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ORIGINAL ARTICLE

QTL mapping for sexually dimorphic fitness-related traits in wild bighorn sheep

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Dissecting the genetic architecture of fitness-related traits in wild populations is key to understanding evolution and the mechanisms maintaining adaptive genetic variation. We took advantage of a recently developed genetic linkage map and phenotypic information from wild pedigreed individuals from Ram Mountain, Alberta, Canada, to study the genetic architecture of ecologically important traits (horn volume, length, base circumference and body mass) in bighorn sheep. In addition to estimating sex-specific and cross-sex quantitative genetic parameters, we tested for the presence of quantitative trait loci (QTLs), colocalization of QTLs between bighorn sheep and domestic sheep, and sex×QTL interactions. All traits showed significant additive genetic variance and genetic correlations tended to be positive. Linkage analysis based on 241 microsatellite loci typed in 310 pedigreed animals resulted in no significant and five suggestive QTLs (four for horn dimension on chromosomes 1, 18 and 23, and one for body mass on chromosome 26) using genome-wide significance thresholds (Logarithm of odds (LOD) >3.31 and >1.88, respectively). We also confirmed the presence of a horn dimension QTL in bighorn sheep at the only position known to contain a similar QTL in domestic sheep (on chromosome 10 near the *horns* locus; nominal $P<0.01$) and highlighted a number of regions potentially containing weight-related QTLs in both species. As expected for sexually dimorphic traits involved in male–male combat, loci with sex-specific effects were detected. This study lays the foundation for future work on adaptive genetic variation and the evolutionary dynamics of sexually dimorphic traits in bighorn sheep.
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INTRODUCTION

Dissecting the genetic architecture of ecologically important traits is key to understanding evolution as well as the mechanisms allowing the maintenance of adaptive genetic variation (Ellegren and Sheldon, 2008; Nadeau and Jiggins, 2010; Slate *et al.*, 2010). While a variety of approaches can be used to identify relevant loci (Stinchcombe and Hoekstra, 2007; Ellegren and Sheldon, 2008), there is growing interest in performing genomic studies using free-living pedigreed populations (Slate *et al.*, 2010). Apart from enabling work on species that may not be amenable to controlled experiments, the study of wild populations is motivated by unparalleled opportunities to address topics requiring fitness estimates that are minimally influenced by experimental conditions (Ellegren and Sheldon, 2008; Clutton-Brock and Sheldon, 2010; Slate *et al.*, 2010). These include the genetic architecture of fitness in natural environments (Ellegren and Sheldon, 2008), the evolutionary dynamics of sexually selected traits (Chenoweth and McGuigan, 2010), evolutionary stasis (for example, Gratten *et al.*, 2008) and sexually antagonistic genetic variation (Bonduriansky and Chenoweth, 2009; Slate *et al.*, 2010). However, apart from work in humans, studies on the genetic architecture of ecologically important traits in free-living populations remain rare because of difficulties in maintaining multigenerational pedigrees and assembling adequate genotype–phenotype data sets (Slate, 2005; Slate *et al.*, 2010).

The bighorn sheep (*Ovis canadensis*), a mountain ungulate endemic to Western North America, has been the focus of numerous ecological and evolutionary quantitative genetic investigations (for example, Coltman *et al.*, 2003, 2005; Poissant *et al.*, 2008; Réale *et al.*, 2009) and is emerging as an excellent ecological model for studies of evolution in the wild. Two traits of interest, because of their links with fitness, are horn size and body mass. Both traits are sexually selected in males (Coltman *et al.*, 2002), and body mass is associated with offspring survival (Feder *et al.*, 2008) and female lifetime reproductive fitness (Poissant *et al.*, 2008). In the Ram Mountain study population, male horn size and body mass also experience negative directional selection through trophy hunting (Coltman *et al.*, 2003). The identification of chromosomal regions containing genes influencing these traits (quantitative trait loci, QTLs) would therefore open a unique window of opportunity to study the evolutionary dynamics of adaptive molecular variation in wild bighorn sheep.

The study of horn size and body mass in bighorn sheep is also motivated by the presence of notable sexual dimorphism (Poissant *et al.*, 2008). In theory, the evolution of sexual dimorphism depends on the presence of sex-specific genetic variance (Lande, 1980). Although such variance has been documented in a large number of organisms (Poissant and Coltman 2009; Poissant *et al.*, 2010a), including bighorn sheep (Poissant *et al.*, 2008), little is known about its molecular underpinning and micro-evolutionary dynamics. Dissecting the genetic architecture of sexually dimorphic traits in bighorn sheep would thus also provide insights into the molecular mechanisms facilitating the independent evolution of males and females.

Differentiating real QTLs from false positives is a major challenge in any QTL mapping study (Lander and Kruglyak, 1995), especially for

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studies of wild populations in which sample sizes are typically limited (Slate *et al.*, 2010). In bighorn sheep, data interpretation could be facilitated by previous research in domestic sheep (*Ovis aries*, ~3 million years divergence, Bunch *et al.*, 2006). Indeed, one QTL has already been mapped for horn size in domestic sheep (that is, on chromosome 10 near the *horns* locus, Johnston *et al.* 2010). A large number of QTLs have also been identified for weight-related traits (reviewed in Cavanagh *et al.*, 2010). QTLs often appear to be conserved across species (for example, Reid *et al.*, 2005; Moghadam *et al.*, 2007) but expectations for fitness-related traits are unclear, in particular because selection is expected to reduce genetic variation through the fixation of advantageous alleles (Falconer, 1989).

We performed a genome-wide scan for horn dimension (volume, length, base circumference) and body mass QTLs in wild bighorn sheep from Ram Mountain, Alberta, Canada, using a recently developed microsatellite genetic linkage map (Poissant *et al.*, 2010b). As sexually antagonistic selection resulting from sexual selection in one sex is expected to promote the accumulation of sex-specific genetic variance (Poissant *et al.*, 2010a), we searched for QTLs influencing both sexes similarly as well as QTLs having sex-specific effects. We also tested for QTL colocalization between bighorn sheep and domestic sheep to assist with data interpretation and assess whether the same loci could be involved in similar micro-evolutionary processes across species.

MATERIALS AND METHODS

Study population

The Ram Mountain bighorn sheep population is native to a small isolated mountain range located about 50 km east of the Canadian Rockies in Alberta, Canada (52°N, 115°W, elevation 1080–2170 m). This study is based on data collected from 1970 to 2009. Techniques used to capture, mark, measure and monitor animals were described in detail by Jorgenson *et al.* (1993). 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 early in life, so their exact age was known. Individuals captured for the first time as adults were aged by counting horn growth rings. Marked sheep were subsequently monitored throughout their lifetime.

Phenotypic data

Most females and young males were captured multiple (>3) times each year, while males 3 years and older were typically caught one to three times per season, usually in June or July. At each capture, sheep were weighed and the size of their horns was measured. Horn measurements included length along the outside curvature and horn base circumference. As in Poissant *et al.* (2008), horn volume was subsequently 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. Horn length measurements of females with two severely broken horns were excluded. We focused on phenotypes measured in adults aged 2 to 10 to reduce the potentially confounding influence of maternal effects (Wilson *et al.*, 2005; Kruuk and Hadfield, 2007) and age×QTL interactions (Poissant and Coltman 2009).

Pedigree information

Over the entire study period, maternity was inferred in the field using suckling behavior. Genetic analyses (described below) showed that this technique is accurate in >99% of cases. Since 1988, the collection of DNA samples permitted formal genetic parentage analyses. These were based on ~30 microsatellite loci (for details, see Coltman *et al.*, 2005) and the 95% confidence threshold in Cervus (Marshall *et al.*, 1998). In addition, the software Colony (Wang, 2004) was used to infer sibships resulting from sires that were not DNA sampled (for details, see Coltman *et al.*, 2005). The accuracy of parts of the pedigree was also recently assessed using >200 microsatellite loci used for linkage map construction (details below). The current pedigree contains 803 maternal links resulting from 236 dams (mean number of offspring ± 1 s.d.=3.40 ± 2.52) and 454 paternal links resulting from 70 sampled and 36 unsampled sires (mean number of offspring per sire=4.28 ± 4.40).

Only parts of the full pedigree are informative for QTL mapping purposes because genome-wide genotypes have only been obtained for a subset of individuals. We therefore based our QTL mapping analyses on a restricted pedigree composed of 310 fully typed animals (172 females and 138 males). We also included animals that were either untyped (n=18) or only typed at markers used for initial parentage analyses (n=41) if they helped to connect fully typed animals in the pedigree (that is, parents). The QTL mapping pedigree included 201 females and 159 males connected by 301 maternal links (mean number of offspring per dam ± 1 s.d.=2.59 ± 1.49) and 259 paternal links (mean number of offspring per sire=4.05 ± 3.28).

Bighorn sheep linkage map

The bighorn sheep linkage map is based on information from two wild pedigreed populations (Ram Mountain, Alberta, Canada, and National Bison Range, MT, USA) and contains 247 microsatellites ordered along all 26 autosomes and the X chromosome (Poissant *et al.*, 2010b). A total of 241 markers have been genotyped in the Ram Mountain population, and all but three (OarFCB11, BMS1247 and BMS1948, which are located near telomeres of chromosomes 2, 5 and 21 in domestic sheep, respectively) are positioned in the species map. In this study, we used recombination fractions from the integrated species map instead of the Ram Mountain population-specific map because they are likely more accurate (Poissant *et al.*, 2010b). Map distances used in this study differ slightly from those presented in Poissant *et al.* (2010b) because recombination fractions were converted to centimorgans using Haldane's rather than Kosambi's mapping function to accommodate downstream QTL mapping analyses (that is, identity-by-descent (IBD) estimation, details below). These new map distances are presented in Supplementary Appendix S1. Additional details about markers, laboratory techniques, map construction and map characteristics are available in Poissant *et al.* (2009, 2010b).

Quantitative genetic analyses

Phenotypic variance was partitioned into additive genetic and other components using the animal model and restricted maximum likelihood implemented in the program ASReml 3.1. (Gilmour *et al.*, 2009). 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. The method has a long history in animal breeding and is now commonly used for studies of free-living populations because of its ability to optimize the use of information in complex and incomplete pedigrees (Wilson *et al.*, 2010).

In a typical animal model:

$$y = X\beta + Za + e$$

y is the vector of individual phenotypes, X and Z are incidence matrices relating fixed and random effects to each individual, β is a vector of fixed effects, a is a vector of polygenic (additive genetic) effects and e is the vector of residual errors.

We initially analyzed male and female traits separately because the genetic architecture of sexually dimorphic traits is expected to be partly independent between the sexes (Poissant *et al.*, 2010a). However, doing so considerably reduces the amount of phenotypic information included in any given analysis and diminishes the probability of detecting QTLs influencing both sexes similarly. All analyses were therefore repeated treating male and female traits as a single trait. We standardized each trait in each age/sex class to an s.d. of one (that is, trait value divided by age- and sex-specific s.d.) before analysis because phenotypic variance differed between the sexes and increased with age, especially in males.

In sex-specific analyses, fixed effects included age (factor), date of capture (continuous, second-order polynomial, with 24 May as day 0), and the age×date interaction. In analyses where male and female homologous traits were combined, fixed effects also included sex and all possible interactions.

We extended the basic animal model described above in all analyses with the addition of permanent environmental (identity), year of capture and year of birth random effects. The permanent environmental effect was included to

account for inter-individual variation resulting from non-genetic causes (for example, horn breakage) as well as dominance and epistasis. The year of capture and year of birth effects were fitted to account for common environmental conditions (Kruuk and Hadfield, 2007). Phenotypic variance (V_p) was therefore partitioned into five components after having taken fixed effects into account (described below): additive genetic (V_a), permanent environmental (V_{pe}), year of capture (V_y), year of birth (V_{yob}) and residual (V_r). All components were retained in final models even when not significant to prevent biasing V_a upwardly (Wilson *et al.*, 2010).

Heritability (h^2) and other ratios were obtained by dividing individual variance components by V_p where $V_p=V_a+V_{pe}+V_y+V_{yob}+V_r$. Covariances and correlations were obtained using bivariate models. Significance of (co)variance components and ratios was tested using likelihood ratio tests contrasting models including and excluding individual random effects. To test if correlations were significantly smaller than one, we used a similar approach where unconstrained models were contrasted to models in which correlations were constrained to one. All analyses were performed using the full Ram Mountain pedigree as well as the more restricted QTL mapping pedigree for comparative purposes.

QTL mapping

Variance component analysis. We mapped QTLs using a variance component approach (George *et al.*, 2000, Slate 2005). This was done by extending the animal model described above with the addition of a QTL variance component (that is, random effect) estimated using pairwise estimates of IBD for specific genomic locations. IBD matrices were estimated every 2cM (Haldane's mapping function) as well as for unassigned markers using pedigree information, genotypes and map distances with the software Loki (Heath, 1997). Loki does not estimate proper IBD matrices for the sex chromosomes (Lange and Sobel, 2006), but we are unaware of software that will do so in large complex pedigrees. We therefore adopted the approach of Beraldi *et al.* (2007a, b) and estimated IBD matrices for the X chromosome with Loki by treating the Y chromosome as a non-variable X chromosome. After a burn-in period of 50 cycles, 1 million iterations were performed with statistics being stored every two iterations. Significance of QTL effects was determined using logarithm of odds (LOD) scores calculated as

$$LOD = (L_{QTL} - L_{polygenic})/\ln(10)$$

where L was the log likelihood of models with and without a QTL component. As linkage maps of bighorn sheep and domestic sheep are very similar (Poissant *et al.*, 2010b), we adopted significance thresholds previously calculated for domestic sheep by Johnston *et al.* (2010) based on the formula from Lander and Kruglyak (1995). QTL were therefore considered suggestive and significant when LOD scores were >1.88 and 3.31, respectively. Following Lander and Botstein (1989), 95% confidence interval for QTL positions were approximated using the one-LOD drop-off method.

Cross-species QTL colocalization. Following Lander and Kruglyak (1995), we tested for QTL colocalization between bighorn sheep and the closely related domestic sheep using a nominal $P<0.01$ threshold (equivalent to LOD >1.175). More specifically, a QTL was considered to be colocalized between species when a position with LOD >1.175 in bighorn sheep was located within the 95% confidence interval of a significant domestic sheep QTL. This approach is valid for horn size because only one QTL has been mapped for this trait in domestic sheep to date (that is, on chromosome 10 near the *horns* locus, Johnston *et al.*, 2010). On the other hand, it is anticonservative for body mass because of the large number of QTLs that have been mapped in domestic sheep for this trait. Results for body mass should therefore be interpreted with caution. Domestic sheep weight-related QTL information was obtained from Cavanagh *et al.* (2010) and references therein, Beraldi *et al.* (2007b), Margawati *et al.* (2006, 2009) and Hadjipavlou and Bishop (2008).

Sex×QTL interactions. As differences between results from univariate sex-specific models can be artifacts of small sample sizes (Curtsinger, 2002), we explicitly tested for sex×QTL interactions using bivariate animal models. More specifically, we compared the likelihood of models where QTL (co)variance components were left unconstrained with models where QTL variances were constrained to be equal between the sexes and the cross-sex QTL correlation was constrained to one. We tested for significance of sex×QTL interactions using likelihood ratio tests assuming a χ^2 distribution with two degrees of freedom. These tests were restricted to regions identified as potentially containing a QTL using univariate analyses.

RESULTS

All traits showed significant additive genetic, year, year of birth and permanent environmental variance after accounting for fixed effects when analyzing the entire data set for both sex-specific and sexes-combined analyses (Table 1). Similar results were observed when analyzing the smaller QTL mapping data set, except that year of birth and permanent environmental effects were not all significant (Supplementary Appendix S2). The proportion of phenotypic variance explained by each component was similar between data sets, except that heritability tended to be higher in the QTL mapping data set (0.18–0.38 versus 0.21–0.50). In sex-specific analyses, year of capture and year of birth together explained ~20–40% of the phenotypic variance while permanent environmental effects explained ~20–25%. In the sexes-combined analyses, year of capture and year of birth explained ~20–25% of the phenotypic variance while permanent environmental effects explained ~30–50%.

Genetic correlation estimates were generally positive (31 of 34). The only (nonsignificant) negative estimates were between female horn base circumference and male traits. Most genetic correlations were significantly smaller than one (24 of 34, Tables 2 and 3). Of the four cross-sex genetic correlations involving homologous male and female traits, two were significantly smaller than one and close to zero (horn volume and horn base circumference) while two were large and not significantly different from one (horn length and body mass). Estimates obtained using the full and the smaller QTL mapping data set were similar (Tables 2 and 3, Supplementary Appendix S3, Supplementary Appendix S4).

The QTL analysis did not result in the identification of significant QTLs when using the genome-wide significance threshold (LOD >3.31). However, five suggestive QTLs deserving further attention were detected (LOD >1.88, Table 4, Figures 1 and 2). Two of these were identified using male-specific analyses (horn length on chromosomes 1 and 23), one was identified using female-specific analyses (body mass on chromosome 26) and two were identified using sexes-combined analyses (horn volume and base circumference colocalized on chromosome 18). Estimates of individual QTL effects were generally large and comprised most or all of the additive genetic variance (Table 4).

Our test for the cross-species QTL colocalization confirmed the presence of a horn size QTL on chromosome 10 near the *horns* locus across sheep species (nominal $P=0.003$ and 0.005 for male horn volume and base circumference, respectively, Table 4). Similar cross-species comparisons for body mass identified four putative cases of cross-species QTL colocalization. These included one of the suggestive QTLs identified on chromosome 26 and three regions with LOD <1.88 located on chromosomes 2, 23 and 24 (Table 4). As noted earlier, the use of a nominal $P<0.01$ test for the colocalization of body mass QTLs is anticonservative and results should be interpreted with caution.

We tested for the presence of sex×QTL interactions using bivariate models (Table 4). Significant sex-specific QTL effects were observed for the two horn dimension QTLs co-located on chromosome 10 (horn volume and base circumference) as well as a putative body mass QTL on chromosome 23 (all $P<0.05$). A near-significant sex×QTL interaction was also observed for the suggestive body mass QTL on chromosome 26 ($P=0.06$).

Table 1 Proportion of phenotypic variance after having accounted for fixed effects (V_p) explained by additive genetic (h^2), year, year of birth and permanent environmental effects in adult bighorn sheep for horn volume (cm^3), horn length (cm), horn base circumference (cm) and body mass (kg)

Trait	*Ind.*	*Obs.*	*Mean (s.d.)*	*Transformed data mean (s.d.)*	V_p	h^2	*Year*	*Year of birth*	*Perm. env*
Male traits									
Horn volume	261	1711	1546 (1057)	3.36 (3.20)	0.78 (0.08)	0.27 (0.12)**	0.08 (0.02)***	0.31 (0.07)***	0.21 (0.11)**
Horn length	262	1718	52.19 (18.41)	7.20 (7.09)	0.79 (0.08)	0.26 (0.13)*	0.14 (0.03)***	0.26 (0.07)***	0.24 (0.12)**
Horn base circ.	261	1715	30.60 (6.91)	10.12 (15.87)	0.76 (0.08)	0.30 (0.11)***	0.06 (0.02)***	0.30 (0.07)***	0.19 (0.11)*
Body mass	262	1708	72.29 (16.84)	6.69 (2.01)	0.59 (0.05)	0.34 (0.12)**	0.14 (0.04)***	0.13 (0.05)***	0.22 (0.11)**
Female traits									
Horn volume	311	4028	111.6 (32.0)	4.57 (1.81)	0.96 (0.08)	0.28 (0.10)***	0.06 (0.02)***	0.17 (0.05)***	0.33 (0.09)***
Horn length	313	4089	22.54 (4.21)	7.99 (3.01)	1.04 (0.09)	0.22 (0.11)*	0.05 (0.01)***	0.15 (0.06)***	0.49 (0.11)***
Horn base circ.	313	4292	13.55 (1.08)	14.76 (5.49)	0.90 (0.07)	0.38 (0.08)***	0.08 (0.02)***	0.12 (0.04)***	0.16 (0.06)***
Body mass	318	4791	60.10 (9.37)	8.33 (2.33)	0.57 (0.04)	0.20 (0.07)***	0.16 (0.04)***	0.10 (0.04)***	0.22 (0.06)***
Sexes combined									
Horn volume	572	5739	—	—	0.88 (0.06)	0.19 (0.06)***	0.05 (0.01)***	0.18 (0.05)***	0.41 (0.06)***
Horn length	575	5807	—	—	0.91 (0.06)	0.18 (0.06)***	0.06 (0.02)***	0.17 (0.05)***	0.47 (0.07)***
Horn base circ.	574	6007	—	—	0.88 (0.05)	0.23 (0.06)***	0.07 (0.02)***	0.15 (0.04)***	0.31 (0.05)***
Body mass	580	6499	—	—	0.59 (0.03)	0.24 (0.06)***	0.13 (0.03)***	0.07 (0.03)***	0.28 (0.05)***

Standard errors generated by ASReml are presented in parentheses. Number of individuals and observations included in each analysis as well as trait means (s.d. in parentheses) prior and following data transformation (see Materials and methods section) are also presented. Estimates are based on the entire Ram Mountain data set; equivalent estimates for the smaller QTL mapping data set are presented in Supplementary Appendix S2. Significance of ratios was assessed using likelihood ratio tests (*$P<0.05$, **$P<0.01$, ***$P<0.001$).

Table 2 Additive genetic (co)variances and correlations for sex-specific fitness-related traits in adult bighorn sheep

	MHV	*MHL*	*MHB*	*MBM*	*FHV*	*FHL*	*FHB*	*FBM*
MHV	0.21 (0.09)**	0.89 (0.07)*†	0.93 (0.04)**†	0.73 (0.14)*†	0.37 (0.28)††	0.88 (0.37)**	−0.10 (0.25)††	0.24 (0.28)††
MHL	0.18 (0.09)*	0.20 (0.10)*	0.72 (0.15)*†	0.48 (0.20)†	0.40 (0.30)†	1.00 (0.35)**	−0.28 (0.26)††	0.43 (0.31)
MHB	0.20 (0.09)**	0.15 (0.09)*	0.23 (0.09)***	0.86 (0.11)**	0.42 (0.26)††	0.78 (0.34)*	0.03 (0.24)†††	0.22 (0.27)††
MBM	0.16 (0.07)*	0.11 (0.07)	0.18 (0.07)**	0.20 (0.08)**	0.44 (0.28)†	0.82 (0.35)*	−0.07 (0.25)††	0.76 (0.24)**
FHV	0.09 (0.07)	0.09 (0.07)	0.10 (0.07)	0.10 (0.06)	0.27 (0.10)***	0.75 (0.12)†	0.95 (0.07)***	0.71 (0.17)**†
FHL	0.17 (0.07)**	0.21 (0.07)**	0.16 (0.07)*	0.15 (0.06)*	0.17 (0.10)	0.22 (0.12)*	0.37 (0.21)†	0.60 (0.27)
FHB	−0.03 (0.07)	−0.07 (0.07)	0.01 (0.07)	−0.02 (0.07)	0.23 (0.08)***	0.10 (0.08)	0.34 (0.08)***	0.52 (0.16)**†††
FBM	0.04 (0.04)	0.06 (0.04)	0.03 (0.04)	0.11 (0.04)**	0.12 (0.05)**	0.08 (0.05)	0.10 (0.04)**	0.11 (0.04)***

Abbreviations: FBM, female body mass; FHB, female horn base circumference; FHL, female horn length; FHV, female horn volume; MBM, male body mass; MHB, male horn base circumference; MHL, male horn length; MHV, male horn volume.
Variance components obtained from univariate models are on the diagonal while covariance components are below the diagonal and correlations are above the diagonal (shaded area). Significance was assessed using likelihood ratio tests.*Identifies (co)variances and correlations significantly different from zero (*$P<0.05$, **$P<0.01$, ***$P<0.001$) while † identifies correlations significantly smaller than one ($^{\dagger}P<0.05$, $^{\dagger\dagger}P<0.01$, $^{\dagger\dagger\dagger}P<0.001$). Standard errors generated by ASREML are presented in parentheses. Estimates are based on the entire Ram Mountain data set; equivalent estimates for the smaller QTL mapping data set are presented in Supplementary Appendix S3.

Table 3 Additive genetic (co)variances and correlations for fitness-related traits in adult bighorn sheep

	Horn volume	*Horn length*	*Horn base circ.*	*Body mass*
Horn volume	0.17 (0.05)***	0.80 (0.08)**†††	0.94 (0.04)***†	0.74 (0.11)***†††
Horn length	0.13 (0.05)**	0.16 (0.06)***	0.51 (0.16)*†††	0.69 (0.14)**††
Horn base circ.	0.16 (0.05)***	0.09 (0.05)*	0.20 (0.05)***	0.57 (0.12)**†††
Body mass	0.11 (0.04)***	0.10 (0.04)**	0.10 (0.04)**	0.14 (0.04)***

Variance components are on the diagonal while covariance components are below the diagonal and correlations are above the diagonal (shaded area). Significance was assessed using likelihood ratio tests. *Identifies (co)variances and correlations significantly different from zero (*$P<0.05$, **$P<0.01$, ***$P<0.001$) while † identifies correlations significantly smaller than one ($^{\dagger}P<0.05$, $^{\dagger\dagger}P<0.01$, $^{\dagger\dagger\dagger}P<0.001$). Standard errors generated by ASREML are presented in parentheses. Estimates are based on the entire Ram Mountain data set; equivalent estimates for the smaller QTL mapping data set are presented in Supplementary Appendix S4.

DISCUSSION

We studied the genetic architecture of fitness-related traits in free-living bighorn sheep from Ram Mountain, Alberta, Canada. In addition to estimating sex-specific and cross-sex quantitative genetic parameters for horn volume, length, base circumference and body mass, we tested for the presence of QTLs influencing these traits, colocalization of QTLs between bighorn sheep and domestic sheep, and sex×QTL interactions.

Table 4 Genomic position of putative QTL for fitness-related traits in the Ram Mountain bighorn sheep population and their estimated parameters (V_{QTL}, phenotypic variance explained by the QTL after having accounted for fixed effects; q^2, proportion of phenotypic variance explained by the QTL after having accounted for fixed effects; h^2, residual heritability after having fitted the QTL effect)

Trait	*LOD*	*Chr.*	*Pos. (cM)*[a]	*Closest marker*	*1-LOD drop (cM)*	*1.5-LOD drop (cM)*	V_{QTL}	q^2	h^2	*QTL×sex (P-value)*	*Domestic sheep QTL*
Male trait											
Horn volume	1.66	10	0	OarSEJ10, 11	0–6	0–12	0.36 (0.11)	0.39 (0.10)	0.00 (0.00)	0.03	(1)
Horn length	1.91*	1	361	BMS2263	346–361	248–361	0.50 (0.09)	0.60 (0.08)	0.00 (0.00)	0.35	—
	2.82*	23	26	AGLA269	16–38	6–40	0.65 (0.12)	0.73 (0.06)	0.00 (0.00)	0.22	—
Horn base circ.	1.45	10	0	OarSEJ10, 11	0–6	—	0.32 (0.12)	0.37 (0.12)	0.06 (0.16)	0.02	(1)
Body mass	1.35	23	37	RT9	16–80	—	0.25 (0.09)	0.45 (0.13)	0.00 (0.00)	0.03	(2–4)
Female trait											
Body mass	1.32	2	190	BM81124	166–296	—	0.11 (0.04)	0.22 (0.07)	0.00 (0.00)	0.81	(5–7)
	1.44	24	44	BP28	0–54	—	0.12 (0.04)	0.24 (0.07)	0.00 (0.00)	0.16	(8–9)
	2.15*	26	40	JMP58	30–44	2–44	0.13 (0.04)	0.26 (0.07)	0.00 (0.00)	0.06	(10)
Sexes combined											
Horn volume	1.95*	18	9	ILSTS52	0–48	0–52	0.30 (0.09)	0.33 (0.08)	0.00 (0.00)	0.27	—
Horn base circ.	2.35*	18	1	SRCRSP5	0–30	0–46	0.30 (0.08)	0.33 (0.07)	0.00 (0.00)	0.37	—
Body mass	1.47	2	190	BM81124	156–242	—	0.12 (0.04)	0.21 (0.06)	0.00 (0.00)	0.81	(5–7)

Abbreviation: QTL, quantitative trait locus.
[a]Map distances are based on Haldane's mapping function (see Supplementary Appendix S1) and therefore not directly comparable to distances presented in Poissant *et al.* (2010b) where Kosambi's mapping function was used. (1) Horn morphology, Johnston *et al.* (2010), (2) body weight, Margawati *et al.* (2006), (3) carcass weight, no 95% CI, Margawati *et al.* (2009), (4) growth rate, Raadsma *et al.* (2009), (5) muscle development, Laville *et al.* (2004), (6) carcass weight, no 95% CI, Margawati *et al.* (2009), (7) weight, suggestive, Walling *et al.* (2004), (8) muscle mass, Campbell *et al.* (2003), (9) body weight and growth rate, Raadsma *et al.* (2009) and (10) body weight and growth rate, Raadsma *et al.* (2009). *Denotes suggestive QTLs (LOD >1.88). Regions with nominal *P*-values >0.01 (LOD >1.175) that did not exceed genome-wide significance thresholds are also presented when co-located with putatively homologous domestic sheep QTL. All regions with LOD >1.175 are presented in Supplementary Appendix S5.

Horn size

Significant additive genetic variance was detected for all sex-specific horn dimension traits, indicating that QTL detection was possible. The cross-sex genetic correlation for horn base circumference was one of the lowest ever estimated for a pair of homologous male and female traits (Poissant *et al.*, 2010a) while the cross-sex genetic correlation for horn length was large and not significantly different from one. This suggests that the genetic decoupling of male and female horn volume reported in Poissant *et al.* (2008) and this study may in most part be attributable to the evolution of sex-specific genetic variance for horn base circumference. The reason for this is unclear but horn base circumference may have experienced greater sexually antagonistic selection than horn length. While most studies of sexual selection in sheep have focused on male horn length (for example, Coltman *et al.*, 2002; Preston *et al.*, 2003), there is no obvious reason to expect sexual selection to act on horn length more than horn base circumference. Horn base circumference is likely more important than horn length for fighting because males clash their horns near the base. The observed pattern would also be consistent with the presence of sexually antagonistic selection on horn volume or horn mass rather than base circumference or length since a change in horn base circumference will have a greater influence on horn volume than a proportional change in horn length.

We identified six putative horn dimension QTLs including four that were suggestive at the genome-wide level (LOD >1.88). The other two did not surpass genome-wide significance thresholds but were significantly colocalized with the only horn size QTL mapped in domestic sheep to date (LOD >1.175, Johnston *et al.*, 2010). The six putative QTLs likely only represented four loci because horn volume and base circumference QTLs were colocalized on chromosomes 10 and 18. The detection of overlapping QTLs for different horn dimension traits was to be expected given strong positive phenotypic correlations among these traits. The other two QTLs were for horn length and located on chromosomes 1 and 23. The chromosome 10 QTL overlapped with the *horns* locus, a locus controlling discrete horn phenotypes in domestic sheep (that is, presence versus absence of horns, Montgomery *et al.*, 1996). On the other hand, no putative QTL overlapped with loci known to influence discrete horn polymorphisms in other bovid genera (Georges *et al.*, 1993; Vaiman *et al.*, 1996; Asai *et al.*, 2004). This suggests that different genes may be responsible for quantitative and discrete variation in horn morphology among bovids.

Body mass

The presence of additive genetic variance for both sex-specific traits indicated that QTL detection was possible in both sexes. The cross-sex genetic correlation for body mass was large and not significantly different from one, indicating that the detection of QTLs influencing variation similarly in both sexes was likely.

The genome scan for body mass QTLs yielded a single suggestive QTL on chromosome 26. This locus was colocalized with domestic sheep body weight and growth rate QTLs identified by Raadsma *et al.* (2009). Three additional regions (out of 5) with LOD scores smaller than genome-wide significance thresholds appeared to be colocalized with domestic sheep weight-related QTLs. In domestic sheep, these regions contain QTLs for body weight and muscularity (chromosome 2, Laville *et al.*, 2004; Walling *et al.*, 2004; Margawati *et al.*, 2009), body weight and growth rate (chromosome 23, Margawati *et al.*, 2006, 2009; Raadsma *et al.*, 2009) and body weight, growth rate and muscle mass (chromosome 24, Campbell *et al.*, 2003; Raadsma *et al.*, 2009). Possible candidate genes in these regions (genes known to influence weight-related traits in sheep or other species) identified by Raadsma *et al.* (2009) include myostatin, beta-3-adrenergic receptor, melanocortin 4 receptor, erythropoietin, elastin and fibrosin genes. Myostatin (also known as growth differentiation factor 8, GDF8), located in the center of the region on chromosome 2, is perhaps the most promising of these genes because it has been linked to muscle development in domestic sheep (Clop *et al.*, 2006; Kijas *et al.*, 2007) and cattle

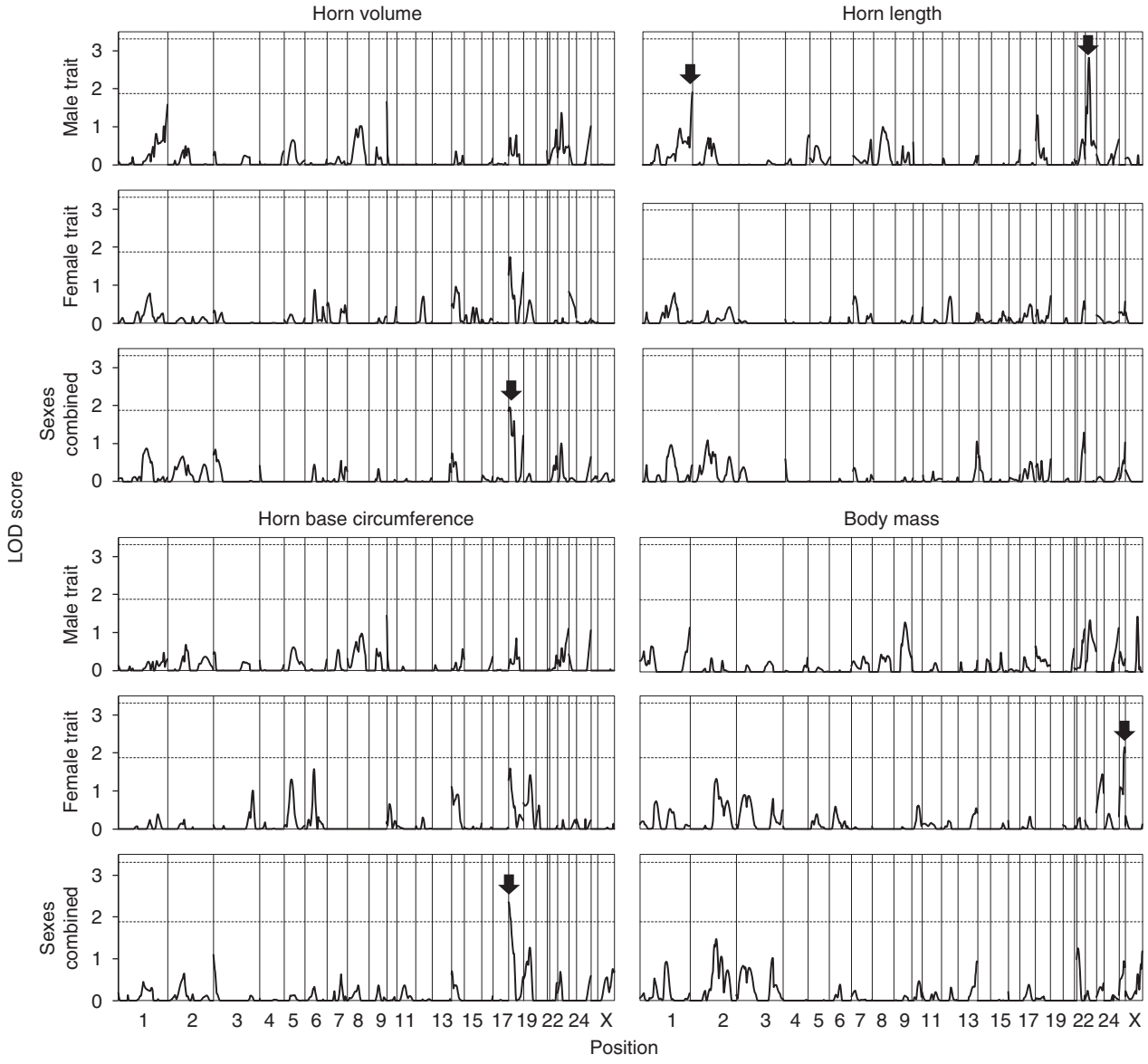

Figure 1 LOD scores along the 26 autosomes and the X chromosome for the presence of horn volume, length, base circumference and body mass QTL in the Ram Mountain bighorn sheep population. Dashed horizontal lines depict genome-wide thresholds used to identify suggestive (LOD > 1.88) and significant (LOD > 3.31) QTLs. Arrows highlight suggestive QTLs.

(Casas *et al*., 1999). Although anti-conservative, our test for the colocalization of body mass QTL nonetheless highlighted chromosomal areas deserving further investigation and suggested that the genetic architecture of body mass may be partially conserved across species.

Sex×QTL interactions

Most QTLs were only identified in one of the two sex-specific analyses. In addition, significant sex×QTL interactions were detected for the horn size QTLs located on chromosome 10. A significant interaction was also detected for the putative body mass QTL on chromosome 23 but this result remains speculative because of uncertainties regarding the presence of a QTL at that position. QTLs with sex-specific effects have been documented in a variety of organisms (for example, Nuzhdin *et al*., 1997; Farber and Medrano, 2007; Moghadam *et al*., 2007) including domestic sheep (Raadsma *et al*., 2009), but to our knowledge had never been documented in a free-living wildlife population. The presence of sex-specific QTL effects in bighorn sheep adds to the accumulating evidence suggesting that sexual selection alters the genetic architecture of quantitative traits by promoting the accumulation of sex-specific genetic variance (Moller 1993; Wilkinson 1993; Bonduriansky and Rowe, 2005; Wright *et al*., 2008; Robinson *et al*., 2009).

QTL number and effect sizes

Our genome-wide analysis yielded no significant and a modest number of suggestive QTLs. Such results are similar to the ones obtained in the three other QTL mapping experiments performed using free-living wildlife populations to date. In Soay sheep, *Ovis aries*, analyses of over 10 traits yielded only one significant (jaw length) and 7 suggestive QTLs (Beraldi *et al*., 2007a, b, Johnston *et al*., 2010).

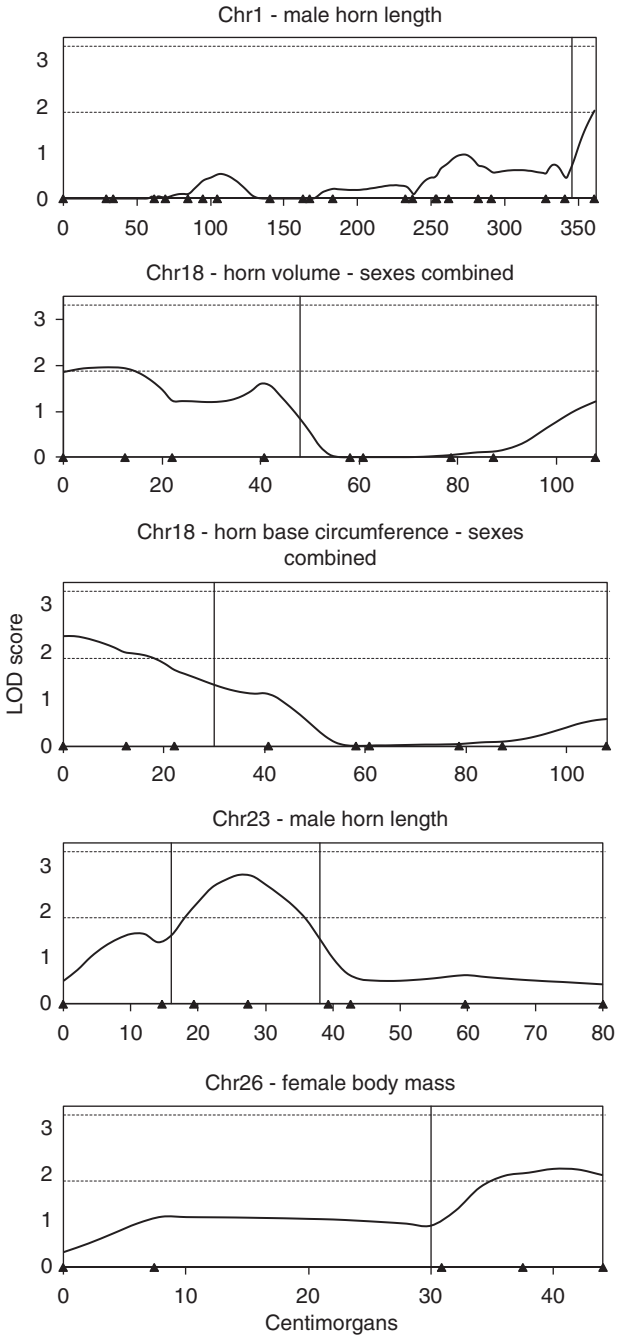

Figure 2 LOD scores along chromosomes for the five suggestive QTLs (LOD >1.88) in the Ram Mountain bighorn sheep population. Triangles on the *X* axis depict marker positions. Dashed horizontal lines depict genome-wide thresholds used to identify suggestive (LOD >1.88) and significant (LOD >3.31) QTLs. Vertical lines depict 1-LOD 95% confidence intervals.

In red deer, *Cervus elaphus*, a test for birth weight QTLs yielded a single suggestive QTL (Slate *et al*., 2002). Finally, in great reed warblers, *Acrocephalus arundinaceus*, analyses of wing length and tarsus length resulted in the identification of a single significant QTL (Tarka *et al*., 2010). This study as well as the ones just mentioned demonstrated that QTL mapping in free-living wildlife populations was feasible. However, it is becoming clear that larger sample sizes and marker densities will be needed to improve QTL detection.

All QTLs appeared to explain all or most of the additive genetic variation. Such results are typical of QTL studies in free-living wildlife populations (Slate *et al*., 2010) and likely a consequence of small sample sizes (Beavis, 1998) combined with the upward bias occurring when QTL effects are estimated in the population in which they were discovered (Goring *et al*., 2001). Further research based on larger sample sizes will be necessary to obtain more reliable estimates (Slate *et al*., 2010).

Future directions

Upcoming research will focus on refining genome-wide QTL searches and test if QTLs identified in this study are valid. This will be accomplished by increasing the number of animals analyzed as well as marker coverage using single-nucleotide polymorphisms identified using the ovine OvineSNP50 BeadChip (Miller *et al*., 2011) and/or novel approaches based on next-generation sequencing technologies such as restriction-site-associated DNA sequencing (Baird *et al*., 2008). Linkage disequilibrium methods will also be used to test the presence of QTL in additional non-pedigreed populations.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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