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 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 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_q). 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_q > 0. Conflict would also be present when selection is in the same direction in both sexes but where r_q < 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
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 ASRem 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 ($MRS = LRS \times \text{longevity}^{-1}$). 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).
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-PLUS 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.)

<table>
<thead>
<tr>
<th>trait</th>
<th>$h^2$</th>
<th>year</th>
<th>year of birth</th>
<th>perm. env.</th>
</tr>
</thead>
<tbody>
<tr>
<td>MBM</td>
<td>0.24 (0.09)</td>
<td>0.11 (0.03)</td>
<td>0.25 (0.07)</td>
<td>0.27 (0.08)</td>
</tr>
<tr>
<td>MHV</td>
<td>0.11 (0.05)</td>
<td>0.30 (0.06)</td>
<td>0.28 (0.07)</td>
<td>0.14 (0.04)</td>
</tr>
<tr>
<td>FBM</td>
<td>0.24 (0.09)</td>
<td>0.11 (0.03)</td>
<td>0.25 (0.07)</td>
<td>0.27 (0.08)</td>
</tr>
<tr>
<td>FHV</td>
<td>0.32 (0.12)</td>
<td>0.13 (0.04)</td>
<td>0.20 (0.07)</td>
<td>0.21 (0.11)</td>
</tr>
</tbody>
</table>

Table 4. Sex-specific standardized directional selection differentials ($S'_i$) and gradients ($\beta'_i$) 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.

<table>
<thead>
<tr>
<th>trait</th>
<th>fitness metric</th>
<th>n</th>
<th>$S'_i$</th>
<th>$\beta'_i$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>male body mass</td>
<td>LRS</td>
<td>72</td>
<td>-0.09 (0.25)</td>
<td>-0.12 (0.36)</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>longevity</td>
<td>129</td>
<td>-0.02 (0.04)</td>
<td>0.04 (0.05)</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>MRS</td>
<td>72</td>
<td>0.03 (0.21)</td>
<td>-0.02 (0.29)</td>
<td>0.91</td>
</tr>
<tr>
<td>male horn volume</td>
<td>LRS</td>
<td>72</td>
<td>-0.05 (0.26)</td>
<td>0.03 (0.38)</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td>longevity</td>
<td>128</td>
<td>-0.08 (0.05)</td>
<td>-0.11 (0.06)</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>MRS</td>
<td>72</td>
<td>0.06 (0.21)</td>
<td>0.07 (0.31)</td>
<td>0.86</td>
</tr>
<tr>
<td>female body mass</td>
<td>LRS</td>
<td>137</td>
<td>0.13 (0.06)</td>
<td>&lt;0.05</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>longevity</td>
<td>137</td>
<td>0.09 (0.04)</td>
<td>&lt;0.05</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td>MRS</td>
<td>137</td>
<td>0.08 (0.04)</td>
<td>&lt;0.05</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>female horn volume</td>
<td>LRS</td>
<td>133</td>
<td>0.06 (0.05)</td>
<td>0.29</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>longevity</td>
<td>133</td>
<td>0.03 (0.03)</td>
<td>-0.01</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>MRS</td>
<td>133</td>
<td>0.01 (0.04)</td>
<td>-0.02</td>
<td>0.22</td>
</tr>
</tbody>
</table>

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).

**Selection analysis**

(4) 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; Colman 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 ($h^2=0.24±0.09$ 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 Colman 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 (Colman 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% oframs 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.

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