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Age-dependent sexual selection in bighorn rams

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Although mating systems and sexual selection have been intensively studied in ungulate model systems, very few studies have combined genetic paternity analysis with individual phenotypic data over several breeding seasons. We used microsatellite paternity analysis to determine the parentage of 83 bighorn sheep (*Ovis canadensis*) born between 1995 and 2000 at Ram Mountain, Alberta, Canada. We could assign the paternity of 64 lambs at a high level of statistical confidence (95%). Within each season, the most successful ram sired an average of 35.5% of the lambs with assigned paternity, and a single ram sired 26.1% of all lambs over the six mating seasons. Although a few large-horned, mature (age 8+ years) rams had very high reproductive success, younger rams sired *ca.* 50% of the lambs. Mixed-effects models indicated that mating success increases as a nonlinear function of age, with horn length increasingly positive in correlation with mating success in older rams. These results indicate that young or small rams possibly achieve mating success through alternative mating tactics that are less dependent on body and weapon size, such as coursing and blocking. Sexual selection is therefore likely to have age-dependent effects on traits such as agility, body and horn size.

Keywords: *Ovis*; paternity; horn; dominance rank; alternative mating tactic

1. INTRODUCTION

In most mammalian species, male reproductive success is constrained only by the ability to sire offspring (Trivers 1972). Thus, male mammals usually compete intensely for mates, creating the potential for a high variance in male mating success (Emlen & Oring 1977), and in turn a high opportunity for sexual selection (Wade & Arnold 1980; Arnold & Wade 1984). Sexual selection, however, can only occur if variation in mating success is correlated with phenotypic variation. Many conspicuous secondary sexual traits that are expressed in male ungulates, such as horns, antlers and tusks, are thought to have arisen as a consequence of their advantage, either as weapons or as indicators of strength, fighting ability or quality via sexual selection (Darwin 1871; Geist 1966). There is wide acceptance of the idea that sexual dimorphism in body size and weaponry evolved as adaptations for mate competition in species in which males contest access to females (Andersson 1994). Many studies have considered the importance of male body size to paternity in size-dimorphic species (Stockley *et al.* 1996; Coltman *et al.* 1999*b*; Fisher & Lara 1999; Kruuk *et al.* 1999; Topping & Millar 1999). But, surprisingly few studies have actually demonstrated a systematic relationship between variation in a secondary sexual trait and genetic paternity in wild ungulates after correcting for age-related variation (except Preston *et al.* 2001). Systematic relationships between mating success and trait variation are evidence of continued sexual selection on secondary trait variation.

Bighorn sheep (*Ovis canadensis*) exhibit a sequentially polygynous and promiscuous mating system, in which rams compete for access to individual oestrus ewes (Geist 1971). A high variance in male mating success is indicated both by well-developed sexual dimorphism (rams are 65% heavier than ewes by age 6 yr; Festa-Bianchet *et al.* 1996) and by more extensive sexual dimorphism in horn development. Bighorn rams possess massive curled horns (constituting up to 15% of their total body weight) that are used in combat, both to establish dominance hierarchies and in direct conflict over access to mates (Geist 1971). Although dimorphism indicates a possible direct mating advantage for large body and/or horn size, the situation is complicated by the expression of alternative mating strategies in bighorn sheep.

Hogg (1984, 1987) and Hogg & Forbes (1997) showed that bighorn rams use three distinct mating tactics. 'Tending' rams defend a single oestrus ewe from other rams in an apparently cooperative courtship that is successfully practised only by rams of high dominance rank, which are the largest mature individuals with well-developed horns. 'Coursing' rams attempt to gain transient access to oestrous ewes by attempting to bypass the tending ram. 'Blocking' rams attempt to forcefully sequester ewes away from the tending area until they become receptive. Coursing and blocking tactics are the major mating tactics of subordinate, younger rams (Hogg 1987). Using paternity analysis, Hogg & Forbes (1997) found that approximately equal numbers of lambs were fathered by coursing versus tending rams in two bighorn sheep populations. The distribution of paternities, however, was strongly skewed in favour of high-ranking, older rams because the mating success of tending rams was concentrated in the top few ranks, whereas paternities obtained through alternative tactics were distributed largely independent of rank among

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many younger rams. The relationship between body size, horn size and mating success is therefore likely to be complicated in bighorn sheep if alternative tactics are common to all populations. Large body size and massive horns are traits that are likely to be important for attaining high dominance rank and successfully defending tended ewes, whereas agility, endurance and speed are likely to be important for successful coursing (Hogg & Forbes 1997).

We used microsatellite paternity analysis to estimate male mating success in a natural population of bighorn sheep at Ram Mountain, Canada. Unlike the Sheep River (SR) and National Bison Range (NBR) populations previously studied by Hogg (1984, 1987, 1988) and Hogg & Forbes (1997), Ram Mountain is inaccessible during the rut; therefore, observation of rutting behaviour is not possible and we must rely entirely on genetic paternity analysis for estimating male mating success. The advantage of the Ram Mountain study, however, is that detailed phenotypic data are available from permanently marked individuals that are captured and weighed each year. It is, therefore, possible to analyse phenotypic sources of variation in male mating success in a quantitative statistical framework. The objectives of this study were to: (i) estimate the variance and characterize the distribution of annual mating success among rams, and (ii) estimate the extent to which variation in annual mating success can be attributed to phenotypic variation. More specifically, extrapolating patterns observed elsewhere by Hogg, we proposed a skewed distribution of male mating success and a nonlinear, increasing relationship between phenotypic traits related to dominance rank (age, weight and horn size) and mating success.

2. METHODS

(a) *Study site, data collection, and sampling*

The study population inhabits Ram Mountain, Alberta, Canada (52° N, 115° W, elevation 1080–2170 m), a mountainous outcrop *ca.* 30 km east of the main range of the Rocky Mountains. Ram Mountain includes *ca.* 38 km² of alpine and subalpine habitat, surrounded on three sides by coniferous forest and on the fourth side by the North Saskatchewan River.

The Ram Mountain population has been monitored intensively since 1971, during which time its numbers ranged from 30 to 104 adult ewes. Each year, from late May to early October, sheep were captured in a corral trap baited with salt, and marked with coloured plastic ear tags or canvas collars for individual identification. A regular census, by foot, of the study area was carried out during the summer months. At each capture, sheep were weighed to the nearest 250 g with a Detecto (Webb City, MO, USA) spring scale. Horn length along the outside curvature was measured using tape. Adult rams were captured once or twice in most summers, mostly from early June to mid-July.

Bighorn males on Ram Mountain can legally be harvested by resident hunters from late August to the end of October. Until 1995, hunting was limited to rams with horns describing at least four-fifths of a curl, a horn size that is attained at four to eight years, and one to three rams were harvested in most years (Jorgenson *et al.* 1993). During our study, however, two factors greatly reduced ram-hunting mortality: density dependence in horn growth meant that most rams never achieved the minimum

horn size required for hunting, and a change in regulations in 1996 limited the harvest to 'full-curl' rams. Consequently, only three rams were shot between 1995 and 1999.

Here, we use data from rams captured from 1994 to 2000. Individual weight and horn-length measurements were adjusted to 5 June using individual linear growth rates for rams caught more than once during the period 25 May to 1 August. For rams caught only once during this period, we adjusted the measurement using age-specific linear regressions on capture date (Festa-Bianchet *et al.* 1996). For horn length, the longer of the left or right horn measurements was taken because rams may have varying amounts of horn removed by wear or 'brooming'. For individuals not captured in year *t*, we estimated weight and horn length as the mean of the date-corrected measurements recorded in the years $t-1$ and $t+1$. Nine observations from seven individuals were interpolated in this way.

(b) *DNA sampling and microsatellite typing*

Tissue sampling for DNA analyses started in 1997, when hair samples were removed from all captured sheep by plucking 50–100 hairs, including roots, from the back or flank. Hairs were kept either in paper envelopes or plastic bags containing *ca.* 5 g of silica at room temperature. From 1998 to 2000, 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% dimethyl-sulphoxide–saturated NaCl at −20 °C.

DNA was extracted, either from 20–30 hairs including follicles, or *ca.* 5 mg of ear tissue, using the QIAamp tissue extraction kit (Qiagen Inc., Mississauga, Ontario). Two microlitres of extract were used for PCR amplification with 4 pmol of each primer, 120 μM dNTPs, 2 mM MgCl, 0.3 units Taq polymerase (isolated as per Engelke *et al.* (1990)), and 1 × PCR buffer (10 mM Tris buffer, pH 8.8, 0.1% Triton-X 100, 50 mM KCl and 0.16 mg ml⁻¹ BSA). Cycling was carried out in a 9600 thermal cycler (Perkin–Elmer, Princeton, NJ, USA) under conditions of 1 min at 94 °C, 3 cycles of 30 s at 94 °C, 20 s at 54 °C, and 5 s at 72 °C, followed by 33 cycles of 15 s at 94 °C, 20 s at 54 °C, and 1 s at 72 °C, and a final extension of 30 min at 72 °C. PCR products were pooled (0.25 μl per FAM or TET-labelled product, 0.50 μl per HEX-labelled product), added to 1.8 μl of buffer containing formamide and TAMRA-labelled size standard made up of amplified products of 80, 130, 180, 230, 280, 330 and 380 bp lengths. All 15 loci could be resolved in two lanes (see Appendix A for details of primer label and lane information). PCR products were resolved on a model 377 DNA sequencer and analysed using GENESCAN and GENOTYPER software (Applied Biosystems, Foster City, CA, USA).

(c) *Statistical analyses*

Exact tests for allelic and genotypic disequilibria by the Markov chain method were implemented in GENEPOP v. 3.2a (see http://wbiomed.curtin.edu.au/genepop/) (Raymond & Rousset 1995). Disequilibrium tests were based on the genotypic data from all yearlings and older sheep that were alive when DNA sampling was initiated (i.e. 1997) to avoid including known mother–offspring pairs. Table-wide significance levels for both allelic and genotypic disequilibria were adjusted by the Bonferroni method.

Paternity was assigned using the likelihood-based approach described in Marshall *et al.* (1998). Simulations were carried out in CERVUS 2.0b (see http://helios.bto.ed.ac.uk/evolgen/cervus) to estimate the critical difference in log-likelihood score (the δ-statistic) for assignment of paternity at 95% statistical confidence. Because input parameters varied between years, we
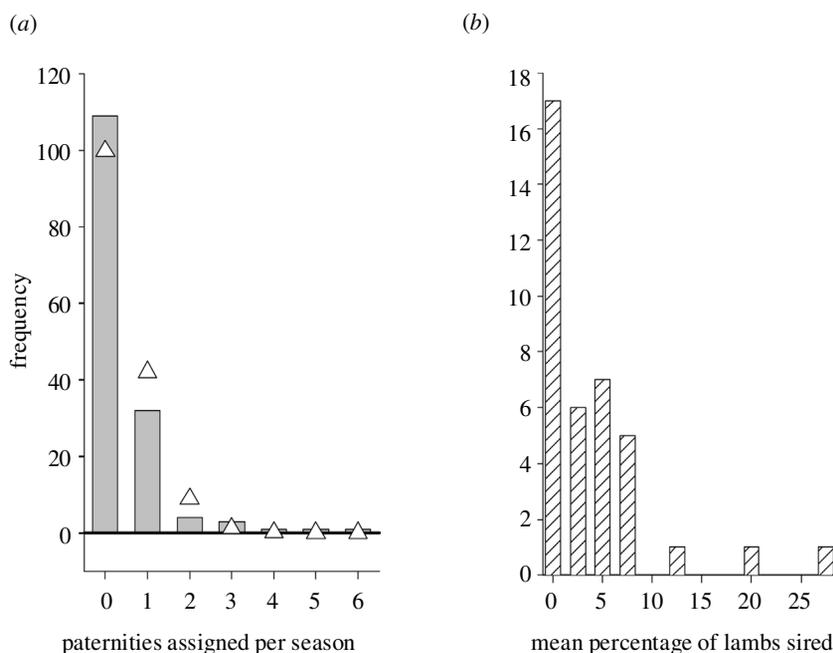
Figure 1. The distribution of the number of paternities assigned to bighorn rams that rutted over all six seasons ($n = 151$ ram years). (*a*) Triangles indicate expected numbers assuming that paternity was randomly distributed among rams. (*b*) The distribution of mean relative mating success (mean percentage of assigned paternities per season) among all 38 sampled rams. Mean = 0.43; s.d. = 0.91; $p < 0.001$; $\chi^2_3 = 21.5$.

Table 1. Within-season variation in mating success and Spearman's rank correlations between mating success and age, horn length and weight of bighorn rams (*$p < 0.05$, **$p < 0.01$, ***$p < 0.005$).

year	number of rams	maximum assigned paternity (%)	I (var/mean^2)	correlation with		
				age	horn length	weight
1994	24	3 (27.3)	2.88	0.656***	0.657***	0.513**
1995	27	2 (22.2)	2.78	0.516**	0.408*	0.274
1996	28	3 (27.3)	3.60	0.127	0.171	0.151
1997	34	4 (44.4)	8.32	0.395*	0.416*	0.294
1998	26	6 (46.2)	7.09	0.500*	0.341	0.448*
1999	12	5 (45.5)	2.45	0.597*	0.651*	0.576
mean	25.2	3.8 (35.5)	4.52	0.465	0.441	0.376

carried out a separate simulation to estimate δ for each year. Simulation input parameters common to all years included the observed marker allele frequencies (estimated from all typed samples), a 1% rate of typing error, 97% of loci typed (observed rate of missing data) and 10 000 cycles. The number of candidate males, and the proportion of candidates sampled, varied between years. All rams aged two years or older, and not known to have died before November, were considered to be candidates in a given year. Even though all of the known candidate males were sampled in some years, for the simulation we assumed that there was at least one non-sampled candidate to allow for the possibility that one or more immigrant rams could have rutted on Ram Mountain (Hogg 2000).

We used mixed-effect models implemented in the linear mixed-effects module of Splus (Insightful, Seattle, WA, USA) to analyse the extent to which phenotypic characteristics determine the variance in annual male mating success. To account for differences between years in the number of offspring tested, we standardized the number of paternities assigned to each individual in each year by subtracting the mean number of

paternities assigned to all individuals in that year. This measure was then log transformed ($\log_e [x + 2]$) to reduce positive skew. Individual identity and year were fitted as random effects, while age, relative weight and relative horn length were fitted as fixed effects. Because weight and horn length are correlated with age, we calculated relative measures of weight and horn length by subtracting the mean age-specific measurements for ages of two to eight years and for rams aged nine years or greater from the observed data. Weight and horn length approach an asymptote before age 10 years (Festa-Bianchet *et al.* 1996; Jorgenson *et al.* 1998). We modelled the within-individual variance function as a power of age (i.e. as age^x) to account for age-related heteroscedasticity. Goodness of fit was evaluated using the Akaike information criterion (AIC), which is calculated as:

$$AIC = -2\log \text{ likelihood} + 2n_{\text{par}}, \qquad (2.1)$$

where n_{par} is the number of parameters estimated (Pinheiro & Bates 2000). A smaller AIC value corresponds to a better fit of the model to the data.
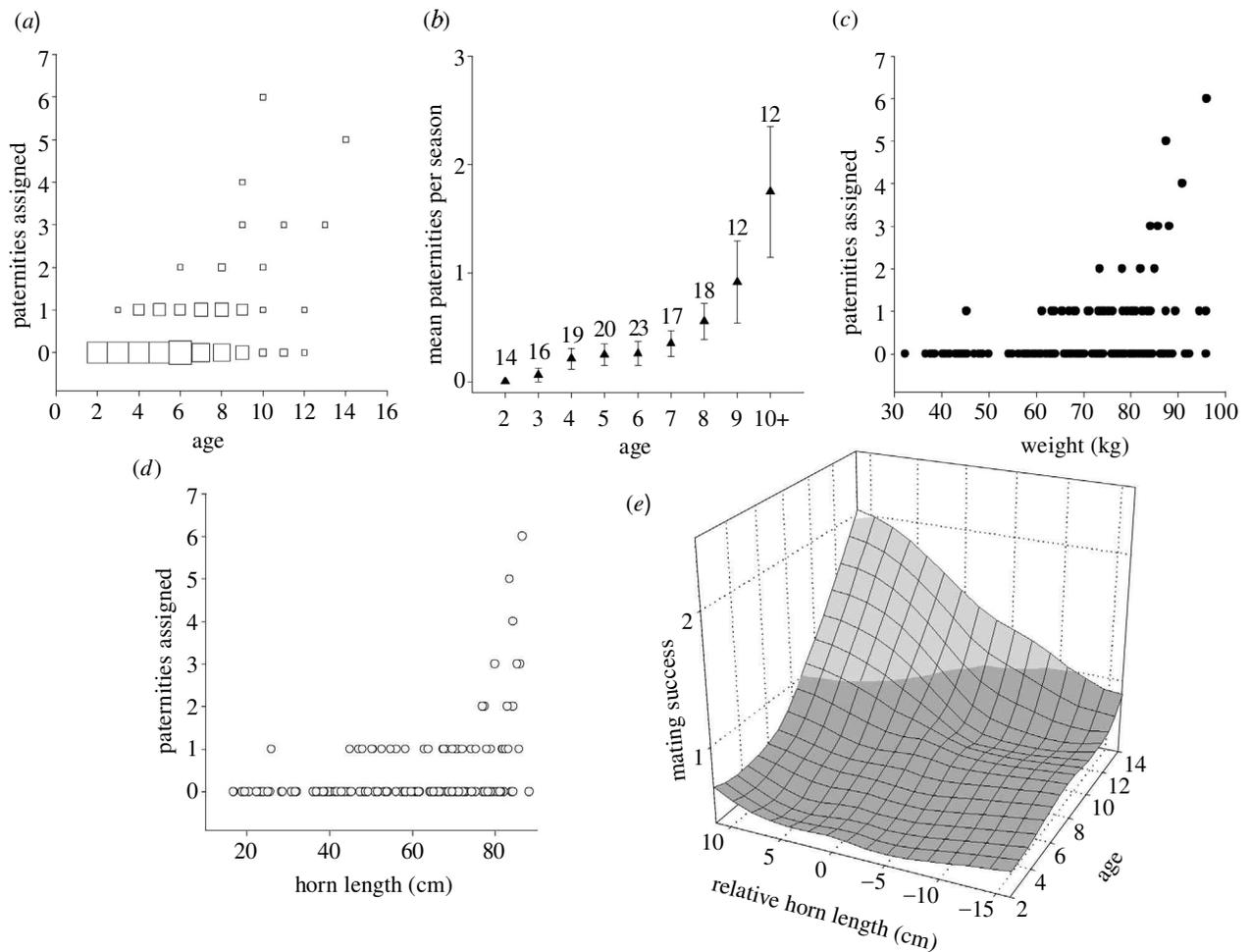
Figure 2. The number of paternities assigned in relation to (*a,b*) ram age, (*c*) weight and (*d*) horn length. (*a*) The area of the open square is directly proportional to the number of individuals represented by each point; (*b*) as means with bars indicating standard error and numbers giving sample size. (*e*) Surface plot of fitted mating success predicted by a linear mixed-effects model as a function of age and horn length. The surface was interpolated from the observed fits using a loess smoother function.

3. RESULTS

Hair, or tissue samples, were collected from 167 individuals. Between three and nine alleles were found at the 15 microsatellite loci typed, and the observed heterozygosity ranged from 0.49 to 0.87 (Appendix A). There was no significant departure from the Hardy–Weinberg equilibrium at any single locus or over all loci combined ($p > 0.05$). There was no evidence for significant linkage disequilibrium between any pair of loci following correction for multiple comparisons (105 tests, critical $p = 0.0005$; minimum observed $p = 0.008$). The probability of identity over all 15 loci was 4.4×10^{-13}, and the probability of exclusion, assuming one parent was known, (Marshall *et al.* 1998) was 0.999 85.

DNA samples were available from 83 sheep born between 1995 and 2000 (Appendix B). The mother's identity was known for 79 of these individuals from behavioural observations. Four lambs of uncertain maternity born in 1996 were caught as yearlings in 1997, when they no longer associated with their mothers. We unambiguously identified their mothers using simple genetic exclusion. DNA samples were available for all mothers and for 38 out of the 49 (77.6%) candidate rams. Most of the non-sampled rams were present only during the first year or two of the study, and the proportion of sampled rams increased from 1994

to 1999 (Appendix B). The Cervus paternity simulations predicted success rates ranging from 70 to 100% over the course of the study (mean = 87%), with higher success rates predicted in years when relatively more rams were sampled. The actual success rate was slightly lower (77%, Appendix B) than the predicted rate but the difference was not significant ($\chi^2 = 1.99$, $p = 0.16$).

The maximum number of paternities assigned to a single ram in a year ranged from two (1995) to six (1998). In each year, the standard deviation in the number of paternities assigned per ram exceeded the mean, and as a consequence the opportunity for selection, defined as the square of the coefficient of variation in reproductive success, *I*, (Crow 1958; Arnold & Wade 1984) was always greater than one. The distribution of yearly mating success combined over all six years deviated from a Poisson distribution of the same mean ($p < 0.001$, figure 1*a*), indicating that mating success was not randomly distributed among rams. Seventeen out of the 38 rams tested were not assigned a paternity over the study period, whereas the three most successful rams were assigned the paternity of more than 50% of all lambs with known paternity (figure 1*b*), and one ram sired over 25% of the assigned lambs per season on average (mean = 26.1%, figure 1*b*).

Two rams dominated mating success over the six years

Table 2. ANOVA indicating coefficients and *t*-statistics for terms in the best linear mixed-effects model. (Terms with $p < 0.05$ explained significant variation in mating success. $R^2 = 0.374$, AIC = 3.47.)

term	coefficient	s.e.	d.f.	t	P
intercept	0.584	0.068	1108	8.56	<0.001
age	−0.046	0.029	1108	−1.57	0.12
age^2	0.008	0.003	1108	2.90	<0.005
horn length	0.022	0.016	1108	1.34	0.18
age $\times$ horn length	−0.014	0.006	1108	−2.34	0.023
age^2 $\times$ horn length	0.0016	0.0005	1108	2.93	<0.005

of the study. Ram 28Q sired a total of 17 lambs, and was the most successful ram in 1994 (three paternities), 1995 (two paternities), 1996 (three paternities) and in 1999 (five paternities). 28Q was relatively large (mean deviation from age-specific body weight = +2.2 kg or 2.6%) and long horned (mean deviation from age-specific horn length = +4.4 cm or 5.6%). 35T became the most successful ram in 1997 (four paternities) and sired six lambs during the 1998 rut before being illegally shot at age 11 yr the following year. 35T was also relatively large (mean deviation from age-specific body weight = +9.10 kg or 11%) and long horned (mean deviation from age-specific horn length = +5.0 cm or 6.3%).

Mating success was positively correlated with age, weight and horn size within years (table 1). Within-year correlations were strongest for age (5 out of 6 seasons $p < 0.05$), followed by horn size (4 out of 6 seasons $p < 0.05$) and then weight (2 out of 6 seasons $p < 0.05$). When the data were pooled across years, a very similar pattern was evident (figure 2) with mating success generally increasing with age, horn length and weight in a nonlinear fashion. Although rams as young as three years old, and with small to moderate weight and horn size, occasionally sired lambs, rams that sired several offspring within a breeding season were usually among the oldest and heaviest, and had a horn length greater than 76 cm (figure 2).

Linear mixed-effects modelling revealed that variation in mating success was best explained by a second-order polynomial function of age and relative horn length, and their interaction terms. This model had the lowest AIC (3.47), indicating the best fit to the data weighted by the number of parameters estimated, and explained virtually the same amount of variance as a model including age and both relative horn length and weight ($R^2 = 0.375$, AIC = 8.43). Significant interaction terms between age, age^2 and horn length indicate that horn size becomes relatively more important for mating success with increasing age (table 2, figure 2).

4. DISCUSSION

The variance in the distribution of paternities among bighorn rams indicates a moderate degree of reproductive skew in this population. The annual opportunity for selection (I, table 1) ranged from 2.45 (1999) to 8.32 (1997), which brackets the range of values obtained using paternity analysis in other polygynous ungulates, such as Soay sheep, in which I ranged from 2.91 to 6.92 over six seasons (Coltman *et al.* 1999*b*), and red deer (7.21 in one season; Pemberton *et al.* 1992). The distribution of mating success among rams when plotted according to age (figure 2) is also very similar

to the distribution of mating success according to the dominance rank observed by Hogg & Forbes (1997) in two other bighorn sheep populations. Age and rank are strongly correlated in bighorn rams (Hass & Jenni 1991).

The similar distributions of mating success observed here and in the SR and NBR populations by Hogg & Forbes (1997) indicate that successful alternative mating tactics may be characteristic of the species over a fairly broad range of ecological and social environments. At NBR and SR, individuals of low dominance rank frequently sired offspring using the coursing tactic, but they rarely sired more than one offspring per season, and their success was independent of their dominance rank. Similarly, in this study, mating success was not solely restricted to the oldest and largest rams. Hogg & Forbes (1997) found that the minimum age of a successful ram was two years, and in this study the youngest successful ram was three years at the time of conception.

If tending and coursing tactics were used by rams at Ram Mountain, with successful tending restricted to the oldest and largest rams, we would expect to observe the complex age-dependent relationship between mating success and body and horn size traits seen here. Horn size is, relatively, the most important trait for mating success among the oldest rams (figure 2), which are also most likely to exhibit the tending mating tactic. Large horns would therefore appear to be a prerequisite to achieve multiple paternity within a season (figure 2). However, large-horned and socially dominant rams do not monopolize mating success. Similarly, in Soay sheep, lifetime (Coltman *et al.* 1999*b*) and seasonal mating success are correlated with horn length and body size (Preston *et al.* 2001), and younger subordinate rams rarely hold oestrus ewes, yet subordinates may mate successfully following chases and opportunistic copulations (Coltman *et al.* 1999*a*; Pemberton *et al.* 1999). Hogg (1984) suggested that the evolution of the coursing tactic in bighorn sheep depended on the prior existence of concussive rather than piercing weaponry, and rapid copulation. As a consequence, individuals of low dominance rank can afford to attempt to reproduce via the coursing tactic because brief combat is less risky and insemination more rapid than in other ungulate taxa, such as deer, that can gore or kill opponents with their antlers (Geist 1986). Using DNA fingerprinting, Pemberton *et al.* (1992) showed that observed harem-holding behaviour accurately predicted paternity in red deer, suggesting that alternative mating tactics may be less successful in such taxa.

Alternative mating tactics in bighorn sheep have several important implications for evolution, population genetics,

conservation and management. First, although there is considerable reproductive skew, mating success is not restricted to a few top ranking rams each year. The effects of the mating system on effective population size are thus less severe than they would be if mating was monopolized by a few older, dominant rams (Nunney 1993). Second, sexual selection is likely to affect different traits in an age-dependent fashion. Large body size and massive horns are important for attaining high dominance rank and successfully defending tended ewes for fully mature rams, whereas agility, endurance and speed may be more important for successful coursing earlier in life (Hogg & Forbes 1997). Weight and horn length are sexually selected traits that show surprisingly high levels of additive genetic variation in this population (Reale *et al.* 1999; D. W. Coltman, J. T. Jorgenson and M. Festa-Bianchet, unpublished data). It is possible that genetic variation may be maintained if traits associated with successful coursing are negatively genetically correlated, or traded off with the expression of sexually selected traits that are associated with dominance and successful tending. A test of this idea, however, requires more extensive pedigree data than is available at present.

Finally, these results are highly relevant to wild sheep management. Many bighorn sheep populations across North America are managed with the explicit purpose of producing large-horned trophy rams for hunters. Current hunting regulations based on a minimum horn-curl development favour the harvest of rams with rapidly growing horns, which can be shot as young as four years (Jorgenson *et al.* 1998). If such individuals are removed from the gene pool before they have reached sufficient age and experience to attain high dominance rank and mating success, then selective hunting could rapidly erode genetic variation for large, fast-growing horns, particularly because the reproductive success of young rams is independent of horn size. A limited harvest of 'full curl' rams should allow more high-quality rams to attain their reproductive potential than the 3 out of 4 or 4 out of 5 curl restrictions now used in many jurisdictions.

APPENDIX A

Microsatellite loci used in paternity analysis of bighorn sheep at Ram Mountain. (Ch, chromosomal assignment in domestic sheep; k, number of alleles observed; H_o, observed heterozygosity; H_e, expected heterozygosity.)

locus (label)	Ch	k	allele size range (bp)	H_o	H_e	reference
OarAE16 (Hex)[a]	13	9	82–104	0.869	0.853	Penty *et al.* (1993)
BM1225 (Tet)[a]	16	5	245–259	0.638	0.606	Bishop *et al.* (1994)
BM1818 (Hex)[b]	20	8	257–273	0.713	0.768	Bishop *et al.* (1994)
BM4505 (Fam)[b]	22	5	265–277	0.563	0.578	Bishop *et al.* (1994)
BM4513 (Tet)[b]	9	4	139–153	0.594	0.617	Bishop *et al.* (1994)
BM848 (Fam)[a]	15	7	219–237	0.787	0.768	Bishop *et al.* (1994)
BMC1222 (Tet)[b]	13	4	286–292	0.494	0.491	de Gortari *et al.* (1997)
OarCP26 (Hex)[b]	4	7	131–163	0.811	0.801	Ede *et al.* (1995)
OarFCB266 (Tet)[b]	25	5	88–100	0.669	0.660	Buchanan & Crawford (1993)
MAF209 (Hex)[a]	17	4	111–121	0.745	0.713	Buchanan & Crawford (1992)
MAF36 (Fam)[b]	22	3	96–100	0.646	0.643	Swarbrick *et al.* (1991)
RT9 (Tet)[a]	?	5	117–137	0.653	0.619	Wilson *et al.* (1997)
TGLA122 (Fam)[a]	18	5	134–150	0.776	0.676	Georges & Massey (1992)
TGLA126 (Fam)[b]	?	4	116–124	0.558	0.583	Georges & Massey (1992)
TGLA387 (Hex)[a]	20	5	134–154	0.695	0.670	Georges & Massey (1992)
mean		5.3		0.681	0.670	

[a],[b] Indicate PCR products pooled for ABI analysis in a single lane.

APPENDIX B

Summary of population census and paternity analysis parameters for bighorn sheep at Ram Mountain, Canada. (LOD, logarithm of the odds.)

rut year	number of ewes 2+ yr	lambs tested	number of rams 2+ yr	number of rams sampled	critical ΔLOD statistic	predicted success rate	paternities assigned
1994	90	20	31	24 (77%)	1.89	14 (70%)	11 (55%)
1995	79	10	30	27 (90%)	0.75	9 (90%)	9 (90%)
1996	73	15	33	28 (85%)	1.53	13 (87%)	11 (73%)
1997	75	12	38	34 (89%)	1.07	11 (92%)	9 (75%)
1998	54	13	27	27 (100%)	0.00	13 (100%)	13 (100%)
1999	45	13	12	12 (100%)	0.00	12 (92%)	11 (85%)
total		83				72 (87%)	64 (77%)

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