morphometric traits. The second eigenvector accounted for 22.2% of the variance and was negatively associated with horn growth. The third eigenvector (8.8% of variance) showed contrasting signs for coefficients of female adult body weight to male and offspring weights in June. None of the three major axes were oriented collinearly with the vector of directional selection gradients, with incident angles of 116.7°, 72.9°, and 103.4° (Table 7).

DISCUSSION

Comparison to previous estimates and the role of maternal effects

Heritability estimates from this population have been previously reported for age-specific weight (Réale et al. 1999), life-history traits (Réale and Festa-Bianchet 2000b) and reproductive investment (Réale and Festa-Bianchet 2000a) in ewes using a smaller pedigree without paternal links. Heritability of age-specific ewe weights in June and September ranged from -0.15 ± 0.15 to 0.59 ± 0.19 using offspring-parent regressions, and from 0.001 to 0.81 ± 0.03 using an animal model (Réale et al. 1999). Here we treated seasonal body weight as one general trait related to body size, with repeated measures at different ages. Heritability estimates from this approach in ewes (June: 0.20 ± 0.05, September: 0.32 ± 0.07) were in the lower range of those found previously (Réale et al. 1999).

Heritability of June weight in rams was similar to that in ewes, and weights were strongly genetically correlated between the sexes (Table 4). The high genetic correlation between the sexes, which constrains the further evolution of sexual size dimorphism, is not unusual (Jensen et al. 2003; Lynch and Walsh 1998; Merilä et al. 1998; Roff 1997). Our data suggest there is a limited capacity for independent evolution of body size measured as June weight in bighorn rams (conditional $h^2 = 0.10$) and ewes (conditional $h^2 = 0.08$). However, the development of size dimorphism in bighorn

TABLE 3. Phenotypic correlation matrices for traits measured in male (above diagonal) and female (below diagonal) bighorn sheep. Significance of difference from 0 is denoted by *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, and ns (not significant). Traits defined in Table 1.

			HL	MWT	MS	MLG	MLRS	Male traits
LWS	$+0.43$***		$+0.75$***	$+0.63$***	$+0.10$ ns	-0.11 ns	-0.07 ns	HB
FWJ	$+0.08$ ns	$+0.10$ ns		$+0.61$***	$+0.17$ ns	-0.20**	-0.13 ns	HL
FWS	$+0.18$*	$+0.15$*	$+0.76$***		$+0.25$**	-0.04 ns	-0.10 ns	MWT
AP	$+0.09$ ns	-0.11 ns	-0.11 ns	-0.09 ns		0.01 ns	$+0.34$**	MS
FEC	$+0.11$ ns	$+0.03$ ns	$+0.15$*	$+0.16$*	-0.09 ns		$+0.52$***	MLG
WS	-0.06 ns	-0.11 ns	$+0.07$ ns	$+0.03$ ns	-0.10 ns	$+0.27$***		
FLG	-0.01 ns	$+0.02$ ns	$+0.23$**	$+0.17$*	-0.19*	$+0.00$ ns	$+0.07$ ns	
FLRS	$+0.10$ ns	$+0.06$ ns	$+0.16$*	$+0.08$ ns	$+0.02$ ns	$+0.26$**	$+0.28$**	$+0.55$***
Female traits	LWJ	LWS	FWJ	FWS	AP	FEC	WS	FLG

TABLE 4. Genetic variance-covariance matrix for traits with heritability >0. Below the diagonal are additive covariances, along the diagonal are additive genetic variances, and above the diagonal are additive genetic correlations (SE). Significance of difference from 0 is denoted by *P < 0.05, **P < 0.01, ***P < 0.001. [1]Standard error not returned due to nonconvergence of the model. Traits defined in Table 1.

	HB	HL	MWT	LWJ	LWS	FWJ	FWS	FEC
HB	2.94	0.84*** (0.10)	0.76*** (0.17)	0.52* (0.24)	0.64*** (0.20)	0.45* (0.19)	0.44* (0.19)	0.10 (0.29)
HL	4.82	11.95	0.39* (0.20)	0.46* (0.23)	0.59*** (0.21)	0.46* (0.21)	0.40* (0.19)	0.16 (0.30)
MWT	3.65	4.57	10.01	0.82*** (0.18)	0.95*** (0.13)	0.78*** (0.20)	0.72*** (0.22)	0.50 (0.33)
LWJ	0.76	1.37	2.68	0.72	0.85*** (0.08)	0.37* (0.14)	0.46** (0.13)	0.22 (0.20)
LWS	2.19	4.14	7.53	1.56	4.08	0.39* (0.14)	0.52*** (0.11)	0.38* (0.14)
FWJ	1.66	3.37	5.31	0.72	1.67	4.47	0.90 (nc)[1]	0.59*** (0.15)
FWS	2.13	3.90	6.61	1.23	3.08	5.68	8.59	0.45*** (0.14)
FEC	0.013	0.041	0.118	0.015	0.059	0.088	0.098	0.005

sheep is a complex function of differing age-specific growth rates and sensitivity to environmental effects in the sexes (Festa-Bianchet et al. 1996; LeBlanc et al. 2001). We plan to conduct a more detailed analysis of the quantitative genetics of the development of sexual dimorphism using age-specific analyses and random regression techniques that allow for age-specific environmental effects and genetic differences in the shape of each individual growth curve (Lewis and Brotherstone 2002).

Our finding of strong permanent environmental effects on ewe (June: 0.23 ± 0.04, September: 0.31 ± 0.06) and ram weights (June: 0.37 ± 0.09) and significant heritable variation for offspring weight in ewes (Table 1) suggests that maternal effects could be an important source of variation in morphometric traits. (Réale and Festa-Bianchet 2000a) found significant heritability estimates for age at primiparity (0.53 ± 0.33), fecundity (0.66 ± 0.32), weaning success (0.81 ± 0.34) and lifetime reproductive success (0.62 ± 0.28), and strong positive genetic correlations between most pairs of life-history traits at Ram Mountain using mother-daughter regressions. In contrast, in this study we only found evidence for heritable variation in fecundity (0.07 ± 0.02). It is possible that life-history traits in ewes may be strongly influenced by shared environmental and maternal genetic effects that will upwardly bias heritability and genetic correlation estimates from mother-daughter regressions. Significant maternal effects on female life-history characters have been found in other studies of long-lived large mammals (Kruuk et al. 2000). We did not fit maternal effects explicitly in this study because they are likely to vary with age. However, the heritability estimates presented here are unlikely to be upwardly biased by maternal effects because the permanent environmental effect will account for much of the maternal effect variation, and the animal model uses information from the whole pedigree including patrilineal relationships.

Genetic (co)variances and selection at Ram Mountain

Our analyses of relative fitness suggest that morphometric traits in females are weakly selected (Table 6), at strength ($\beta < 0.1$) often found in natural populations (Hoekstra et al. 2001; Kingsolver et al. 2001; Hereford et al. 2004). However, these findings should not be taken as meaning that morphometric variation is unimportant. Body and horn size are correlated with life-history traits such as mating success, fecundity, and longevity (Table 3), which may be regarded as integral components of fitness. Morphometric traits tended to exhibit higher heritability than life-history traits, primarily due to the latter possessing higher residual variance rather than low additive genetic variance (Tables 1 and 2). Our analyses of trait variation in relation to selection (Fig. 1) also suggest that traits associated with fitness do not always exhibit low levels of genetic variance (Merilä and Sheldon 1999). Selection has apparently not depleted additive genetic variance for all fitness-related traits, a finding which closely mirrors those of (Kruuk et al. 2000) in red deer (*Cervus elaphus*) and (Merilä and Sheldon 2000) in collared flycatchers (*Ficedula albicollis*). Some traits closely associated with lifetime reproductive success, such as fecundity, show significant levels of additive genetic variation (Table 1). How-

TABLE 5. Effects of conditioning on trait heritability. Values are the heritability of trait *x* conditioned on trait *y* with the percentage of additive genetic variance remaining after conditioning given in parentheses. Values on the diagonal are univariate heritability. The average value refers to the mean heritability of the trait *y* on that row conditioned by *x*. Traits defined in Table 1.

Trait *y*	Heritability conditioned upon trait *x*								Average
	HB	HL	MWT	LWJ	LWS	FWJ	FWS	FEC	
HB	0.42	0.12 (29%)	0.15 (42%)	0.31 (73%)	0.24 (59%)	0.34 (79%)	0.33 (80%)	0.42 (99%)	0.27 (66%)
HL	0.11 (29%)	0.39	0.37 (85%)	0.31 (79%)	0.26 (66%)	0.31 (79%)	0.32 (84%)	0.38 (97%)	0.29 (74%)
MWT	0.09 (42%)	0.20 (85%)	0.23	0.09 (42%)	0.03 (10%)	0.10 (40%)	0.12 (49%)	0.19 (77%)	0.12 (48%)
LWJ	0.12 (73%)	0.13 (79%)	0.06 (32%)	0.16	0.05 (27%)	0.15 (86%)	0.14 (79%)	0.16 (95%)	0.12 (67%)
LWS	0.15 (59%)	0.16 (66%)	0.03 (10%)	0.07 (27%)	0.25	0.21 (85%)	0.18 (74%)	0.22 (87%)	0.15 (58%)
FWJ	0.17 (79%)	0.17 (79%)	0.08 (40%)	0.19 (86%)	0.17 (85%)	0.20	0.04 (19%)	0.12 (63%)	0.13 (65%)
FWS	0.25 (80%)	0.26 (84%)	0.15 (49%)	0.26 (79%)	0.23 (74%)	0.06 (19%)	0.32	0.25 (78%)	0.21 (66%)
FEC	0.07 (99%)	0.07 (97%)	0.06 (77%)	0.07 (95%)	0.07 (86%)	0.04 (63%)	0.05 (78%)	0.07	0.06 (85%)

ever, we did not detect significant additive genetic variance for other life-history traits including longevity, age at primiparity, and lifetime reproductive success (Table 1).

The predominance of positive genetic correlations among heritable traits and the first major axis of genetic variation (Table 7) with positive coefficients for body weight in both sexes as well as offspring weight could be interpreted as a major genetic axis of overall body size or condition. At the phenotypic level, the heaviest ewes tended to have heavier lambs, increased longevity and fecundity, earlier age at primiparity, and higher lifetime reproductive success (Table 3). Significant positive genetic correlations between weight, fecundity, and offspring weight support the idea that reproductive and somatic allocations are not traded-off in ewes. On the contrary, higher quality ewes may be heavier and tend to produce heavier offspring (Table 4). However, the third principal axis of genetic variation (Table 7) suggests another underlying antagonistic genetic relationship between offspring weight and maternal weight in June that may explain why the correlation between maternal and offspring weight, albeit positive, is weak (Réale and Festa-Bianchet 2000a).

The selection pressures affecting rams differ greatly from those for ewes. Mating success increases as a complex function of horn length and age, with relatively large-horned rams achieving high rates of paternity if they survive to about eight years, an age at which they can achieve social dominance (Coltman et al. 2002; Hogg and Forbes 1997). However, trophy hunting superimposes a countervailing selection pressure on horn and body size, as hunters selectively harvest rams with fast growing horns as young as four years (Coltman et al. 2003; Festa-Bianchet et al. 2004). Since 1972, 57 rams have been harvested by hunters from the Ram Mountain population under a minimum horn length restriction. Hunting therefore probably drives the negative phenotypic correlation between longevity and horn length (Table 3). Furthermore, hunting leads to a negative correlation between horn length breeding value and both longevity and lifetime reproductive success in trophy-harvested rams (Coltman et al. 2003). The fact that the mean longevity of trophy-harvested rams is not significantly different from the mean longevity of rams that survived to age four and subsequently died from natural causes (trophy harvested rams mean longevity = 6.5 ± 0.2 years, nonharvested rams mean = 6.4 ± 0.3, t_{171} = −0.32, P > 0.05) strongly suggests that horn growth, weight, longevity, mating success, and lifetime reproductive success would be positively associated in the absence of hunting selection (von Hardenberg et al. 2004). The selection pressure imposed by hunting likely explains the negative selection coefficients on male morphometric traits (Table 6), which are reasonably high compared to most published estimates for morphological

TABLE 6. Standardized selection differentials (directional *S*, and nonlinear *c*) and gradients (directional β) estimated from univariate and multivariate regression analyses. Gradients were not estimated for HB and FWS due to their high correlation with other measured traits. The predicted response to selection (in standard deviations per generation) based on multivariate selection gradients is given for traits with heritability significantly greater than 0. Traits defined in Table 1.

		Univariate					Multivariate		Predicted response
	n	*S*	SE	*c*	SE	R^2	β[1]	SE	
HB	74	−0.175	0.277	0.082	0.177	0.01			
HL	74	−0.331	0.294	0.299	0.209	0.04	−0.240	0.388	−0.113
MWT	80	−0.295	0.316	0.172	0.217	0.02	−0.206	0.436	−0.059
MS	74	1.165**	0.386	0.052	0.310	0.11	1.165**	0.342	
MLG	82	1.296***	0.236	0.286	0.178	0.30	1.384***	0.275	
LWJ	118	0.134	0.129	−0.116	0.083	0.03	0.078	0.153	−0.034
LWS	113	0.088	0.137	−0.026	0.101	0.00	0.069	0.155	−0.050
FWJ	158	0.195*	0.099	−0.080	0.069	0.03	−0.047	0.140	−0.038
FWS	154	0.106	0.103	−0.048	0.065	0.01			
AP	127	0.025	0.132	0.163	0.103	0.02	0.230	0.158	
FEC	127	0.380**	0.129	0.111	0.109	0.07	0.359	0.183	0.008
WS	127	0.412**	0.125	0.019	0.076	0.08	0.499*	0.206	
FLG	175	0.686***	0.080	−0.219**	0.080	0.33	0.458*	0.186	

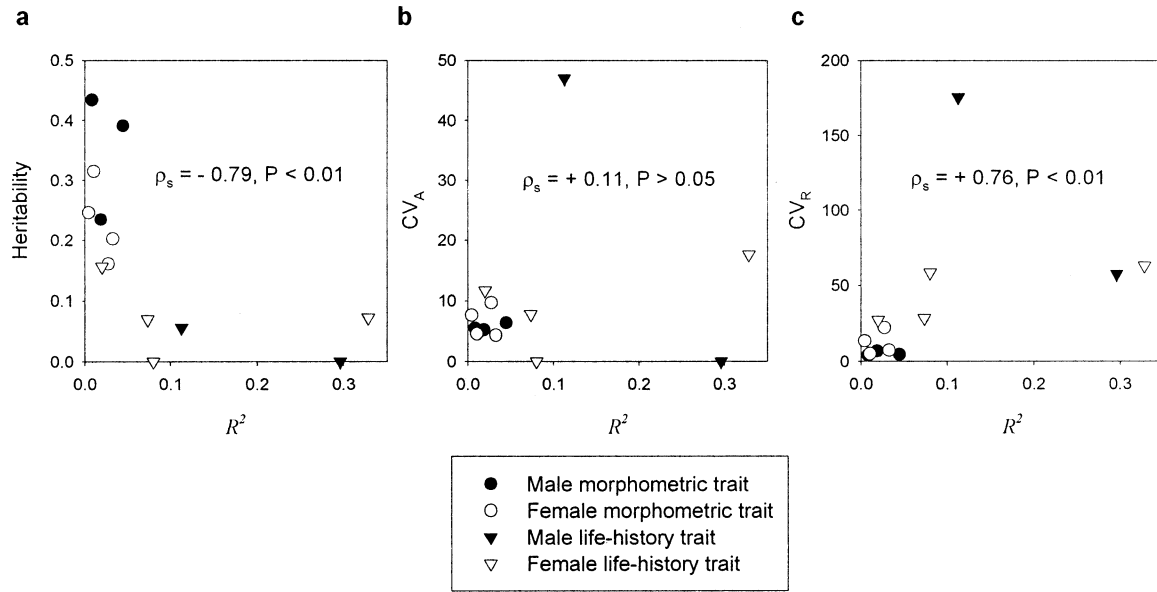[1] *n* = 73 for males and 103 for females.

FIG. 1. Heritability (a), coefficient of additive genetic variation (b), and coefficient of residual variation (c) plotted versus the amount of variance explained by that trait in reproductive success when fitted as a second order polynomial (R^2).

traits (Hereford et al. 2004), and contributes to the angular mismatch between the axes of selection and genetic variation (Table 7). It is therefore important to note that the current selection regime, which is clearly influenced by harvesting, may not accurately reflect the historical selection patterns under which the genetic (co)variances evolved. The current selection regime on the traits we have measured predicts a rate of decline in horn length of -0.113 standard deviations per generation. This is very close to the rate of phenotypic change that we have observed (-0.15) after correcting for changes in resource availability (Coltman et al. 2003).

All genetic correlations estimated between males and females were positive, and both ram weight and horn size were strongly positively genetically correlated with ewe weight and offspring weight (Table 4). The analyses of conditional genetic variance (Table 5) and principal components (Table 7) also suggest a significant level of integration among the morphometric traits we have measured. It would therefore seem likely that the alleles that are associated with large body size and maternal performance in ewes are also associated with large body and horn size in rams. An important implication of this finding is that the undesirable consequences of intensive trophy hunting, which selectively removes rams with high breeding values for horn length and weight (Coltman et al. 2003), could have correlated negative effects on maternal performance characteristics such as offspring weight. We may therefore see a long-term decline in ewe and lamb weights in intensively harvested trophy-hunted populations, and the total response to selection predicts a modest rate of decline for ewe and lamb morphometric traits (Table 6). However, we also note that the second major axis of genetic variation suggests a partially antagonistic genetic relationship between horn size and adult weight (Table 7).

In summary, the positive covariance among many of the traits we measured may be a consequence of their dependence on an underlying trait such as "condition" which may be interpreted as a general pool of resources that can be allocated to various traits (Rowe and Houle 1996). Variance in condition is then expected to lead to positive genetic covariance among traits (Rowe and Houle 1996). Because a large number of loci could conceivably contribute to condition, it therefore constitutes a very large mutational target and a dispersed target of selection. Therefore, even if selection was stronger than our analyses suggest, genetic variation could be maintained at the point of balance between the continuous input of deleterious mutations and the erosion of selection (Houle 1991; Houle et al. 1996). However, to this interpretation we must add three important caveats. First, current patterns of selection may not reflect the historical selection regime due to the effects of recent human harvesting. Secondly, we cannot rule out undetected trade-offs between components of fitness that we did not measure. Third, most of the heritable traits we considered are related to body size; thus it is perhaps unsurprising that they are positively genetically correlated because they may be expected to share a common underlying genetic architecture.

TABLE 7. Loadings for the first three eigenvectors (**g**) of the genetic covariance matrix in the bighorn sheep population, and the angles (θ) between **g** and the vector of multivariate selection gradients (β).

Trait	g_1	g_2	g_3
Horn length	0.49	−0.87	0.04
Male June weight	0.57	0.31	0.68
Lamb June weight	0.13	0.03	0.34
Lamb September weight	0.39	0.19	−0.27
Female June weight	0.51	0.34	−0.59
Fecundity	0.01	0.01	0.00
% variance explained by **g**	67.3	22.2	8.8
θ_β	116.7°	72.9°	103.4°

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