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Male mating effort in a polygynous ungulate

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Abstract Survival and mating success are key fitness components of mammalian males. Because energy is limited, life history theory predicts trade-offs between current and future reproduction. While many studies have examined fitness trade-off in females, we know little about trade-offs faced by males. In polygynous species, male mating success is largely dependent upon intrasexual competition. Consequently, males have greater uncertainty over the benefits of a given allocation than over its costs, and the correlation between mating effort and success is likely much weaker in males than in females. We analyzed 14 years of data on the mating effort and survival of marked bighorn rams to investigate fitness trade-offs. Dominant rams defended single estrous ewes (“tending”) while subordinates attempted to copulate after separating the tending pair (“coursing”). We estimated the participation in tending and coursing for each ram and the effort in searching for breeding opportunities by each ram each year. We compared these three behavioral indices of male mating effort to demographic parameters, individual characteristics, and both yearly and long-term survival. Mating effort during the rut was unrelated to ram overwinter survival, but longevity was positively correlated with mating effort

between 2 and 5 years of age. Persistent variation among rams is likely to explain this pattern, suggesting that in natural populations a few high quality males enjoy both high mating success and high survival.

Keywords Rut · Male mating effort · Ungulates · Bighorn sheep · Life history

Introduction

Life history theory predicts a trade-off in resource allocation between reproduction and survival based on the assumption of limited resources (Stearns 1992). Several studies, however, documented substantial individual heterogeneity in resource acquisition in wild populations, such that some individuals can consistently allocate large amounts of energy to both reproduction and survival, leading to positive correlations between life history traits (Partridge and Farquhar 1983; Van Noordwijk and De Jong 1986; Service 2000; Cam et al. 2002). It was also suggested that individual variation in resource acquisition may be more important than individual variation in trade-offs occurring at the level of resource allocation, leading to “increasing returns” as superior individuals achieve both high reproductive success and increased survival (Houle 1991; Dobson et al. 1999; Reznick et al. 2000). While that reasoning appears sensible for females (Bérubé et al. 1999), it may not apply to males of species where both reproductive effort (the relative amount of energy devoted to reproduction) and reproductive success (the number of offspring fathered) mostly depend on a male’s ability to defeat potential competitors. Because of the high risk of injury (Geist 1967; Gosling et al. 1987), males may not challenge clearly superior competitors for access to receptive females and therefore a dominant male may obtain high reproductive success without much mating effort. Consequently, mating effort is not necessarily greater for males that use the most profitable mating tactics (such as mate guarding or harem holding; McElligot et al. 2003).

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A striking feature of the population dynamics of most mammals is that adult mortality differs between the sexes. Greater male than female mortality is common in ungulates, especially when resources are limited (Owen-Smith 1993a,b; Loison et al. 1999; Toïgo and Gaillard 2003). The most widely accepted explanation for male-biased adult mortality is that males take higher risks than females to obtain mating opportunities because they can have several mating partners and therefore a potentially greater fitness payoff (Andersson 1994). An alternative explanation is that sexual dimorphism leads to higher maintenance costs for males and impaired male survival (Ralls et al. 1980; Promislow 1992). In temperate ungulates, male-biased mortality was also attributed to the high-energy expenditure by males during the rut, which typically occurs just before the onset of winter. Males are thought to enter the winter in poorer condition than females, and then suffer higher mortality through starvation (Clutton-Brock et al. 1982; Festa-Bianchet 1989; Stevenson and Bancroft 1995). Although male mating effort is typically considered as one of the most important factors affecting differential adult survival, very few studies have assessed how individual mating effort affects male survival in ungulates.

The scarcity of studies investigating trade-offs between reproduction and survival in male mammals partly arises from difficulties in quantifying male reproductive effort (Mysterud et al. 2004). Female reproductive effort can be assessed by the production, number, and growth of offspring, but in species without paternal care, quantifying the amount of energy devoted to reproduction by males is not straightforward. Several studies used behaviors such as reduced foraging, mate guarding, or fighting frequency to indirectly quantify male mating effort (see Mysterud et al. 2004 for review). Other studies used mass loss during the rut as a measure of male mating effort (Yoccoz et al. 2002; McElligott et al. 2003; Forsyth et al. 2005). Because experimental studies of reproductive effort are almost impossible to conduct in wild ungulates (see Stevenson and Bancroft 1995), an examination of reproductive strategies must rely on indirect measures of fitness cost (Festa-Bianchet et al. 1998).

Two hypotheses predict how male reproductive investment should vary over the lifetime. The “terminal investment” hypothesis suggests that as males age, their residual reproductive value decreases and consequently they should increase their investment in current reproduction (Williams 1966; Pianka and Parker 1975). The “mating strategy-effort” proposes that reproductive effort should peak in males using the most rewarding tactics [such as harem holding in red deer (*Cervus elaphus*) or tending in bighorn] because those males can obtain more matings than either younger or senescent males (Yoccoz et al. 2002; Mysterud et al. 2005). Based on our results and on work by McElligott et al. (2003), we suggest that males with more resources (such as greater age-specific body mass) at the start of the rut should invest more in reproduction, regardless of the mating tactic they use. We term this the “individual quality hypothesis.” Under this hypothesis,

mating effort will not necessarily be correlated with reproductive success (McElligott et al. 2003).

Here, we estimated individual mating effort with three independent measurements: the distance traveled by a ram during the rut, the proportion of time spent in coursing activities, and the proportion of time spent tending ewes. We tested whether mating effort varied with social rank and demography [female number, operational sex ratio (OSR), and male age structure]. We also evaluated the effect of mating effort on annual survival and longevity using a 14-year database on marked rams. We argue that the individual quality hypothesis is likely to explain patterns of mating effort for bighorn rams and possibly other male ungulates.

Materials and methods

Study area and population

We studied the mating behavior of bighorn rams in the Sheep River Provincial Park, Alberta from 1989 to 2002. Since 1981, this population was intensively monitored (Festa-Bianchet 1986a; Hogg and Forbes 1997; Loison et al. 1999). Lambs (4 to 6 months old) were captured by chemical immobilization (Jorgenson et al. 1990; Pelletier et al. 2004) and individually marked using colored ear tags. Exact age is known for all marked animals and more than 95% of the sheep are individually recognizable each year. Detailed monitoring of rutting behavior started in 1989 (Hogg and Forbes 1997). Bighorn sheep in the Park rut in cliffs and open grasslands that are easily reached and mostly within sight of a road (Festa-Bianchet 1986b; Hogg and Forbes 1997; Pelletier 2005).

Male bighorn sheep use three main tactics (Hogg 1984, 1987; Hogg and Forbes 1997). The most successful tactic, tending, involves defending a single estrus ewe. The tending male will consort with the ewe for up to 2 days and use courtship behaviors leading to repeated copulations that are accepted by the ewe. Only the dominant ram among those near an estrus ewe can tend her (Hogg 1984, 1987; Hogg and Forbes 1997). An alternative mating tactic used by subordinate rams is “coursing.” Coursing rams try to separate the dominant male from the ewe by engaging the consort male in physical combats. When a coursing ram successfully breaks the defense, a rapid chase develops during which the coursing male attempts to force copulations (Hogg 1984, 1987). Although coursing is much less successful than tending for individual rams, coursing males collectively can obtain up to 40% of paternities within one breeding season (Hogg and Forbes 1997). During the rut, males spend considerable time “searching,” looking for mating opportunities by sampling groups of females that may be a few kilometers apart (Pelletier 2005). A third tactic, blocking, involves sequestering the estrus ewe outside the main mating area. At Sheep River, rams are rarely successful in blocking ewes (Pelletier 2005).

Every day from mid-November to mid-December, two to five observers censused the Park to locate males and females and monitor their behavior (Hogg and Forbes 1997). We considered the rut to begin the day the first copulation was observed (Pelletier 2005). The earliest estrus observed was on November 13, but on average, the rut started on November 21±4 days. Observations typically ended around December 14 (range December 7–23). During daily censuses, each time a group of sheep was seen, identities of all individuals were recorded. Locations were recorded on a 1:50,000 map. Focal observations of at least 1 h/day and up to 8 h were made to record the mating history of estrous ewes, which included identification of the tending and coursing rams. Only one ram at a time could tend a ewe, but a tending ram could be displaced if a more dominant ram joined a mating group. When that happened, the former tending ram usually left the group to search for other females or remained as a coursing ram. We defined “coursing rams” as all nontending males within 50 m of an estrous female. Given the opportunity, these males could be actively involved in a chase, during which they may copulate. For more details on mating behavior, see Hogg (1984, 1987, 1988) and Hogg and Forbes (1997). From 1989 to 2002, an average of 36 (SD=11 and range 10–51) ewes 2 years and older were seen in estrus each year. The mean number of ewes present during the rut was 41 (SD=14 and range 12–59). Each year, an average of 83±8% of females 2 years and older were observed in estrus (see Table 1), suggesting that we documented most of the breeding season each year.

From daily censuses, we reconstructed demographic parameters such as the number of ewes and rams in the park, OSR, and male age structure during each rut (Table 1). Male age-structure was measured as the proportion of males 6 years and older divided by the total number of males present during the rut. Survival was determined by repeated census of marked individuals (Jorgenson et al. 1997; Loison et al. 1999). Rams sometime left the park during the rut to breed in other sheep populations 6–25 km away (Hogg 2000). Our analyses

included only marked males with at least 7 days of behavioral observations at Sheep River during the rut [average observation days per individual=23 (SD=6)]. Our sample included 349 ram-years of observations of 103 different individuals monitored for one to nine ruts [average 3.4 (SD=2.5) and range 1 to 12 years].

Index of male mating effort

Tending effort index To estimate each male’s mating effort via the relative use of tending tactic, we calculated a “tending effort index” based on observed mating histories. We attempted to locate each estrus ewe three times a day (morning, noon, and end of the day). To estimate the tending effort index, we first calculated the number of point samples with ram *i* defending an estrus ewe divided by all observation of tending during each rut (Hogg and Forbes 1997). We observed a total of 532 estruses and each ewe contributed an average of 2.43 point samples. This index estimated the proportion of total estrus time during which ram *i* was the tending ram in each year. To control for variation in total estrus time between years, we then multiplied these proportions by the number of ewes in the study area during the rut. This gave an estimate, for each ram in each year, of the total time spent tending estrous females.

Coursing effort index Similar to the tending effort index, to determine an individual coursing effort index, we first calculated for each ram the number of times it was recorded as a coursing ram in point samples of estrous ewes divided by the total number of observations of coursing during each rut. This definition of coursing includes observations in which males were involved in a coursing chase and observations in which they were not actively coursing but simply present, showing interest in the estrous ewe and apparently waiting for coursing opportunities (Pelletier 2005). This index estimated the proportion of total estrus time during which ram *i* was

Table 1 Sex-age structure of the Sheep River bighorn sheep population during the rut from 1989 to 2002

Year	Number of rams rutting at Sheep River	Number of females	Operational sex ratio M/F	Rams 6 years and older	Proportion of estrous ewes observed
1989	31	61	0.51	13	0.62
1990	33	62	0.53	7	0.84
1991	40	62	0.65	3	0.93
1992	45	72	0.63	4	0.83
1993	45	59	0.76	3	0.80
1994	33	54	0.61	5	0.88
1995	24	46	0.52	6	0.77
1996	31	44	0.70	11	0.70
1997	29	45	0.64	10	0.94
1998	42	54	0.78	11	0.80
1999	24	37	0.65	7	0.79
2000	21	39	0.54	7	0.95
2001	18	34	0.53	5	0.97
2002	9	12	0.75	2	0.83

present as a coursing ram in each year. To obtain an estimate of total time spent as a coursing ram, we again multiplied these proportions by the number of ewes in the study area during the rut.

Searching effort index To quantify the degree in which rams searched for mating opportunities, we defined the “searching rate index” as the individual travel distance divided by the number of observation days. From daily censuses, we selected the first sighting of each ram each day from the start of the rut to the end of the field season. Locations were digitized in Arcview GIS 3.2 software (Economic and Social Research Institute) on a topographic map. We estimated the shortest distance traveled between successive locations for 103 individuals observed in at least one rut for a total of 349 individual traveling distances over 14 years [24.3 (SD=8.6) locations per ram each year]. Total minimum distance traveled by each ram was estimated using the animal movement tools (Hooge and Eichenlaub 1997). We drew a polyline between all successive locations for each male and estimated their length. Because each line between two successive locations is the shortest possible distance, the actual distance traveled is underestimated. The period of time during which the rut was observed each year changed, we then divided the total travel length by the number of days of observation to estimate average daily travel in meters per day for each individual (unit: m/day). Absolute distance traveled ranged between 2.6 and 85.4 km. More than 90% of males were seen every day (Hogg and Forbes 1997; Pelletier 2005).

Social rank

From 1989 to 2002, rams were observed during the pre-rut (end of September to early November) while they congregated in large groups and frequently interacted. Interactions were recorded ad libitum to determine individual social rank, as described in detail in Hogg and Forbes (1997), Pelletier (2005), and Pelletier and Festa-Bianchet (2006). Briefly, we built yearly dominance matrices and tested hierarchy linearity using Matman 1.0 for Windows (de Vries et al. 1993; de Vries 1995, 1998). We recorded on average 585 interactions per year (range 189–1,098) involving 46.2% of possible dyads (range 29 to 67.6%).

Data analysis

All models were fitted using GenStat for Windows 8.0 (VSN International). Because we analyzed repeated observations of the same individual over several years, we included ram identity and year of observations as random terms in linear mixed effect models (LMMs, for the searching and coursing indexes) and generalized linear mixed effect models (GLMMs, for the tending index). For all GLMMs, we used a logarithmic link function and

assumed Poisson error distribution. For all LMMs we used the identity link function and assumed a normal error distribution. For all models, the proportion of variance explained by the final model was estimated using the difference in residual deviance between a null model and the final model (Schemper 1990). Correlations between demographic parameters were done using linear models. Bonferroni corrections were made in cases of multiple comparisons (Sokal and Rohlf 1981).

To test for the effect of activity during the rut on age-specific overwinter survival, we used the Cox regression model in S-Plus 6.0 (Insightful, Seattle, WA, USA), which allows for time-dependent covariables. Twelve rams, poached or legally killed by hunters, were excluded from this analysis, leaving 91 marked individuals. We used linear regression to evaluate the relation between longevity and male mating effort. As explanatory variables, we used the average coursing and searching index for each ram between the ages of 2 and 5 years. Body mass and social rank of rams in that age range are strongly correlated (Pelletier and Festa-Bianchet 2006), and it was rare for rams aged 5 years or less to tend ewes. We excluded yearling males because they rarely attempted to mate (Pelletier 2005) and were assigned a single paternity over all years (Hogg and Forbes 1997; J. T. Hogg, unpublished data).

Results

Indices of mating effort were not independent of each other. Males that often tended ewes were less involved in coursing than other males [$r = -0.50$, $y = -1.71 - 0.15x$ (SE=0.02), Wald statistic (W)=58.37, and $p < 0.001$]. The tending and searching indices were not correlated [$r = 0.01$, $y = -2.09 - 0.00004x$ (SE=0.00001), $W = 0.09$, and $p = 0.76$], but searching increased with coursing [$r = 0.28$, $y = 963.5 + 46.8x$ (SE=7.9), $W = 34.92$, and $p < 0.001$]. A male's mating effort during year t was positively correlated with his mating effort in year $t-1$: for coursing [$r = 0.29$, $y = 5.02 + 0.31x$ (SE=0.06), $W = 22.77$, and $p < 0.001$] and searching [$r = 0.42$, $y = 1,153 + 0.40x$ (SE=0.06), $W = 47.10$, $p < 0.001$, and $N = 231$ records with information on successive years]. The degree in which a male was able to tend ewes in 1 year was also a predictor of its tending success the following year [$r = 0.64$; $y = 5.73 + 0.79x$ (SE=0.10), $W = 58.65$, $p < 0.001$, and $N = 79$ records of rams observed tending in consecutive years]. All estimates remained significant after Bonferroni corrections.

Effects of individual characteristics

Much of the variation in tactic-specific effort was explained by variation in social rank (Fig. 1). Rank explained 22.5% of variance in the searching index [$y = 1,053 + 2,448$ rank (SE=396.0), $W = 107.5$, and $p < 0.001$; $-1,457$ rank² (SE=380.7), $W = 14.65$, and $p < 0.001$; Fig. 1a], 23.4% of variance in the coursing index [$y = 4.26 + 29.76$ rank (SE=2.50), $W = 141.43$, and

$p < 0.001$; -28.78 rank^2 ($SE=2.41$), $W=142.56$, and $p < 0.001$; Fig. 1b], and 96.2% of variance in the tending index [$y=2.06+11.16 \text{ rank}$ ($SE=1.79$), $W=38.66$, and $p < 0.001$; Fig. 1c]. Age and social rank are highly correlated in bighorn rams ($r=0.94$), although the correlation weakens substantially for rams aged 6 years and older ($r=0.26$; Pelletier and Festa-Bianchet 2006). A reanalysis using age instead of rank showed that age (Fig. 2, analysis not presented) explained less variance in the tending index (89.4%) and coursing index (16.5%), and explained a slightly higher proportion of variance in the searching index (26.7%). All estimates remained significant after Bonferroni corrections.

Sex-age structure effects

The population sex-age structure during the rut varied substantially during our study (Table 1). The number of females was not correlated with the OSR ($r=-0.16$, $F_{1,12}=0.323$, and $p=0.580$) or male age structure ($r=0.16$, $F_{1,12}=0.298$, and $p=0.595$) and OSR was not significantly related to male age structure ($r=-0.30$, $F_{1,12}=1.167$, and $p=0.301$). The demographics parameters considered explained little of the variability in individual mating effort (Table 2). Ewe density had a negative effect on the coursing effort index (Table 2). No other demographic variable was significant.

Survival and longevity

Controlling for age, rams with greater mating effort index did not suffer greater mortality over winter than other individuals (Table 3). We also tested models including the three indices and their possible interactions and found none. There was a positive correlation between a ram's average coursing index from 2 up to 5 years and its longevity ($r=0.29$, $t=2.21$, $p=0.03$, and $n=55$; Fig. 3a). The searching index of rams aged between 2 and 5 years was also positively correlated with longevity ($r=0.57$, $t=5.16$, $p < 0.001$, and $n=55$; Fig. 3b). When rams that died before 5 years of age were excluded ($n=17$), the relation between mean coursing index and longevity remained positive but was no longer significant ($r=0.19$, $t=1.17$, $n=38$, and $p=0.25$), while the searching index remained positively correlated with longevity ($r=0.46$, $t=3.15$, $n=38$, and $p=0.003$).

Discussion

Despite substantial variation in sex-age structure during our study, male mating effort was only weakly affected by the number of females present. A ram's individual characteristics, especially social rank, are better predictors of its mating effort during the breeding season than demographic parameters. Changes in sex-age structure are more likely to affect the degree of competition between

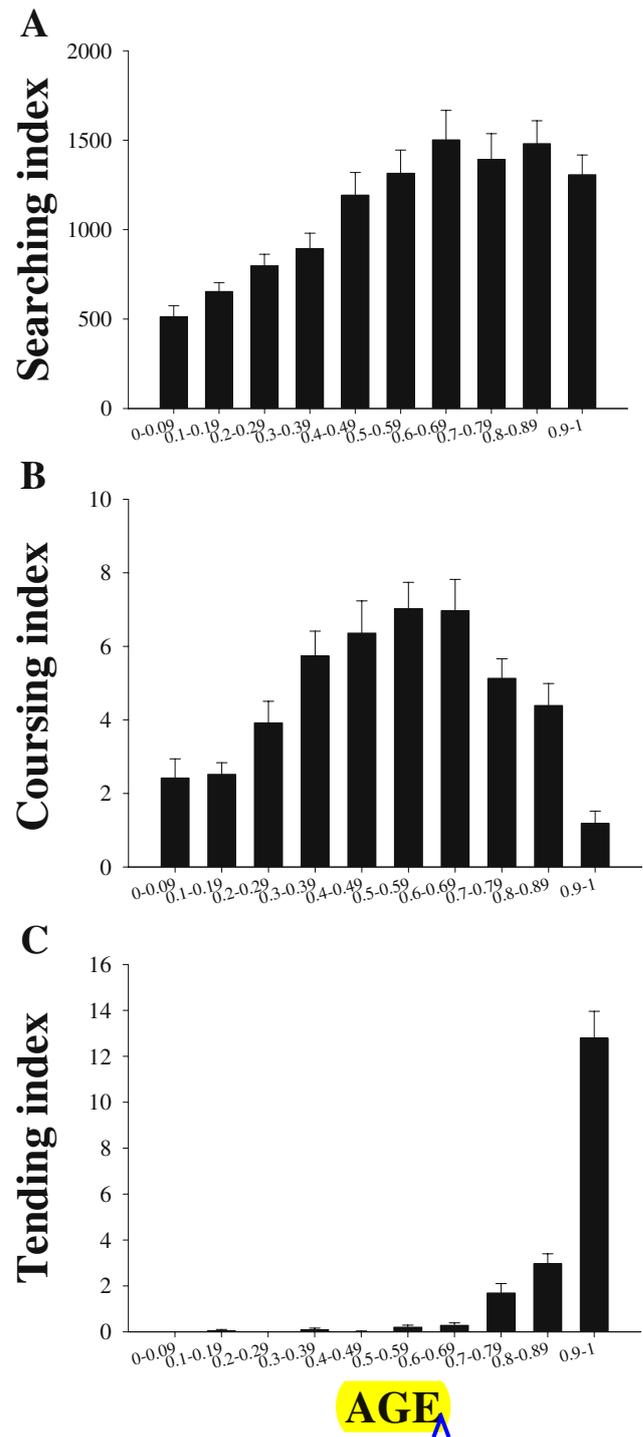


Fig. 1 Rank-specific male mating behavior ($\pm SE$) for bighorn sheep rams during 14 breeding seasons (1989–2002) at Sheep River, Alberta. **a** Searching index (m/day), **b** coursing index, and **c** tending index

males (Clutton-Brock et al. 1997) than an individual male's mating effort within a given mating tactic. Overwinter survival was not affected by a ram's mating effort during the previous rut. Contrary, to our expectations, there was no evidence of trade-offs between any index of mating effort and short-term survival after accounting for age effects.

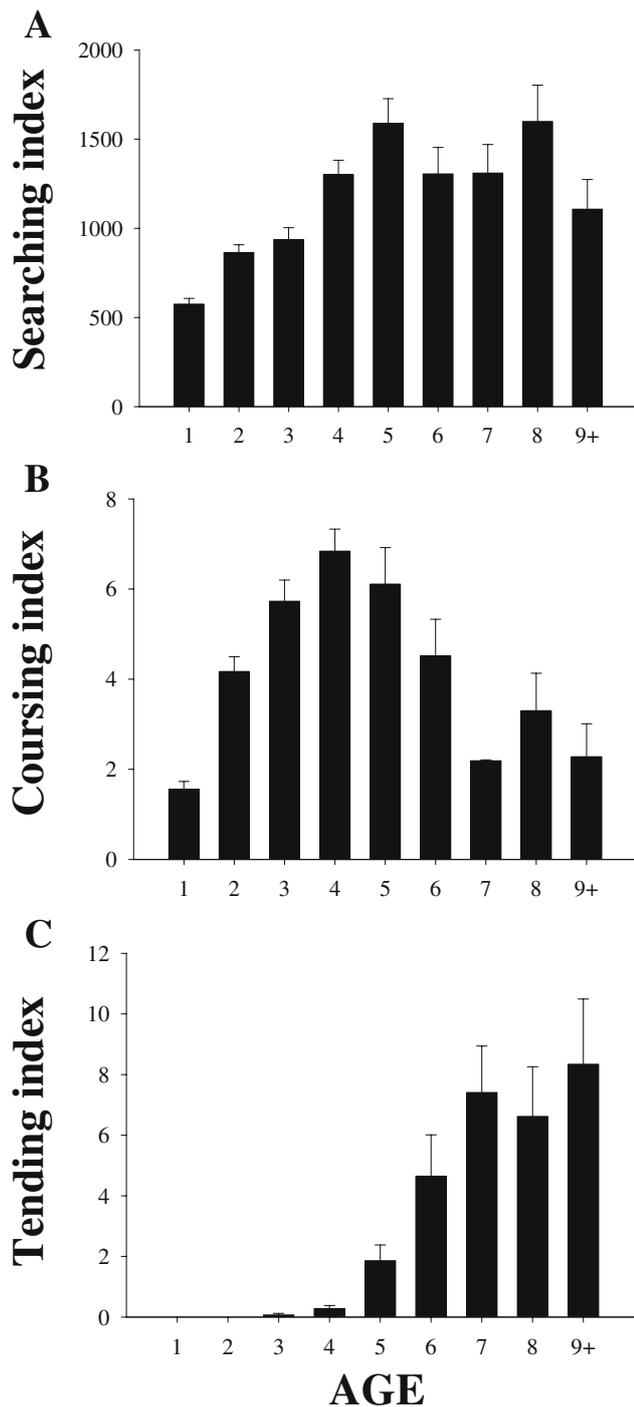


Fig. 2 Age-specific male mating behavior (\pm SE) for bighorn sheep rams during 14 breeding seasons (1989–2002) at Sheep River, Alberta. **a** Searching index (m/day), **b** coursing index, and **c** tending index

More surprisingly, long-term survival was positively associated with indices of coursing and searching during early adulthood. The positive correlation between coursing and searching at 2–5 years of age and longevity suggests that rams that made a greater mating effort were in superior body condition because they also enjoyed higher survival. Alternatively, the index of mating effort may not

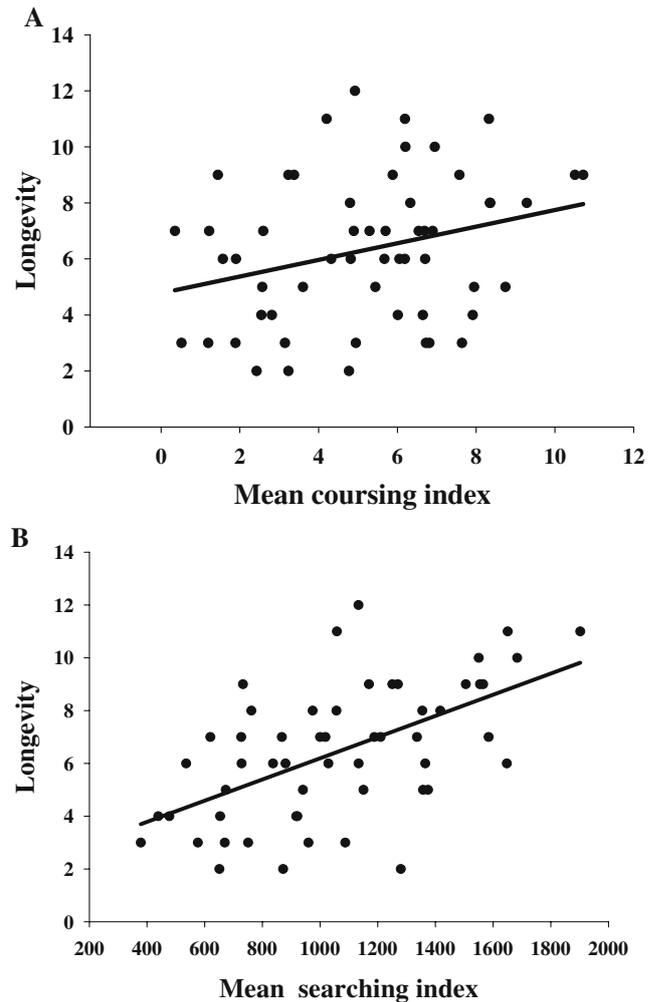


Fig. 3 Mean rutting indices while aged 2 to 5 years and longevity for rams 2 years and older. **a** Relation between the mean coursing index and longevity. **b** Relation between mean searching index and longevity

adequately represent rutting effort, but we previously reported that rams that spend more time searching and coursing decrease their time foraging and that the time spent searching for estrus ewes is correlated with an increase in fecal counts of lungworm larvae during the rut. Rams' activity during the rut is also correlated with mass loss (Pelletier 2005). Therefore, we suggest that our behavioral indices reflect male mating effort.

Stevenson and Bancroft (1995) showed that precocial male maturity in Soay sheep (*Ovis aries*) lambs led to high survival costs during years of high density. In the same population, Jewell (1997) found that castrated males had much greater survival than noncastrated males. In our study, however, males that made a greater mating effort early in life did not suffer from higher phenotypic costs of reproduction. Other studies of large mammals support this finding. In fallow deer (*Dama dama*), a male's reproduction during 1 year was positively associated with both survival and probability to reproduce the following year (McElligott et al. 2002). Finally, a study on elephant seals (*Mirounga angustirostris*) showed a survival cost for males

Table 2 Effect of demographic parameters on three indices of male behavior (after controlling for social rank) during the rut, 1989–2002, Sheep River, Alberta

Dependent variables	Explanatory variables	Estimates	Wald test	<i>P</i> value
Coursing index	Intercept	4.17 (0.33)		
	Ewe number	−0.04 (0.027)	2.34	0.0126
	OSR	−5.25 (3.79)	1.92	0.166
	Male age structure	−4.09 (2.78)	2.17	0.140
Searching index	Intercept	1,056 (107.5)		
	Ewe number	0.34 (8.08)	0.00	0.967
	OSR	823.5 (1,268.1)	0.42	0.516
	Male age structure	−533.2 (925.6)	0.33	0.565
Tending index	Intercept	2.07 (0.15)		
	Ewe number	0.003 (0.015)	0.04	0.837
	OSR	−0.74 (1.77)	0.17	0.676
	Male age structure	−0.91 (1.39)	0.43	0.511

Coursing and searching indices were modeled using a LMM using the identity link function and assuming normal distribution of error, while the tending index was modeled using a GLMM using a logarithmic link function and assuming Poisson error distribution. Both models included year and identity as random terms

that bred for the first time, whereas for older males there was a positive, but not significant, result between mating success and survival (Clinton and Boeuf 1993).

Van Noordwijk and De Jong (1986) suggested that the sign of correlations between life history traits will depend on the relative variation in the acquisition and in the allocation of resources. Some individuals are “better” than others because they have acquired more resources and can afford to invest in current reproduction without compromising their future reproductive potential. Studies of senescence have long underlined this problem (low-quality individual dies younger: Service 2000; Cam et al. 2002). Heterogeneity in individual quality is also likely to affect studies of male reproduction in species where access to mates is determined through intrasexual contests because high quality males can monopolize several mating partners over consecutive years (Clinton and Boeuf 1993; McElligott et al. 2002). Our study emphasized the importance of accounting for heterogeneity in phenotypic quality among individuals (Reznick et al. 2000) to understand reproductive trade-offs in males, especially in species where individual quality determines access to mates.

Our results support a model of energy trade-offs with large individual differences in the amount of resources available for reproduction (Tuomi et al. 1983). We suggest that males adjust their behavior during the rut according to

their condition. Similarly, Pelletier (2005) showed that heavier yearling and 2-year-old rams were more active during the rut than lighter ones. Fitness trade-offs, where an increase in reproductive effort is made at the expense of survival due to lowered body reserves (Stearns 1992), are reduced when some individuals have sufficient body resources to sustain the energy costs of reproductive activity (including mass loss, decreased foraging, and increased parasite activity; Pelletier 2005) without compromising their survival (Tuomi et al. 1983).

Further evidence that individual quality affected mating effort is provided by the correlations of indices for individual rams in successive years: Rams that were seen tending more often in 1 year were also likely to be observed to be tending more often in the following year. In bighorn sheep, access to females is determined by intrasexual competition and is monopolized by individuals of high phenotypic quality (Coltman et al. 2002, 2005). Higher-ranking bighorn rams are heavier than subordinates (Pelletier and Festa-Bianchet 2006) and heavy rams apparently can afford to lose more mass during the rut (Pelletier 2005). Only high-ranking males can use tending, a tactic with much higher reproductive success (Hogg and Forbes 1997) and with lower feeding constraints than coursing (Pelletier 2005). Those individuals of high phenotypic quality that reach adult size can use a high-

Table 3 Winter survival compared to indices of reproductive effort for 103 male bighorn sheep 2 years and older at Sheep River, Alberta, 1989–2002

Term	Coefficient (SE)	Exp (coef) ^a	<i>z</i>	<i>P</i> value
Coursing index	0.00025 (0.02)	1.00	0.012	0.99
Searching index	0.00007 (0.0001)	1.00	0.572	0.57
Tending index	−0.013 (0.02)	0.99	−0.669	0.50

The estimated effect of male reproductive effort on survival represents the predicted change in the log risk of mortality per unit increase of each index fitted in the model. None of these indices affected survival even when considered alone or testing for possible interactions

^aExp (coef) is then an estimate of the predicted change in the relative risk of death at each age per unit increase in each index

benefit tactic without incurring greater fitness costs than subordinates. Thus, for species where reproductive success is monopolized by a few individuals, positive associations between fitness components appear likely.

The natural survival of male bighorn sheep peaks at about 85–90% a year between 2 and 7 years of age, then declines gradually with age to about 65% for rams older than 9 years (Jorgenson et al. 1997; Loison et al. 1999). In our study population, males reach about 90% of their asymptotic autumn mass by 5 years of age when the heaviest rams can successfully challenge conspecifics that are older but lighter, and can sometimes tend estrous ewes (Pelletier and Festa-Bianchet 2006). Our results partially support the “male mating strategy” hypothesis because mating effort was associated with mating tactic (Yoccoz et al. 2002). For bighorn rams, however, the more rewarding tactic of tending appeared to be the least costly. This contrasts with the suggestion that those males that could achieve higher reproductive success by using the most rewarding mating tactic should invest more in reproduction than other males. In bighorn sheep, this hypothesis predicts peak effort by dominant males (mostly aged 6 years and older) that can tend ewes. Instead, rams restricted to the coursing tactic (mostly aged 2 to 5 years) incur the highest energy expenditure (Pelletier 2005), while tending rams have much higher reproductive success (Hogg and Forbes 1997). The terminal investment hypothesis predicts that male reproductive investment should increase with age. For bighorn rams, coursing appears to be costly and is mostly used by young rams. Dominant rams aged 6 years and older switch from coursing to the lower-cost and higher-benefit tactic of tending. Consequently, the age-specific pattern of mating effort by bighorn rams does not support the terminal investment hypotheses because reproductive effort does not appear to increase with age, even though rams suffer increasing age-related mortality (Loison et al. 1999). The individual quality hypothesis provides the best interpretation of our results: High-quality males of any age can afford a large mating effort (regardless whether that effort involves tending, coursing, or searching for estrous ewes) and although they incur large energy expenditure, they have higher survival than low-quality individuals. Some males may be better than others at obtaining resources or at using them to increase their reproductive success (Tuomi et al. 1983). In this case, a measure of individual quality is essential to investigate reproductive trade-offs.

Changes in body mass during parental care were suggested to measure reproductive effort for capital breeders (Festa-Bianchet 1998) that partly rely on stored fat reserve for reproduction (Jönsson 1997). In most temperate ungulates, males use a capital breeding strategy by relying on stored reserve during the rut (Miquelle 1990; Mysterud et al. 2005). Consequently, changes in male body mass during the rut were used to assess reproductive effort (Yoccoz et al. 2002; McElligott et al. 2003; Mysterud et al. 2004, 2005). Mass loss, however, is mainly determined by initial body mass (Festa-Bianchet et al. 1996; McElligott et al. 2003; Pelletier 2005), which will lead to the conclusion

that bigger individuals have greater reproductive effort than smaller ones. Even relative mass loss may not fully account for differences in individual phenotypic quality because for a given amount of energy expenditure some males may be better at acquiring mates than others (McElligott et al. 2003). The loss of a given proportion of body mass could have stronger effects for a small male than for a large one. In male fallow deer, mass loss during the rut was independent of reproductive success (McElligott et al. 2003). Therefore, to control for individual quality to quantify reproductive investment, one should monitor both mass loss and the degree of participation in reproduction by marked individuals over their lifetime. It is unclear to what extent individual mass loss (either absolute or relative) should be considered a fitness cost. In both bighorn sheep and fallow deer, highly successful males lose a substantial amount of mass during the rut (McElligott et al. 2003; Pelletier 2005) but enjoy high survival and successful reproduction over the following rut (McElligott et al. 2002). Clearly, any consideration of the evolution of male reproductive strategies in polygynous mammals must take into consideration the fact that fitness costs (such as reduced survival) and benefits (reproductive success) may not be correlated. In these species, females may suffer a cost of reproduction, but males may mostly suffer a cost of trying to reproduce.

Given the correlation in mating effort across years for the same individuals, the apparently higher survival of high-quality individuals (Gaillard et al. 2000; McElligott et al. 2002) and the lack of compensatory growth in most male ungulates (Toïgo et al. 1999; Festa-Bianchet et al. 2000), most subordinate young males in natural populations face poor prospects of ever becoming successful breeders. In these systems where individual male reproductive success is highly skewed, one may expect reproductive investment (possibly leading to greater mortality) to be negatively correlated with individual quality.

In conclusion, male reproductive strategies in polygynous species are more likely to have been shaped by individual ability to acquire resources rather than variability in allocation of those resources (Dobson et al. 1999). Males with a small initial advantage at acquiring resources (of environmental, maternal, or genetic origin) could gain increasing returns in fitness by allocating a large amount of metabolic resources to reproduction. That strategy would likely be selected for if it does not greatly reduce survival. Because most ungulates are capital breeders, body mass is likely to be a good surrogate of individual quality. Any factors known to affect body mass (such as population density in the year of birth or during early development) are therefore likely to play an important role in determining phenotypic differences among individual. Phenotypic costs are difficult to measure because males may adjust their participation in reproductive activities according to individual quality. Therefore, accounting for individual quality is essential to obtain further insights on reproductive trade-offs for males. In species where reproduction is monopolized by a few males, positive association between fitness components should be expected and male repro-

ductive success may not be correlated with reproductive investment (McElligott et al. 2003).

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