Quantitative genetics and sex-specific selection on sexually dimorphic traits in bighorn sheep

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Sexual conflict at loci influencing traits shared between the sexes occurs when sex-specific selection pressures are antagonistic relative to the genetic correlation between the sexes. To assess whether there is sexual conflict over shared traits, we estimated heritability and intersexual genetic correlations for highly sexually dimorphic traits (horn volume and body mass) in a wild population of bighorn sheep (*Ovis canadensis*) and quantified sex-specific selection using estimates of longevity and lifetime reproductive success. Body mass and horn volume showed significant additive genetic variance in both sexes, and intersexual genetic correlations were 0.24 ± 0.28 for horn volume and 0.63 ± 0.30 for body mass. For horn volume, selection coefficients did not significantly differ from zero in either sex. For body weight, selection coefficients were positive in females but did not differ from zero in males. The absence of detectable sexually antagonistic selection suggests that currently there are no sexual conflicts at loci influencing horn volume and body mass.

Keywords: animal model; genetic correlation; heritability; lifetime reproductive success; selection; sexual conflict

1. INTRODUCTION

The widespread occurrence of sexual dimorphism suggests that optimal trait values often differ between the sexes (Fairbairn 2007). Because traits shared by the sexes are typically influenced by the same genes (Roff 1997), sexual conflicts at loci influencing shared traits (intralocus sexual conflicts; Arnqvist & Rowe 2005) may be common. While negative cross-sex genetic correlations for fitness in many laboratory and wild populations (Chippindale *et al.* 2001; Brommer *et al.* 2007; Foerster *et al.* 2007) suggest that such sexual conflicts may be common (Arnqvist & Rowe 2005), they have very rarely been studied in nature (Arnqvist & Rowe 2005; Rowe & Day 2006).

Since Darwin's (1871) suggestion that certain conspicuous male traits may have evolved through male–male combat, the massive sexually selected horns of male bighorn sheep (*Ovis canadensis*; figure 1) have attracted much attention from evolutionary biologists (Geist 1966; Fitzsimmons *et al.* 1995; Coltman *et al.* 2002, 2003, 2005; Festa-Bianchet *et al.* 2004). On the other hand, the smaller horns of females have almost never been studied and have no clearly known fitness benefit. The presence of horns in females could result from a genetic correlation with male horns. Alternatively, horns may be useful to both sexes but differ in size if they have different functions. For example, female horns may play an important role in defence against predators and intraspecific competition (Packer 1983; Roberts 1996).

The aim of this study was to test for the presence of sexual conflict at loci influencing horn size and body weight in a pedigreed population of wild bighorn sheep studied extensively for over 35 years (Coltman *et al.* 2005). Because a sexual conflict at the genetic level requires heritable traits, we first quantified additive genetic variance in both sexes. We then assessed the importance of genetic constraints on the evolution of sexual dimorphism by estimating intersexual genetic correlations (r_g). Finally, we quantified sex-specific selection using field estimates of longevity and reproductive success. Significant heritability in both sexes for a shared trait could lead to sexual conflict at the genetic level if it was combined with sexually antagonistic selection and an intersexual $r_g > 0$. Conflict would also be present when selection is in the same direction in both sexes but where $r_g < 0$. We included body mass in our analyses not only to control for the influence of body size on horn size, but also to contrast quantitative genetic parameters and selection at traits varying in their degree of sexual dimorphism (horn size being much more dimorphic than body mass). This study represents a rare test of sexual conflict at loci influencing shared traits (Arnqvist & Rowe 2005; Rowe & Day 2006) and provides much needed information on the importance of genetic constraints on the evolution of sexual dimorphism in nature (Rice & Chippindale 2001; Fairbairn 2007).

2. MATERIAL AND METHODS

(a) *Study site and data collection*

The study population inhabits Ram Mountain, Alberta, Canada (52° N, 115° W, elevation 1080–2170 m). Techniques used to capture, mark, measure and monitor individuals are
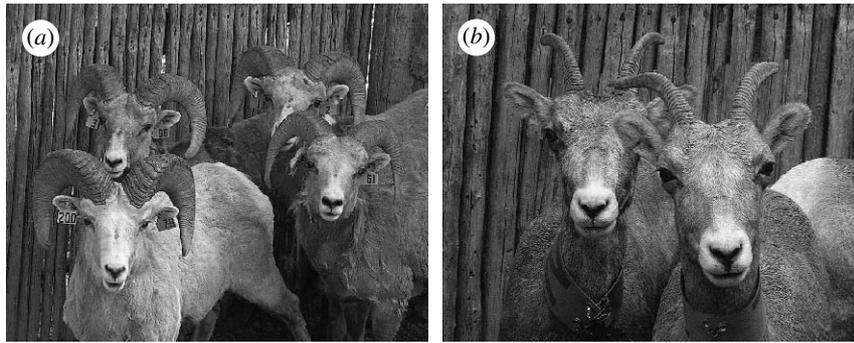
Figure 1. (*a*) Adult male and (*b*) female bighorn sheep from Ram Mountain, Alberta, Canada. Photos by Julien Martin.

described in detail elsewhere (Jorgenson *et al.* 1993). The data presented here were collected from 1970 to 2006. Briefly, animals were captured in a corral trap baited with salt from late May to September or early October each year. Almost all animals were marked as lambs or yearlings, so that their exact age was known. Individuals first captured as adults were aged by counting horn growth rings. Marked sheep were monitored throughout their lifetime.

Ewes and young rams are usually captured multiple times each year, while rams 3 years and older are typically caught only one to three times per season, usually in June or July. At each capture, sheep are weighed to the nearest 250 g with a Detecto spring scale. The horn length along the outside curvature and the horn base circumference are measured to the nearest millimetre for both horns using tape. Horn volume (cm^3) was calculated assuming a conical shape using the average horn base circumference of both horns and the length of the longest horn to reduce the influence of horn breakage.

(b) Pedigree information

The pedigree used in this study includes 764 maternal and 435 paternal links. It differs from the one in Coltman *et al.* (2005) by the addition of individuals born between 2003 and 2006. Maternity was accurately determined from field observations of suckling behaviour. Paternity was determined using paternity test and half-sib reconstruction based on genotypes at approximately 30 microsatellite loci for samples collected from 1988 to 2006. The laboratory and statistical methods are detailed in Coltman *et al.* (2005).

(c) Quantitative genetic analysis

Phenotypic variance in horn volume and body mass was partitioned into additive genetic and other components using an animal model and restricted maximum likelihood with the program ASREML v. 2.0 (Gilmour *et al.* 2006). The animal model is a form of mixed model incorporating pedigree information where the phenotype of each individual is modelled as the sum of its additive genetic value and other random and fixed effects. This method is particularly useful for the study of natural populations because it optimizes the use of information from complex and incomplete pedigrees when estimating quantitative genetic parameters (Kruuk 2004).

Prior to analysis each trait for each age/sex class was standardized to a standard deviation of unity. We then partitioned the phenotypic variance left after taking into account fixed effects into five components: additive genetic (V_a), permanent environmental (V_{pe}), year (V_y), year of birth (V_{yob}) and residual (V_r). We also attempted to include a maternal effect component but this often caused convergence problems for bivariate models. Since the influence of maternal

effects for body size is known to be negligible by age 2 in the study population (Wilson *et al.* 2005), we decided not to include maternal effects and to restrict our analysis to adult sheep (2 years old and older). We also excluded animals older than 5 years because the distribution of phenotypes in older males is biased by trophy hunting (Coltman *et al.* 2003; Festa-Bianchet *et al.* 2004) and most rams become vulnerable to hunting at 5–7 years of age depending on their rate of horn growth. Year and year of birth were fitted to account for the influence of environmental variation (Postma 2006; Kruuk & Hadfield 2007). Since different individuals were sampled at different points within sampling seasons, we included day of capture (continuous, second-order polynomial, with 24 May as day 0) as a fixed effect. Since growth patterns differ between age classes, we also fitted age (factor) and the age×date interaction. We used bivariate models to estimate covariances and correlations within and between the sexes. The significance of (co)variance components was assessed using likelihood ratio tests. Narrow sense heritability (h^2) and other ratios were calculated by dividing the appropriate variance component by V_p (e.g. V_a/V_p for h^2), where $V_p = V_a + V_{pe} + V_y + V_{yob} + V_r$. The significance of ratios and correlations was not explicitly tested but was instead inferred from the significance of their associated (co)variance components. Since a main objective of this study was to assess the importance of genetic constraints, we also verified whether genetic correlations were smaller than unity using likelihood ratio tests. The number of individuals and measurements included in the animal models are presented in table 1.

(d) Selection analysis

Our selection analyses were based on estimates of lifetime reproductive success (LRS, number of lambs produced that survived to weaning), longevity (in years) and mean reproductive success (MRS = LRS × longevity^{-1}). Separate analyses were performed for males and females. We only included animals that were born before 1996 so that every individual had the opportunity to reach 10 years of age. For LRS and MRS, we only included genotyped males that have been DNA sampled and therefore included in paternity analyses. Females that had received contraceptive implants and individuals removed for translocations or research purposes were excluded from the analysis. To account for changes in density and environmental conditions, we fitted year of birth as a factor in all models. Cohorts comprising a single informative individual were therefore omitted (1968 and 1994 for male longevity, 1980 and 1994 for male reproductive success and 1974 for female longevity and reproductive success).

Table 1. Phenotypic data for body mass (kg) and horn volume (cm^3) in bighorn sheep. (Number of individuals and observations included in the animal models are indicated as well as age-specific trait means and variation (s.d.). Each sex/age class was standardized (s.d. of unity) prior to analysis.)

trait/age	males				females			
	2	3	4	5	2	3	4	5
body mass								
individuals	203	169	142	119	235	222	199	177
observations	502	340	237	184	703	695	609	544
mean	56.6	69.1	77.3	83.5	48.6	56.3	60.0	62.5
s.d.	10.5	10.1	10.4	10.6	7.9	7.4	7.1	7.2
horn volume								
individuals	201	169	145	121	225	210	189	164
observations	498	339	240	186	620	596	526	457
mean	486.8	1133.7	1877.8	2412.6	70.6	103.2	120.0	124.9
s.d.	237.4	431.1	597.6	592.2	24.2	25.7	27.2	25.6

Table 2. Additive genetic, year, year of birth and permanent environmental (co)variance components and correlations within and between the sexes for body mass and horn volume in adult bighorn sheep. (Variance components are on the diagonal while covariance components are below the diagonal and correlations are above the diagonal. Variance components were obtained with sex-specific univariate animal models whereas covariances where obtained from bivariate models. Significance of (co)variance components was tested with likelihood ratio tests. $^*p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$. The significance of genetic correlations (in italics when different from zero) was inferred from the significance of associated covariance components. †Identifies genetic correlations significantly smaller than unity ($^†p < 0.05$ and $^{††}p < 0.01$). Standard errors generated by ASRᴇᴍʟ are also presented. MBM, male body mass; MHV, male horn volume; FBM, female body mass and FHV, female horn volume.)

	MBM	MHV	FBM	FHV
additive genetic				
MBM	0.19 (0.07)**	*0.74 (0.15)*	*0.63 (0.30)*	0.27 (0.30)†
MHV	0.15 (0.07)*	0.22 (0.09)**	0.02 (0.29)††	0.24 (0.28)†
FBM	0.08 (0.04)*	0.00 (0.05)	0.10 (0.04)**	*0.63 (0.20)*†
FHV	0.06 (0.06)	0.06 (0.07)	0.10 (0.05)*	0.25 (0.10)**
year				
MBM	0.08 (0.02)***	*0.70 (0.11)*	*0.51 (0.16)*	*0.53 (0.15)*
MHV	0.06 (0.02)***	0.10 (0.03)***	*−0.56 (0.14)*	−0.23 (0.20)
FBM	0.07 (0.03)*	−0.11 (0.04)*	0.28 (0.08)***	*0.90 (0.04)*
FHV	0.05 (0.02)*	−0.02 (0.02)	0.19 (0.06)***	0.11 (0.03)***
year of birth				
MBM	0.12 (0.05)***	*0.96 (0.04)*	0.10 (0.26)	0.30 (0.25)
MHV	0.15 (0.06)***	0.18 (0.06)***	−0.10 (0.23)	0.37 (0.22)
FBM	0.02 (0.04)	−0.03 (0.06)	0.26 (0.08)***	*0.93 (0.04)*
FHV	0.05 (0.04)	0.08 (0.06)	0.29 (0.09)***	0.26 (0.09)***
permanent environment				
MBM	0.12 (0.06)**	*0.75 (0.20)*	—	—
MHV	0.10 (0.06)*	0.14 (0.08)*	—	—
FBM	—	—	0.13 (0.04)***	0.32 (0.17)
FHV	—	—	0.06 (0.04)	0.28 (0.08)***

We estimated sex-specific standardized linear and quadratic selection differentials and gradients using linear regression (Lande & Arnold 1983). For phenotypic values, we used body mass and horn volume at age 4 corrected to 5 June. These corrected values were obtained using individual linear regressions for individuals sampled multiple times and using mean population growth rate for individuals sampled only once. The significance of coefficients was tested using generalized linear models with negative binomial error for LRS and Poisson error for longevity. For MRS, we used a linear model with a square root transformation. Neither quadratic nor interaction terms were statistically significant and are therefore not shown. These analyses were performed using S-Pʟᴜs v. 7.0 (Insightful).

3. RESULTS

(a) *Quantitative genetic parameters*

Body mass and horn volume showed significant additive genetic variance in both sexes (table 2). The proportion of phenotypic variance explained by additive genetic effects after accounting for fixed effects ranged from 0.11 ± 0.05 for female body mass (FBM) to 0.32 ± 0.12 for male body mass (MBM) and male horn volume (MHV; table 3). Year and year of birth were also significant for all traits and combined they explained 33–58% of the variation (tables 2 and 3). Finally, permanent environmental effects which include non-additive genetic variance were also significant for all traits and accounted for 14–27% of the variation (tables 2 and 3).

Table 3. Sex-specific proportions of phenotypic variance explained by additive genetic (h^2), year, year of birth and permanent environmental effects. (Standard errors generated by ASREML are also presented. MBM, male body mass; MHV, male horn volume; FBM, female body mass and FHV, female horn volume.)

trait	h^2	year	year of birth	perm. env.
MBM	0.32 (0.12)	0.13 (0.04)	0.20 (0.07)	0.21 (0.11)
MHV	0.32 (0.12)	0.14 (0.04)	0.25 (0.07)	0.20 (0.11)
FBM	0.11 (0.05)	0.30 (0.06)	0.28 (0.07)	0.14 (0.04)
FHV	0.24 (0.09)	0.11 (0.03)	0.25 (0.07)	0.27 (0.08)

Table 4. Sex-specific standardized directional selection differentials (S_i') and gradients (β_i') for body mass and horn volume in bighorn sheep. (Male and female data were analysed separately. Analyses were based on phenotypic values on 5 June at 4 years old. Fitness was defined as LRS (number of lambs produced that survived to weaning over an individual's lifetime), longevity (in years) and mean reproductive success (MRS, LRS×longevity^{-1}).) Significant coefficients ($p < 0.05$) are italicized.

trait	fitness metric	n	S_i'	p	β_i'	p
male body mass	LRS	72	−0.09 (0.25)	0.68	−0.12 (0.36)	0.87
	longevity	129	−0.02 (0.04)	0.72	0.04 (0.05)	0.49
	MRS	72	0.03 (0.21)	0.99	−0.02 (0.29)	0.91
male horn volume	LRS	72	−0.05 (0.26)	0.50	0.03 (0.38)	0.58
	longevity	128	−0.08 (0.05)	0.15	−0.11 (0.06)	0.13
	MRS	72	0.06 (0.21)	0.89	0.07 (0.31)	0.86
female body mass	LRS	137	*0.13 (0.06)*	*< 0.05*	*0.16 (0.07)*	*< 0.01*
	longevity	137	*0.09 (0.04)*	*< 0.05*	*0.11 (0.04)*	*< 0.05*
	MRS	137	*0.08 (0.04)*	*< 0.05*	*0.10 (0.05)*	*< 0.05*
female horn volume	LRS	133	0.06 (0.05)	0.29	0.01 (0.06)	0.97
	longevity	133	0.03 (0.03)	0.39	−0.01 (0.04)	0.87
	MRS	133	0.01 (0.04)	0.73	−0.02 (0.04)	0.22

The r_g estimates were relatively large and significantly positive for three pairs of traits (table 2). These included r_g for pairs of traits within each sex (body mass versus horn volume) and between male and FBM. On the other hand, intersexual r_g involving horn volume was all relatively small and significantly smaller than unity (table 2).

With the exception of covariance between MHV and female traits, year and year of birth appeared to affect pairs of traits similarly (table 2). In particular, year and year of birth correlations were close to unity for pairs of traits within each sex. The within-sex correlation for permanent environmental effects was close to unity in males (0.75 ± 0.20) and negligible in females (0.06 ± 0.04; table 2).

(b) Selection analysis
Selection coefficients were relatively small in both sexes (table 4). In males, none of the selection coefficients for body mass and horn volume were significant. However, MHV showed a non-significant trend for a negative association with longevity after accounting for selection on body mass (-0.11 ± 0.06, $p = 0.13$; table 4). In females, selection differentials and gradients for body mass were all positive and significant. There was no evidence for directional selection on female horn volume (FHV).

4. DISCUSSION
(a) Quantitative genetic parameters
Body mass and horn volume showed significant additive genetic variance in both sexes. Quantitative genetic parameters had previously been estimated for FBM and male traits (Réale *et al.* 1999; Coltman *et al.* 2003, 2005; Pelletier *et al.* 2007) but not for female horn size. Heritability of horn volume in females was comparable

with the male estimate ($h^2 = 0.24 \pm 0.09$ versus 0.32 ± 0.12, respectively).

Our estimates of the genetic correlation between horn size and body mass in females were significantly smaller than unity. This is important because it suggests that horn volume can evolve relative to body size in that sex. In contrast, the same genetic correlation was not significantly smaller than unity in males (0.74 ± 0.15, $p = 0.11$). This is consistent with the results of Coltman *et al.* (2003, 2005) and suggests that the evolution of horn size relative to body mass may be more constrained in males.

One of our main goals was to evaluate the importance of genetic constraints on the evolution of sexual dimorphism in bighorn sheep. As previously shown (Coltman *et al.* 2003, 2005), we found that the evolution of body size sexual dimorphism may be constrained by a large intersexual r_g (0.63 ± 0.30). On the other hand, r_g was smaller than unity for many other pairs of traits, which suggests that horn volume should be able to evolve partly independently in each sex and that sex-specific optima could be reached more readily (Lande 1980). In particular, the intersexual r_g for horn volume was quite small (0.24 ± 0.28) and similar to estimates reported for other highly sexually dimorphic traits in other species (e.g. fat deposition in humans, Comuzzie *et al.* 1993; antenna length in the fly *Prochyliza xanthostoma*, Bonduriansky & Rowe 2005). This is consistent with the prediction that sexual dimorphism and intersexual r_g should be negatively correlated in response to sexually divergent selection (Bonduriansky & Rowe 2005; Fairbairn & Roff 2006).

(b) Selection analysis
None of the selection coefficients differed significantly from zero in males. However, rams with fast-growing

horns are artificially selected against by trophy hunters in the study population (Coltman *et al.* 2003; Festa-Bianchet *et al.* 2004). Each year approximately 40% of rams with horns that satisfy the legal definition of a harvestable ram are shot. The trend towards a negative association between horn volume and longevity after controlling for selection on body mass (-0.11 ± 0.06, $p = 0.13$) probably results from hunting pressure. A similar negative relationship between horn volume and longevity was documented in Soay sheep where it probably results from the cost of growing and carrying large horns (Robinson *et al.* 2006). In our study population, any natural selection against large horns is unlikely to be expressed because of trophy hunting (Coltman *et al.* 2003; Festa-Bianchet *et al.* 2004). It may also be that artificial selection more effectively targets total horn length or morphology rather than horn volume in bighorn sheep. For example, harvest restrictions are based on horn length and shape, not on horn volume. Similarly, horn length is a good correlate of mating success in rams after accounting for age (Coltman *et al.* 2002). Horn volume may reflect the metabolic costs of growing and carrying horns, however, total horn length may be more relevant in terms of artificial and sexual selection.

Selection differentials and gradients for body mass were all significantly positive in females. Coltman *et al.* (2005) and Pelletier *et al.* (2007) also observed positive relationships between body mass in June and female fitness. On the other hand, horn volume does not appear to be under directional selection in females. This contrasts with the negative association observed between horn size and LRS in female Soay sheep (Robinson *et al.* 2006). It may be that female horns in bighorn sheep are so small relative to body size that they do not incur an easily detectable fitness cost.

In summary, we tested for intralocus sexual conflict in a wild population of bighorn sheep by estimated quantitative genetic parameters and selection coefficients for two sexually dimorphic traits. Because all traits showed significant additive genetic variance and all genetic correlations were positive, sexual conflicts at the genetic level are possible in the presence of sexually antagonistic selection. However, the absence of detectable sexually antagonistic selection suggests that there are currently no such conflicts.

REFERENCES

Arnqvist, G. & Rowe, L. 2005 *Sexual conflict*. Princeton, NJ: Princeton University Press.

Bonduriansky, R. & Rowe, L. 2005 Intralocus sexual conflict and the genetic architecture of sexually dimorphic traits in *Prochyliza xanthostoma* (Diptera: Piophilidae). *Evolution* **59**, 1965–1975.

Brommer, J. E., Kirkpatrick, M., Qvarnström, A. & Gustafsson, L. 2007 The intersexual genetic correlation for lifetime fitness in the wild and its implications for sexual selection. *PLoS ONE* **2**, e744. (doi:10.1371/journal.pone.0000744)

Chippindale, A. K., Gibson, J. R. & Rice, W. R. 2001 Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila. Proc. Natl Acad. Sci. USA* **98**, 1671–1675. (doi:10.1073/pnas.041378098)

Coltman, D. W., Festa-Bianchet, M., Jorgenson, J. T. & Strobeck, C. 2002 Age-dependent sexual selection in bighorn rams. *Proc. R. Soc. B* **269**, 165–172. (doi:10.1098/rspb.2001.1851)

Coltman, D. W., O'Donoghue, P., Jorgenson, J. T., Hogg, J. T., Strobeck, C. & Festa-Bianchet, M. 2003 Undesirable consequences of trophy hunting. *Nature* **426**, 655–658. (doi:10.1038/nature02177)

Coltman, D. W., O'Donoghue, P., Hogg, J. T. & Festa-Bianchet, M. 2005 Selection and genetic (co)variance in bighorn sheep. *Evolution* **59**, 1372–1382.

Comuzzie, A. G., Blangero, J., Mahaney, M. C., Mitchell, B. D., Stern, M. P. & Maccluer, J. W. 1993 Quantitative genetics of sexual dimorphism in body fat measurements. *Am. J. Hum. Biol.* **5**, 725–734. (doi:10.1002/ajhb.1310050616)

Darwin, C. 1871 *The descent of man and selection in relation to sex*. London, UK: J. Murray.

Fairbairn, D. J. 2007 Introduction: the enigma of sexual size dimorphism. In *Sex, size and gender roles. Evolutionary studies of sexual dimorphism* (eds D. J. Fairbairn, W. U. Blanckenhorn & T. Székely), pp. 1–15. Oxford, UK: Oxford University Press.

Fairbairn, D. J. & Roff, D. A. 2006 The quantitative genetics of sexual dimorphism: assessing the importance of sex-linkage. *Heredity* **97**, 319–328. (doi:10.1038/sj.hdy.6800895)

Festa-Bianchet, M., Coltman, D. W., Turelli, L. & Jorgenson, J. T. 2004 Relative allocation to horn and body growth in bighorn rams varies with resource availability. *Behav. Ecol.* **15**, 305–312. (doi:10.1093/beheco/arh014)

Fitzsimmons, N. N., Buskirk, S. W. & Smith, M. H. 1995 Population history, genetic variability, and horn growth in bighorn sheep. *Conserv. Biol.* **9**, 314–323. (doi:10.1046/j.1523-1739.1995.9020314.x)

Foerster, K., Coulson, T., Sheldon, B. C., Pemberton, J. M., Clutton-Brock, T. H. & Kruuk, L. E. B. 2007 Sexually antagonistic genetic variation for fitness in red deer. *Nature* **447**, 1107–1110. (doi:10.1038/nature05912)

Geist, V. 1966 The evolutionary significance of mountain sheep horns. *Evolution* **20**, 558–566. (doi:10.2307/2406590)

Gilmour, A. R., Gogel, B. J., Cullis, B. R. & Thompson, R. 2006 *ASReml user guide. Release 2.0.* Hemel Hempstead, UK: VSN International.

Jorgenson, J. T., Festa-Bianchet, M. & Wishart, W. D. 1993 Harvesting bighorn ewes: consequences for population size and trophy ram production. *J. Wildl. Manage.* **57**, 429–435. (doi:10.2307/3809267)

Kruuk, L. E. B. 2004 Estimating genetic parameters in natural populations using the 'animal model'. *Phil. Trans. R. Soc. B* **359**, 873–890. (doi:10.1098/rstb.2003.1437)

Kruuk, L. E. B. & Hadfield, J. D. 2007 How to separate genetic and environmental causes of similarity between relatives. *J. Evol. Biol.* **20**, 1890–1903. (doi:10.1111/j.1420-9101.2007.01377.x)

Lande, R. 1980 Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**, 292–305. (doi:10.2307/2407393)

Lande, R. & Arnold, S. J. 1983 The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226. (doi:10.2307/2408842)

Packer, C. 1983 Sexual dimorphism: the horns of African antelopes. *Science* **221**, 1191–1193. (doi:10.1126/science.221.4616.1191)

Pelletier, F., Reale, D., Garant, D., Coltman, D. W. & Festa-Bianchet, M. 2007 Selection on heritable seasonal phenotypic plasticity of body mass. *Evolution* **61**, 1969–1979. (doi:10.1111/j.1558-5646.2007.00160.x)

Postma, E. 2006 Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. *J. Evol. Biol.* **19**, 309–320. (doi:10.1111/j.1420-9101.2005.01007.x)

Réale, D., Festa-Bianchet, M. & Jorgenson, J. T. 1999 Heritability of body mass varies with age and season in wild bighorn sheep. *Heredity* **83**, 526–532. (doi:10.1038/sj.hdy.6885430)

Rice, W. R. & Chippindale, A. K. 2001 Intersexual ontogenetic conflict. *J. Evol. Biol.* **14**, 685–693. (doi:10.1046/j.1420-9101.2001.00319.x)

Roberts, S. C. 1996 The evolution of hornedness in female ruminants. *Behaviour* **133**, 399–442.

Robinson, M. R., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M. & Kruuk, L. E. B. 2006 Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in soay sheep. *Evolution* **60**, 2168–2181.

Roff, D. A. 1997 *Evolutionary quantitative genetics*. New York, NY: Chapman & Hall.

Rowe, L. & Day, T. 2006 Detecting sexual conflict and sexually antagonistic coevolution. *Phil. Trans. R. Soc. B* **361**, 277–285. (doi:10.1098/rstb.2005.1788)

Wilson, A. J., Kruuk, L. E. B. & Coltman, D. W. 2005 Ontogenetic patterns in heritable variation for body size: using random regression models in a wild ungulate population. *Am. Nat.* **166**, E177–E192. (doi:10.1086/497441)