Paternal reproductive success drives sex allocation in a wild mammal

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Parents should bias sex allocation toward offspring of the sex most likely to provide higher fitness returns. Trivers and Willard proposed that for polygynous mammals, females should adjust sex-ratio at conception or bias allocation of resources toward the most profitable sex, according to their own body condition. However, the possibility that mammalian fathers may influence sex allocation has seldom been considered. Here, we show that the probability of having a son increased from 0.31 to 0.60 with sire reproductive success in wild bighorn sheep (*Ovis canadensis*). Furthermore, our results suggest that females fertilized by relatively unsuccessful sires allocated more energy during lactation to daughters than to sons, while the opposite occurred for females fertilized by successful sires. The pattern of sex-biased offspring production appears adaptive because paternal reproductive success reduced the fitness of daughters and increased the average annual weaning success of sons, independently of maternal allocation to the offspring. Our results illustrate that sex allocation can be driven by paternal phenotype, with profound influences on the strength of sexual selection and on conflicts of interest between parents.

Trivers and Willard (1973) suggested that in polygynous mammals where maternal condition has a stronger effect on the fitness of sons than of daughters, females in relatively good condition should preferentially produce sons, whereas females in relatively poor condition should bias their birth sex ratio in favor of daughters. This idea has generated much interest and is among the most scrutinized topics in evolutionary biology (Carranza 2002; West 2009). Despite the logical appeal of this theory, however, empirical tests produced mixed results (Hewison and Gaillard 1999; Brown and Silk 2002; Sheldon and West 2004). Many species that fit all the assumptions of the model do not show the predicted response (e.g., Birgersson 1998; Lindström et al. 2002; Blanchard et al. 2004), leading to suggestions that sex ratio is affected by multiple selective pressures (Kruuk et al. 1999; Cockburn et al. 2002; West and Sheldon 2002).

The logic of the Trivers and Willard hypothesis can apply to any trait that parents transmit to offspring and that differentially influences the fitness of sons and daughters (Frank 1990; West 2009; Komdeur 2012). Thus, females breeding with more attractive males should produce more sons, who may inherit from their father characters increasing their attractiveness and will achieve high reproductive success (Burley 1981; Fawcett et al. 2007; Komdeur 2012). On the other hand, females breeding with less attractive males should produce more daughters (Fawcett et al. 2007; Booksmythe et al. 2013). A recent meta-analysis (Booksmythe et al. in press) provides weak support for the mate attractiveness hypothesis, but 84% of the studies it examined were on birds (for case studies, see Ellegren et al. 1996; Sheldon et al. 1999; Korsten et al. 2006) and only one was conducted on mammals. Thus, we know much less about whether and how fathers contribute to sex-ratio variation in mammals (Gomendio et al. 2006; Røed et al. 2007; Edwards and Cameron 2014). In birds, females are the heterogametic sex and may control egg sex ratio. In mammals, males may have more control over the mechanisms of sex determination because they are the heterogametic sex, hence, both parents may be involved in sex-ratio manipulation (Grant and Chamley 2010; Edwards and Cameron 2014). A landmark study showed that in red deer (*Cervus elaphus*) the likelihood

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of producing a son increased both with a sire's fertility and his proportion of normal spermatozoa (Gomendio et al. 2006). In that experiment all hinds were inseminated at the same time in relation to ovulation. If females are conceived later in the estrous cycle as observed in humans (Weinberg et al. 1995), however, this manipulation may have limited the conception of females (Grant and Chamley 2010). Gomendio et al. (2006) suggested that sex-ratio bias in relation to sire fertility is likely to occur in natural contexts, but this prediction has not been tested.

Primary sex ratio is not the only component of sex allocation. In species with parental care, parents should allocate more energy to the most profitable sex (Trivers and Willard 1973; Frank 1990; Hewison and Gaillard 1999). Parental care has important fitness consequences for both parents and offspring, since early development has profound effects on juvenile survival and adult phenotype (Lindström 1999; Metcalfe and Monaghan 2001; Lummaa and Clutton-Brock 2002). Studies on birds have found support for differential maternal allocation of resources to offspring in response to mate quality (Cunningham and Russell 2000; Pryke and Griffith 2009). Whether or not mothers modulate energy expenditure toward sons and daughters according the quality of their mate remains, however, an open question.

Measuring the evolutionary implications of fathers on sex allocation is a challenge because there are very few natural systems where detailed pedigrees, measures of resource allocation to offspring, and fitness of both sexes are known. Not only do paternal effects on sex ratio and allocation of resources to male and female offspring need to be tested, but the underlying assumption that paternal traits differentially influences the relative fitness of sons and daughters also needs to be examined (West 2009; Cox and Calsbeek 2010). This is particularly important because sex-biased early mortality may create a correlation between parental characteristics and offspring sex ratio and thus, be an alternative mechanism to explain sex-ratio bias (Clutton-Brock et al. 1985; Martins 2004; Orzack et al. 2015).

Here, we used the exceptionally detailed long-term monitoring of wild bighorn sheep (*Ovis canadensis*) at Ram Mountain, Canada, to examine the adaptive effects of paternal success on mammalian sex allocation. Bighorn sheep are highly polygynous and strongly sexually dimorphic (Leblanc et al. 2001). Males compete intensely for estrous females but provide no parental care, as typical for mammals. Each estrous female is defended by a dominant male that has a 60% chance of fathering her lamb; subordinate males attempt to break up the pair and fertilize 40% of females (Hogg 1984; Hogg and Forbes 1997). We used male reproductive success to measure paternal influence on sex allocation because it encapsulates several morphological, behavioral, and physiological traits that can have differential fitness effects on sons and daughters. Males with higher reproductive success have longer horns and larger mass, two heritable traits (Coltman

et al. 2002, 2005). Horn volume does not influence reproductive success or longevity of females (Poissant et al. 2008). Male reproductive success also includes ability to fertilize a female after copulation. Very fertile males with a higher proportion of normal spermatozoa may benefit from producing sons who will inherit this trait (Gomendio et al. 2006).

Our aims in this study were: (1) to examine whether both the likelihood of having a son and maternal resource allocation to sons increases as paternal success increases, (2) to test whether sex allocation patterns in relation to paternal success affected future reproductive success of mothers (3) to assess the adaptive significance of sex allocation patterns by examining the fitness of sons and daughters as a function of paternal success.

Materials and Methods
STUDY POPULATION
Ram Mountain is about 30 km east of the Rockies in Alberta, Canada (52°N, 115°W, elevation 1080–2170 m). The bighorn sheep population has been studied since 1972. Techniques used to capture, mark, measure, and monitor animals have been described in detail (Jorgenson et al. 1993). In brief, sheep were captured in a corral trap baited with salt from late May to late September each year. Individuals were marked using visual collars and plastic ear tags at their first capture, usually as lambs, so their exact age was known. Various measurements (body mass, horn size) and biopsies for genetic analysis were collected at capture. Marked sheep were subsequently monitored throughout life to quantify survival and reproduction. Animal-handling procedures were approved by the Animal Care Committee of the University of Sherbrooke (MFB2009-01 and FP2012-01), affiliated to the Canadian Council for Animal Care.

PEDIGREE INFORMATION
Maternity was accurately established from field observations of suckling behavior since 1972. Tissue samples were genotyped to determine paternity since 1988. Paternities of lambs that died before capture are unknown. Polymerase chain reaction amplification was performed at approximately 30 microsatellite loci, with no evidence of linkage disequilibrium (Coltman et al. 2005). Paternities were assigned using CERVUS version 3.0 (Marshall et al. 1998) at a > 95% confidence level. Maternity and paternity were known for 359 lambs born between 1988 and 2013 to 126 mothers (mean 2.85 offspring *per* mother) and 86 fathers (mean 4.17 offspring *per* father). Male reproductive success depends upon many factors that vary across years, including age, environmental conditions, and the number and characteristics of competitors (Hogg and Forbes 1997). Therefore, we considered paternal reproductive success on an annual basis, measured as the percentage of paternities assigned to each male in a given year, log transformed to reduce skewness.

MEASURING SEX ALLOCATION

Females produce a maximum of one offspring per year and a 6-month gestation is followed by 5 months of lactation. Sex was assessed at first capture, when lambs were aged from 1 week to 3 months. In agreement with previous studies (Bérubé et al. 1996, Blanchard et al. 2004), we assumed that sex ratio at capture reflected birth sex ratio. Neonatal mortality (deduced for ewes that lactated but were not seen with a lamb) at 17% was lower than subsequent juvenile mortality (45%), with no evidence that it was sex-specific. Woodgerd (1964) sexed 43 bighorn lambs aged a few days old and found 22 males and 21 females. Similar result was obtained in captive population (Geist 1971). Assuming that equal numbers of males and females were born, we would expect a proportion of sons different from 0.5 at capture if neonatal mortality varies between the sexes. This is not the case (proportion test: $\chi^2 = 0.17$, $P = 0.67$); 461 lambs sexed since 1988 included 235 females and 226 males.

Maternal resource allocation to offspring depends on the total amount of energy available to the mother (King et al. 2011; Hamel et al. 2012). Following Martin and Festa-Bianchet (2010, 2011), maternal reproductive allocation was measured as lamb summer mass gain corrected for maternal mass in June (an indicator of maternal body reserves) and for maternal mass gain over the summer (an indicator of food intake). For a given mass in June and a given mass gain in summer, a female with a fast-growing lamb would allocate more energy to reproduction than one with a slow-growing lamb. Almost all females and lambs were weighed 2–7 times each summer. We adjusted female mass to June 5 and September 15 using linear-mixed models (LMMs). The square root of capture date (considering May 25 as day 1) was fitted as a fixed effect. We included random effects of female identity as an intercept and the interaction between identity and date as a slope representing the rate of mass gain (Pelletier et al. 2007; Martin and Pelletier 2011). We fitted separate regression models for each year. Lamb mass was adjusted to June 15 (as some were born after June 5, Festa-Bianchet et al. 1996) and to September 15 using the same procedure. Summer mass gain was the difference between estimated mass in September and in June.

FITNESS AND FITNESS COMPONENTS

We used lifetime weaning success (LWS; the number of offspring that survived to weaning) to measure fitness of male and female lambs (Clutton-Brock 1988, Brommer et al. 2004). A high LWS can be reached through high longevity and/or by being successful at each reproductive event. Therefore, we tested the effects of sire annual reproductive success on LWS of lambs of each sex, but also on their longevity (in years) and on LWS adjusted for longevity (AWS). We only included offspring that reached the age at which they can reproduce, 2 years for females (Festa-Bianchet et al. 1995) and 3 years for males (Coltman et al. 2005)

in analyses of AWS, because this variable measured the average annual weaning success of sons and daughters. Offspring removed for translocations or research purposes were excluded from fitness analyses. Cohorts born after 2000 for females and after 2005 for males were excluded, because they included individuals still alive in 2014, whose LRS and longevity could not be measured.

STATISTICAL ANALYSES

In all mixed models, we fitted father and mother identity as well as offspring birth year (cohort) as random factors to account for nonindependence of offspring born from the same mother, father or in the same year. All statistical analyses were performed using R v. 3.1.2 R (http://www.r-project.org), and mixed models were fitted using the "lme4" library (Bates et al. 2011). We used likelihood ratio tests and Wald statistics to assess statistical significance of the fixed effects in generalized linear-mixed models (GLMMs) (Bolker et al. 2009). The difference in deviance between two nested models is distributed as a χ^2 with degrees of freedom equal to the difference in degrees of freedom between the two models compared. Statistical significance of the fixed effects in LMMS was assessed using F-tests and Wald statistics with denominator degree of freedom calculated as suggested by Kenward and Roger (1997) in KRmodcomp's function of the pbkrtest library (Halekoh and Højsgaard 2014). We report standardized regression coefficients obtained by standardizing (mean = 0, variance = 1) all continuous explanatory variables, to allow comparison of their effect sizes.

We tested the effects of paternal annual reproductive success on the probability of producing a son that year using GLMMs with a binomial distribution (glmer function). These models also included the fixed effects of relative maternal mass (measured in two different ways, see Blanchard et al. 2004 and Table S1) and maternal reproductive success the previous year (a three-level factor: "failed," "weaned a female," or "weaned a male"). The timing of conception may influence the proportion of sons produced (Holand et al. 2006). This variable was unknown, but birth dates were available from 1992 onwards. We tested the effect of birth date on the probability of producing a son from this restricted dataset to ensure it did not introduce any bias.

To evaluate whether paternal annual reproductive success influenced sex-specific maternal reproductive allocation, we fitted a LMM of lamb summer mass gain using the lmer function. This model included as fixed effects lamb sex (male lambs gain mass faster than female lambs, Leblanc et al. 2001), several maternal traits (summer mass gain, mass in June, quadratic effect of age, and reproductive success the previous year), population density (the number of adult females aged 2 or older in June each year), paternal annual reproductive success and its interaction with lamb sex. Because the model of lamb mass gain included lamb sex, maternal summer mass gain, and maternal mass in June, all others

variables in this model can be interpreted as affecting maternal reproductive resource allocation (Martin and Festa-Bianchet 2010, 2011). This analysis was rerun with lamb birth date as an additional explanatory variable in a restricted dataset.

For sex-biased maternal allocation to constitute sex-biased maternal investment, the differential production and care of one sex of offspring must be associated with a reproductive cost to the mother (Trivers 1972; Hewison and Gaillard 1999). We tested for sex-biased maternal investment in relation to paternal success by examining whether maternal survival and weaning success in year $t + 1$ was related to the interaction between offspring sex and sire success in year t. Survival and weaning success were analyzed using GLMMs with a binomial distribution. Last recorded sighting is a reliable indicator of age at death since the yearly resighting probability was over 0.99 for ewes in this population (Jorgenson et al. 1997).

The effects of paternal success on fitness (LWS) and longevity of sons and daughters were tested using GLMMs with Poisson errors. Poisson models often display overdispersion, where variance of the response variable is greater than the mean, resulting in a poor fit to the data. We tested for possible overdispersion in Poisson GLMMs by calculating the ratio of the sum of the squared Pearson residuals to the residual degrees of freedom (Bolker et al. 2009; Zuur et al. 2009). This ratio corresponds to the dispersion parameter φ, and values > 1 indicate overdispersion. We tested the effects on AWS (i.e., residuals obtained from the model of LWS against longevity) with linear models. As we found evidence for sire effects on offspring sex and maternal resource allocation, we reran these analyses of fitness and fitness components by including adjusted lamb growth as an additional explanatory variable to investigate the adaptive nature for the pattern of offspring sex variation.

Results
VARIATION IN OFFSPRING SEX
The proportion of male lambs with known father did not differ from 0.5 (167 sons, 192 daughters; proportion test: $\chi^2_1 = 1.74$, $P = 0.19$). We found a positive relationship between paternal annual reproductive success and the likelihood of having a son ($\chi^2_1 = 5.18$, $P = 0.02$; Fig. 1; Table S1). Females fertilized by less successful males produced more daughters. In contrast, females fertilized by the most successful males had slightly more sons (Fig. 1). Importantly, the relationship between paternal success and the probability of producing a son did not change with yearly neonatal mortality (interaction between paternal success and neonatal mortality, $\chi^2_1 = 0.67$, $P = 0.41$; additive effect of neonatal mortality, $\chi^2_1 = 1.14$, $P = 0.29$). There was no relationship between birth date and offspring sex (Table S1). Offspring sex was not affected by yearly deviations from mother or pop-
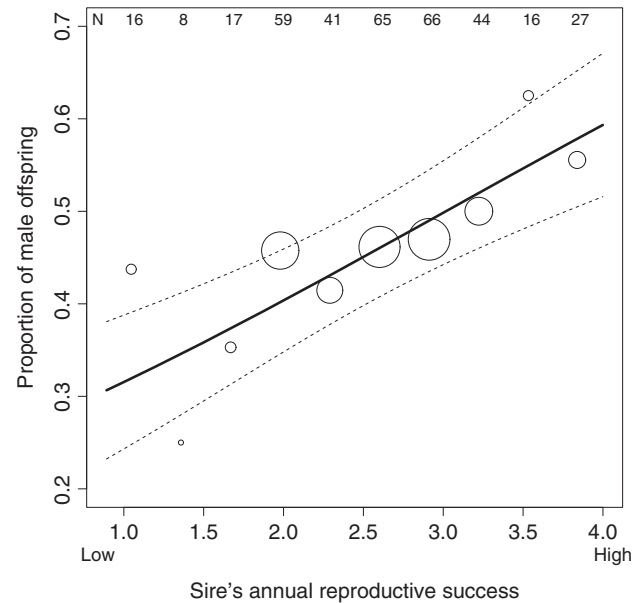

Figure 1. Sex of bighorn sheep lambs born at Ram Mountain, Alberta, Canada between 1988 and 2013 to 126 mothers and 86 fathers as a function of sire annual reproductive success (the log-transformed percentage of paternities assigned to a male in a given year). The solid and dotted lines show the predicted values ± SE from a GLMM. Points (of different size according to the sample size (N) at top of the figure) indicate the observed sex ratio for each class of paternal reproductive success.

ulation average mass (Table S1 and Fig. S1) or by interactions between paternal success and either measure of maternal condition (Table S1). There was also no relationship between paternal success and either measure of maternal condition (both *P*-values > 0.47).

ALLOCATION OF MATERNAL RESOURCES TO SONS AND DAUGHTERS
Lamb summer mass gain was strongly related to maternal traits; it increased with both mother's mass in June and her age until about 9 years before declining (Fig. S2) and decreased if the mother had weaned a son the previous year (Table 1). Maternal and lamb mass gain also tended to be positively correlated. Male lambs gained more mass during summer than female lambs and population density lowered lamb mass gain (Table 1). After controlling for all these effects, we found that paternal success differentially influenced body growth of sons and daughters ($F_{1,303} = 5.87$, $P = 0.016$; Table 1; Fig. 2). Adjusted mass gain of sons increased with sire annual reproductive success (slope $= 0.48 \pm 0.21$, $P = 0.03$), whereas that of daughters did not change (slope $= -0.16 \pm 0.20$, $P = 0.42$). Overall, our results suggest that mothers fertilized by relatively unsuccessful males allocated more energy during lactation to daughters than to sons, while a bias in favor of sons occurred for mothers fertilized by successful males

Table 1. Linear-mixed model of summer mass gain for 342 bighorn lambs with known parents at Ram Mountain, Alberta, Canada between 1988 and 2013.

Parameter	Estimate ± SE	t	P value
Fixed effects:			
Intercept	**18.28 ± 0.53**	**34.20**	**<0.001**
Maternal summer mass gain	0.37 ± 0.21	1.70	0.09
Maternal mass in June	**0.57 ± 0.20**	**2.86**	**<0.01**
Lamb sex (male)	**1.35 ± 0.25**	**5.24**	**<0.001**
Previous maternal reproductive success (failed)			
Weaned a male	***−0.95 ± 0.34***	***−2.73***	***<0.01***
Weaned a female	*−0.45 ± 0.34*	*−1.29*	*0.19*
Maternal age	***2.76 ± 0.73***	***3.72***	***<0.001***
Maternal age²	***−2.52 ± 0.69***	***−3.58***	***<0.001***
Population density	***−1.01 ± 0.50***	***−2.00***	***0.05***
Father's annual reproductive success	*−0.16 ± 0.20*	*−0.81*	*0.41*
Father's annual reproductive success × lamb sex	***0.64 ± 0.26***	***2.42***	***0.01***

	Variance	Ratio	χ^2 (df)	P value
Random effects:				
Mother identity	**0.97**	**0.10**	**10.07 (1)**	**< 0.01**
Father identity	0.13	0.01	0.43 (1)	0.50
Year	**4.46**	**0.45**	**106.53**	**< 0.01**
Residual	4.33			

Because reproductive allocation was measured as lamb summer mass gain corrected for lamb sex, maternal mass in June and maternal mass gain over the summer (Martin and Festa-Bianchet 2010, 2011), the variables in italics test for effects on maternal reproductive resource allocation. Female lambs were the sex of reference, × stands for interactive effect and significant effects are in bold. The *P*-values for the fixed effects are calculated from *t* test based on the Kenward–Roger method of calculating denominator degrees of freedom. For random effects, ratio corresponds to each variance component divided by the sum of all variance components. Rerunning the model with birth date as additional explanatory variable did not affect the interaction between paternal success and lamb sex (see Table S2).
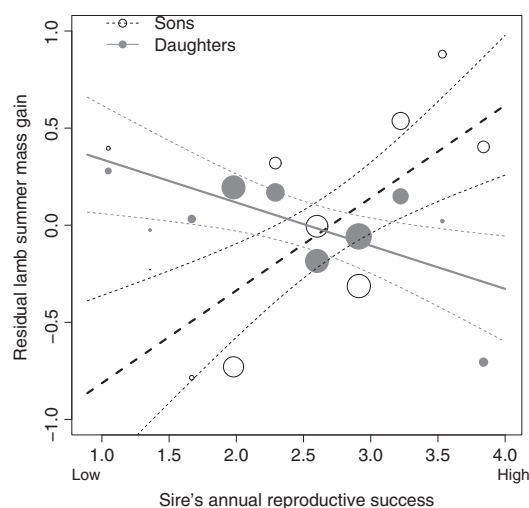

Figure 2. Residual summer mass gain of male and female lambs as a function of sire annual reproductive success in bighorn sheep at Ram Mountain, Alberta, Canada. Values on the *y* axis represent residuals from a linear-mixed model (see Table 1). The solid and dotted lines (black for males and gray for females) show the predicted values ± SE from linear models. Points of different size according to sample size correspond to the average values for each class of sire success.

(Fig. 2). As paternal mass did not influence lamb growth for either sex (interaction between lamb sex and sire mass, $F_{1,153} = 1.19$, $P = 0.28$; additive effect of sire mass, $F_{1,79} = 1.71$, $P = 0.19$), our results were not simply due to heavy males siring fast-growing sons and slow-growing daughters.

SEX ALLOCATION OR SEX INVESTMENT

For mothers of sons, the reproductive success of their mate did not influence subsequent survival ($\chi^2_1 = 0.93$, $P = 0.33$) or weaning success ($\chi^2_1 = 1.60$, $P = 0.21$). Similarly, for mothers of daughters, the success of their mate was not related to subsequent survival ($\chi^2_1 = 1.32$, $P = 0.25$) or weaning success ($\chi^2_1 = 0.29$, $P = 0.59$). Thus, sex-biased maternal allocation in relation to paternal success did not seem to translate to sex-biased maternal investment.

OFFSPRING FITNESS AND FITNESS COMPONENTS

Lifetime weaning success (LWS) of sons was unrelated to the success of their fathers because of antagonistic effects on reproduction and longevity: sons of successful males had higher annual weaning success but suffered reduced longevity compared

to sons of relatively unsuccessful males (Fig. 3, Table 2). By contrast, LWS of daughters decreased with increasing success of their fathers, because of reduced longevity rather than variation in annual weaning success (Fig. 3, Table 2). Although the slope of the relationship between paternal success and LWS did not differ between sons and daughters ($t = 0.27$, $P = 0.78$), females fertilized by less successful males produced daughters with higher fitness relative to their sons (Fig. 3). Repeating these analyses accounting for adjusted lamb mass gain did not change the results (Table S4), since our measure of maternal resource allocation was uncorrelated with fitness of sons and daughters (all $P > 0.42$). For all Poisson GLMMs, there was no evidence of overdispersion ($\varphi = 0.22$ and 0.33 for male and female LWS, respectively, $\varphi = 0.48$ and 0.57 for male and female longevity, respectively; all $P > 0.98$) so these models fitted the data well.

Discussion

At the population level, bighorn sheep produce approximately the same number of male and female lambs. At the individual level, however, offspring sex varies with paternal reproductive success. A recent meta-analysis (Booksmythe et al. in press) found that, as predicted by theory (Fawcett et al. 2007), offspring sex ratio is statistically but weakly associated with various measures of male attractiveness. Available information, however, has a strong taxonomic bias as over 80% of studies are on birds. While overproduction of sons in response to attractive mates is the overriding pattern for birds (Burley 1981; Ellegren et al. 1996; Sheldon et al. 1999; Korsten et al. 2006), sex-biased offspring production for bighorn sheep mainly results from more daughters for females fertilized by less successful males. The likelihood of having a son increased from 0.31 to 0.60 with increasing sire reproductive success. Sex ratio is only one component of sex allocation as envisioned by Trivers and Willard (1973). However, few studies have simultaneously considered the different components of sex allocation and tested its predicted adaptive consequences by measuring the fitness of sons and daughters (Olsson et al. 2005; Cox and Calsbeek 2010; Cox et al. 2011). In addition to offspring sex adjustment, our analyses suggest that females fertilized by less successful sires allocate more energy to daughters than to sons, while the opposite occurs for females fertilized by successful sires. Sires may thus influence the amount of maternal care, even in a species without paternal care.

We did not know sex ratio at birth because lamb sex was usually determined when lambs were aged 1–10 weeks. Paternal effects on offspring sex could be nonadaptive if sons sired by relatively unsuccessful males had a much lower survival than daughters over the first few days or weeks of life. Neonatal
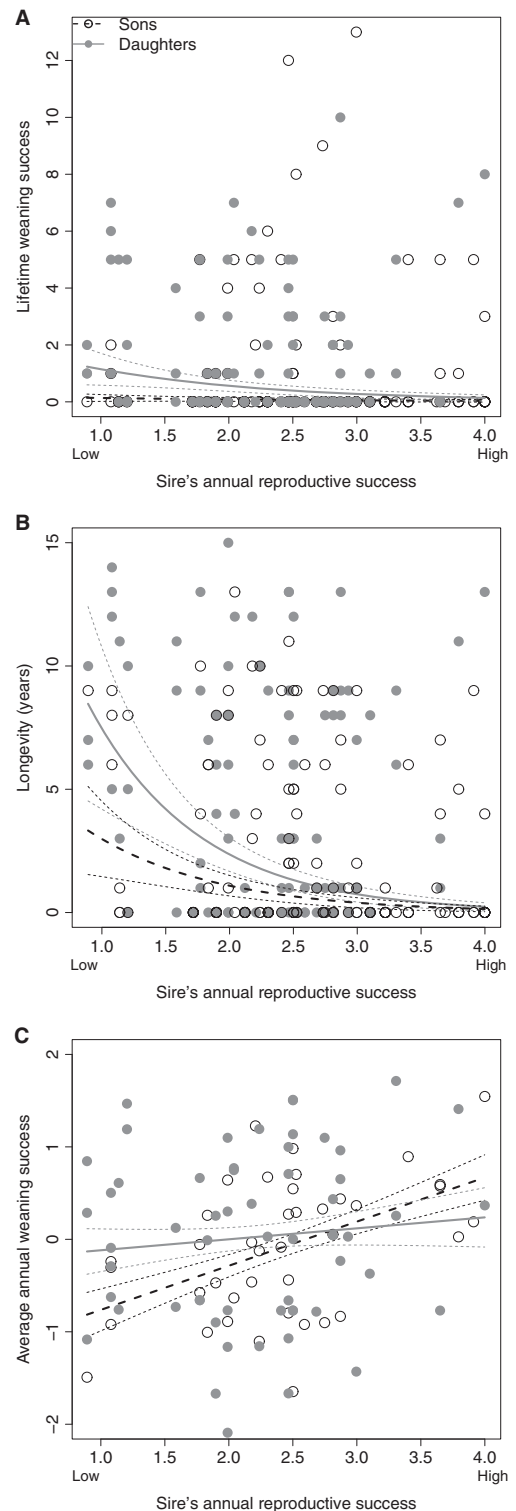

Figure 3. Lifetime weaning success (A), longevity (B), and average annual weaning success (C) of bighorn sheep sons (open circles and dashed black line) and daughters (gray circles and solid gray lines) as a function of paternal reproductive success at Ram Mountain, Alberta, Canada. Thin dashed lines represent standard errors around model's predictions.

Table 2. Effects (± standard error) of sire annual reproductive success on fitness (lifetime weaning success) and fitness components (longevity and average annual weaning success) of bighorn lambs of each sex at Ram Mountain, Alberta, Canada.

Dependant variable	Son			Daughter		
	Estimate	SE	*P* value	Estimate	SE	*P* value
Lifetime weaning success (LWS)	–0.35	0.36	0.33	**–0.46**	**0.23**	**0.04**
Longevity	**–0.76**	**0.26**	**<0.01**	**–0.75**	**0.21**	**<0.01**
Average annual weaning success (AWS)	**0.36**	**0.10**	**<0.01**	0.09	0.12	0.47

Generalized linear-mixed-effects model are based on 111 sons born before 2006 and 109 daughters born before 2001. Significant effects are in bold. The negative association between paternal reproductive success and longevity of sons resulted from natural mortality because the relationship remained unchanged when removing eight sons shot by hunters (estimate ± SE = –0.82 ± 0.28, *P* = 0.003). Interpretation of the results did not change when we considered the same cohorts (before 2001) for both sexes (Table S3).

mortality, however, was relatively low compared to overall juvenile mortality (Portier et al. 1998), we have no evidence that it was sex-biased (see Material and Methods section) and the relationship between paternal success and offspring sex was independent of the yearly rate of neonatal mortality. Furthermore, sex-specific mass of lambs at about 3 weeks of age, an indication of the strength of selection during early life, was not influenced by paternal reproductive success (interaction between sex and sire success, $F_{1,296} = 0.45$, $P = 0.50$; additive effect of sire success: $F_{1,172} = 0.08$, $P = 0.77$). Paternal effects on lamb sex raise the question of the mechanisms involved in this phenomenon. Some female birds and lizards produce more sons when mated to males with elaborate ornaments, larger body size or better condition (Burley 1981; Ellegren et al. 1996; Sheldon et al. 1999; Korsten et al. 2006; Cox and Calsbeek 2010; Cox et al. 2011). Male birds provide parental care and male lizards defend territories. Therefore, attractive males may provide direct benefits, which may have a greater influence on the fitness of sons than of daughters. This explanation is not applicable to bighorn males, which are not territorial and provide no paternal care. Alternatively, sex-ratio adjustment may evolve in response to sexually antagonistic genetic variation (Connallon and Jakubowski 2009; Blackburn et al. 2010). Sexually antagonistic alleles increase the fitness of one sex but are maladaptive for the other. Because daughters receive the father's X chromosome and sexually antagonistic genetic variation is expected to accumulate on the X chromosome, females that mate with relatively unsuccessful males may produce high-fitness daughters, whereas mates of high-fitness males may produce low-fitness daughters (Chippindale et al. 2001; Fedorka and Mousseau 2004; Foerster et al. 2007.; Connallon and Jakubowski 2009). In support of this hypothesis, the fitness functions show that it is advantageous for relatively unsuccessful male bighorn sheep to produce more daughters, independently of maternal resource allocation. Our results are thus most consistent with an adaptive function for sex-ratio bias, although it would be informative to analyze offspring sex at conception.

Analysis of paternal and maternal effects on offspring growth suggests that mothers adjust resource allocation (a trait that cannot be affected by early mortality) to daughters and sons according to paternal annual reproductive success. Studies of birds reveal that females mated with more attractive males lay larger eggs (Cunningham and Russell 2000) and deposit more androgens in egg yolks (Gil et al. 2006). However, whether or not females are selected to modulate sex-specific offspring provisioning in response to characteristics of their mate remains largely unexplored. In blue tits (*Cyanistes caeruleus*), reduced mate ultraviolet coloration led females to reduce feeding effort, decreasing offspring growth but without sex-differential allocation (Limbourg et al. 2004). Among mammals, female pronghorn (*Antilocapra americana*) compensated for mating with a less attractive male by increasing milk transfer to their offspring (Byers and Waits 2006), but the effect of offspring sex was not tested. Offspring body growth is highly dependent on the amount of milk produced by the mother (Gittleman and Thompson 1988; Garcia et al. 1999). In another population of bighorn sheep, Hogg et al. (1992) showed that ewes appeared to have control over lactation because they almost invariability terminated suckling bouts. Mechanistically, females may adjust sex-specific allocation of resources based on whether they mostly mated with a tending male or were often mounted by coursing males during estrus. Tending males, which are dominant, defend a single estrous female against other males. Coursing males attempt to gain access to estrous females by bypassing the tending male. Coursing is the main mating tactic of subordinate rams. Estrous females likely mate with multiple males (Hogg 1988) but, the less they mated with coursing males, the more likely the sire was a male of high reproductive success (Hogg and Forbes 1997; Coltman et al. 2002). Alternatively, sex-specific offspring growth may vary with paternal success because of sexually antagonistic genes from the sire rather than differential maternal resource allocation. In mountain goats (*Oreamnos americanus*) son mass at 1 year of age increased with paternal mass but daughters showed the opposite relationship (Mainguy

et al. 2009). Although an effect of sexually antagonistic genes was not supported by the lack of interaction between lamb sex and paternal mass on adjusted lamb growth, paternal genes may differentially influence behavior or physiology of sons and daughters, which may in turn influence early body growth. This remains a plausible but untested explanation for the contrasting effects of paternal success on adjusted body growth of sons and daughters.

Most studies cannot identify the proximate mechanisms of offspring sex manipulation (Cockburn et al. 2002; Cameron 2004; Helle et al. 2008). Although we also lack a detailed mechanistic understanding of how bighorn sheep manipulate the sex of their offspring, two nonexclusive explanations can be proposed. First, mothers may adjust offspring sex in response to sire reproductive success. Maternal testosterone prior to conception and maternal glucose immediately postconception affect mammalian sex ratio (review in Grant and Chamley 2010). For example, in field voles (*Microtus agrestis*) high maternal testosterone level prior to breeding was associated with an excess of male pups, likely because testosterone favors the mobility/survival of Y-bearing sperm (Helle et al. 2008). Alternatively, fathers could differ in the proportion or competitiveness of X- and Y-bearing sperms. Male mammals may have more control over the mechanisms of sex determination than males of other taxa because they are the heterogametic sex. Thus, for mammals, paternal manipulation may provide a more parsimonious explanation for sex-ratio bias than maternal response to paternal characteristics (Edwards and Cameron 2014). Supporting this view, artificially inseminated captive red deer hinds, with no direct knowledge of sire phenotypes, doubled the proportion of sons from 30 to 60% as sire fertility tripled (Gomendio et al. 2006). Males with high fertility may benefit from having sons who inherit their father's semen quality and therefore obtain high reproductive success, while low-fertility males would benefit from producing daughters that will not inherit their poor sperm quality. That study, however, did not measure the production of X- and Y-bearing sperm in the ejaculate, which could help understand when variation arises.

Paternal sex-ratio manipulation may lead to a conflict of interest between parents. For instance, a relatively unsuccessful male might benefit from producing daughters while a female in good condition would be advantaged by giving birth to sons. Even after accounting for paternal influences, we found no support for the expectation that the probability of having a son increases with relative maternal condition (Trivers and Willard 1973). Also, paternal success did not interact with maternal condition to determine offspring sex. Paternal effects may, however, explain why observed sex ratios in other species often do not correspond or even oppose the pattern predicted by Trivers and Willard (1973). The conclusions of sex allocation studies based solely on maternal characteristics should thus be reconsidered in the light of potential paternal contributions. Furthermore, our results have

important consequences for sexual selection, because sex-ratio adjustment in response to sire characteristics can weaken sexual selection on male traits (Fawcett et al. 2011). By producing more daughters, low-success male bighorn sheep increase their fitness. This tactic makes the "best of a bad job," reduces the benefits of sexually selected traits and could contribute to the maintenance of genetic variation in male reproductive success in natural systems (Kruuk et al. 2000; Merilä and Sheldon 2000). The patterns we report could be widespread but remain poorly documented in wild mammals, because detailed paternity data are available for very few species, highlighting the importance of long-term individual-based studies that monitor the reproductive success of both sexes (Clutton-Brock and Sheldon 2010). A full understanding of sex allocation will require studies of underlying mechanisms, as well as a simultaneous consideration of the roles of mothers and fathers.

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Associate Editor: A. Maklakov
Handling Editor: M. Servedio

Supporting Information
Additional Supporting Information may be found in the online version of this article at the publisher's website:

Supporting information for "Paternal reproductive success drives sex allocation in a wild mammal" including two figures (Figure S1. and Figure S2) and four tables (Table S1., Table S2., Table S3. and Table S4.)

Fig. S1. Probability of producing a male bighorn lamb between 1988 and 2013 as a function of relative maternal condition.

Fig. S2. Residual lamb summer mass gain as a function of maternal age at Ram Mountain, Alberta.

Table S1. Generalized linear mixed model of the probability of producing a son between 1988 and 2013 for bighorn sheep at Ram Mountain, Alberta ($n = 359$ lambs).

Table S2. Linear mixed model of summer mass gain for 210 bighorn lambs with known birth dates at Ram Mountain, Alberta, 1992–2013.

Table S3. Effects (± standard error) of sire annual reproductive success on fitness (measured as lifetime weaning success) and fitness components (longevity and average annual weaning success) of sons and daughters born before 2001 at Ram Mountain, Alberta. Significant effects are in bold.

Table S4. Effects (± standard error) of sire annual reproductive success on fitness (lifetime weaning success) and fitness components (longevity and average annual weaning success) of sons and daughters after accounting for adjusted offspring growth (our measure of maternal resource allocation) at Ram Mountain, Alberta.