Sex-ratio variation and reproductive costs in relation to density in a forest-dwelling population of red deer (*Cervus elaphus*)

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For dimorphic species in which the variance in reproductive success of males is more pronounced than that of females, theories of adaptive variation in sex ratio predict that mothers should invest more heavily in sons than in daughters. By using harvest data from a forest-dwelling red deer population that experienced a marked reduction in population density we tested the hypothesis that adaptive sex-ratio variation should occur only when populations are much below carrying capacity. More specifically, we tested whether at low density, females in better than average condition were more likely to produce male offspring and to invest in individual sons rather than were females in poorer than average condition. We also investigated female reproductive costs arising from a decrease either in body mass or in reproduction. We did not find any support for a biased sex ratio or investment toward male calves by high-quality mothers at any population density. Costs of reproduction in terms of body mass and pregnancy rates were only detectable for females that reproduced as yearlings and not for those that reproduced as adults. Our results therefore do not support the hypothesis of adaptive sex-ratio variation in a population living below carrying capacity. The four-fold difference in party sizes (defined as the number of deer aggregate in the same party in which no individual was more than 50 m from any other) observed in our population living in a closed forest habitat compared with populations living in more open habitats previously studied might account for such a discrepancy. We suggest that a smaller party size may decrease the intensity of sexual selection and could be the proximal cause for the lack of adaptive sex-ratio variation we report for the population studied here. *Key words: Cervus elaphus*, closed habitat, party size, red deer, reproductive costs, sex ratio, Trivers and Willard, ungulates. *[Behav Ecol 14:862–869 (2003)]*

F isher's (1930) theory states that equal investment between sexes should lead to a balanced sex ratio at the population level when sons and daughters are equally costly to produce. Once equilibrium is reached, investment in each sex may deviate from population average among individuals and still be an evolutionary stable strategy (Kolman, 1960; Williams, 1979). Trivers and Willard (1973; hereafter, noted as T&W) proposed that for sexually dimorphic species, maternal quality might determine the pattern of sex-biased maternal investment provided that the following three assumptions are met: (1) the quality of the young correlates with the quality of its mother, (2) differences in quality endure into adulthood, and (3) the reproductive success of sons is differentially enhanced by maternal investment because males compete more intensively for mates. One would then expect that high-quality mothers (with a good condition and/or a high social rank) should produce sons more often or invest more heavily in their sons, because of the potential greater fitness return for an equal investment.

Currently, whether modification of the sex ratio really occurs or not is controversial, and inconsistencies have been regularly reported across (Brown, 2001; Clutton-Brock and Iason, 1986; Hewison and Gaillard, 1999; Hiraiwa-Hasegawa, 1993) and within (roe deer: Wauters et al., 1996 versus Hewison et al., 1999; reindeer: Skogland, 1986 versus Kojola and Eloranta, 1989; red deer: Kruuk et al., 1999a versus Post et al., 1999; and bison: Rutberg, 1986 versus Green and Rothstein, 1991) mammalian species. Various suggestions have been proposed for explaining such contradictions, notably the selective publication of significant results (Festa-Bianchet, 1996; Palmer, 1999), the possibility of a posteriori interpretation of sex-ratio variations (Hewison and Gaillard, 1999), or the violation of underlying assumptions of T&W's model (Hewison and Gaillard, 1999), all of which are complicated by a lack of comprehensive physiological mechanism enabling sex-ratio control (Clutton-Brock and Iason, 1986; Krackow, 1995). It has also been proposed that the selective advantage to invest more heavily in one sex could be affected by more than one factor (Clutton-Brock and Iason, 1986; Hardy, 1997; James, 1998), including nonselective factors. For instance, nonadaptive modifications of sex ratio have been reported in red deer populations during periods of harsh environmental conditions (Mysterud et al., 2000; Post et al., 1999). These studies emphasize the importance of extrinsic and intrinsic factors (such as density or climate) in shaping the sex-ratio variations, which may have been underestimated in the current theory. A possible mechanism would involve a fetal mortality higher in males than in females when mothers are faced with harsh environmental conditions (Kruuk et al., 1999a). Thus, Kruuk et al. (1999a) recently proposed that adaptive variation of the sex ratio, as predicted by T&W, should only occur in populations living much below carrying capacity. Although numerous analyses of T&W effects have been performed in vertebrate populations during the past two decades (Brown, 2001; Clutton-Brock and Iason,

1986; Hewison and Gaillard, 1999), to our knowledge none have tested the generality of the hypothesis of Kruuk et al. (1999a) and/or experimentally assessed the influence of marked changes in density on sex ratio. By using contrasting periods with highly different population density, we aimed to fill this gap by performing a test of the hypothesis proposed by Kruuk et al. (1999a) that the T&W effect should only be seen in populations below carrying capacity.

Ungulates are usually considered ideal candidates for testing evolutionary sex-ratio hypotheses but all species do not fulfill all the three assumptions of T&W's model (Hewison and Gaillard, 1999). Red deer are sexually dimorphic and polygynous and produce one young per breeding attempt. Only males typically disperse, and males exhibit a high variance in reproductive success that largely depends on their fighting ability (Clutton-Brock et al., 1982a; Kruuk et al., 1999b). Accordingly red deer seem to fit all T&W's assumptions (Clutton-Brock et al., 1985; Kruuk et al., 1999a; Mysterud et al., 2000). We thus aimed to test the following predictions.

Prediction 1

According to T&W, females in better than average condition are more likely to produce a son than are females in poorer condition. As the production of a male or a female calf should depend on maternal ability to invest, factors such as primiparity or the previous reproductive attempt are also expected to affect sex ratio, because of a potential decrease in the amount of energy allocated to reproduction (Clutton-Brock et al., 1983; Trivers and Willard, 1973). In addition, adaptive variation of sex ratio should only occur at low density (Kruuk et al., 1999a) when high-quality mothers produce an excess of sons and low-quality mothers produce an excess of daughters.

Prediction 2

T&W concluded that rather than a variation in offspring sex ratio, we may expect a bias in maternal investment toward male calves. An appropriate measure of maternal expenditure is not straightforward (Byers and Moodie, 1990; Pélabon et al., 1995). An alternative to the assessment of maternal investment focuses on reproductive costs (Reznick, 1992). If a male-biased investment occurs, females that weaned a male calf should suffer a higher decrease in body mass and/or fecundity compared with that of a female that weaned a female calf. Although reproductive costs are usually difficult to demonstrate without experimental manipulation, previous studies on ungulates have shown that assessing reproductive costs from observational data becomes possible when a measure of individual differences in phenotypic quality (such as body mass) is available (see Clutton-Brock et al., 1983 on red deer; Festa-Bianchet et al., 1998 on bighorn sheep for study cases).

Prediction 3

Several studies on polygynous ungulates showed a decrease in fecundity as a result of a successful weaning (Mitchell et al., 1977 on red deer; Rutberg, 1986 on bison; Bérubé et al., 1996 on bighorn sheep). We thus expect the pregnancy rates and/ or body mass of females that weaned a calf the previous year to decrease. Furthermore, as female growth continues for at least 3 years (Clutton-Brock et al., 1982a), variations in pregnancy rates or body mass should be more marked for 2-year-old females because of the trade-off between growth and reproduction (Stearns, 1992).

METHODS

Study area

The Petite Pierre National Reserve (PPNR) is a 2800-ha forest located in northeast France (48.5° N, 7° E) in the Vosges mountains at a mean elevation of 300 m. The climate is continental with oceanic influences (mean January and July temperatures are 0.6°C and 18.4°C, respectively) characterized by cold winters and hot summers. The PPNR red deer population inhabits a temperate forest of silver fir (*Abies alba*), Douglas fir (*Pseudotsuga douglasii*), Norway spruce (*Picea abies*), and European beech (*Fagus sylvatica*). Roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) are also present in the reserve, and all the three ungulates are hunted, either based on quotas (both species of deer) or freely (wild boar). During the past 10 years, an average of 35 red deer, 50 roe deer, and 100 wild boar were hunted annually. The study area is free of predators that could selectively influence calf survival and, hence, sex ratio at weaning (Guinness et al., 1978).

Harvest data

Red deer have been harvested since 1977 in PPNR (professional and sport hunters), and the hunting season spans 5 months from September–January. Culled animals are sexed and weighed. Three age classes (calves less than 1 year of age, yearlings between 1 and 2 years of age, and adults more than 2 years of age) have been recognized based on the dental eruption method (Hamlin et al., 2000; Lowe, 1967). A total of 395 hinds have been shot in PPNR. The managers from the Office National de la Chasse et de la Faune Sauvage recorded whether females were "yeld" (i.e., with dry nipples and piebald) or "milk" (i.e., with milk in their nipples), allowing us to assess the female reproductive success of the previous year. We then assessed current reproductive status by sampling uteruses. Sex and mass of 111 fetuses were recorded. More than 97% of the females shot with their calves from the 1 September–19 January showed signs of lactation, so we considered that the female successfully weaned a calf if she was still lactating when shot before 1 December, which was the date corresponding to the end of the lactation period (Clutton-Brock et al., 1982a: 74). Although we did not obtain specific data for any red deer population in a French forest, weaning of red deer calves (sensu Martin, 1984) was expected to occur within the 5 or 6 months after birth as reported by Clutton-Brock et al. (1982a) for a red deer population on Rum Island, Scotland. We thus assumed that calves harvested during the hunting season were mostly weaned, an assumption that was supported by the high survival rate of orphaned calves that lost their mother during the hunting period (Bonenfant C, Hamman JL, Klein F, unpublished data). We accounted for possible growth occurring during the 5-month-long hunting season by standardizing calf body mass to the mean shooting date by using linear regression (for a similar procedure, see Jorgenson et al., 1993).

Managers of the PPNR have monitored population density by using an abundance index (AI; Caughley, 1977; Seber, 1982) derived from road night counts (for further details about the method, see Bonenfant et al., 2002). Managers increased the hunting pressure just before 1983 (an average of 78 deer per year were shot from 1981–1983 versus 37 deer from 1984 onward), so that population density decreased drastically. As a consequence, the AI declined (from 90 deer seen per 100 km before 1983 to only 54 in average after 1983), corresponding to a 40% decrease. Since 1983, the density index has remained quite constant, suggesting that population size has been kept fairly constant by the moderate annual harvest. We used this reduction in density as an experimental

test of density-dependent responses of offspring sex ratio. Because of its low accuracy (CV = 29.7%), we did not use the AI as a continuous variable but instead considered it as a two-level factor, which explained 78% of the total variance in the AI ($F_{1,21} = 74.327$, $p < .0001$). The high-density level includes years from 1977–1983 and the low-density years from 1984–1999.

Relationship between mother and offspring condition

Although polygynous species usually fit T&W's model assumptions (particularly red deer, Hewison and Gaillard, 1999), we first aimed to test for a correlation between maternal and offspring body mass. We could not directly assess the condition of hind, for example, by using the kidney fat index, because such data were not recorded in the present study. Moreover, using a condition index (CI) measured as the residuals from the regression of body mass on jaw length from a restricted data set revealed a marked positive relationship between such a measure of structural size (CI) and body mass (body mass = $0.726 \times$ CI $- 40.45$, $F_{1,232} = 614$, $p < .0001$, $R^2 = .73$). We thus confidently concluded that female phenotypic quality or condition could be reliably assessed by female body mass in that population.

We measured fetal growth rate by fitting a growth equation of the form mass = $\alpha \times$ age$^\beta$, relating the mass (to the nearest gram) to the age of the fetus. Assuming that conception dates are highly synchronized in red deer (Clutton-Brock et al., 1982a: 54), and do not differ between sexes, the age of the fetuses was estimated as the number of days between the peak period of rutting in the population (15 September) and the harvest date of the mother (ranging from 2 November–1 February). A high synchrony of conception dates was more directly supported by the high synchrony of births reported in the only red deer population monitored during this life stage in France (Wassy in east France). Indeed all newborn (i.e., less than 11 kg) calves marked there ($N = 116$) were found from 11–29 May (Bonenfant C, Richard A, Picard A, Klein F, unpublished data). But the occurrence of some outliers suggests that embryos may die soon after conception or that several females may conceive in a second or third oestrus (Guinness et al., 1971) and so conceive later in the rutting season, in disagreement with the synchronization hypothesis. A weighted regression was then performed to minimize the influence of outliers, each point being weighted with the inverse of its residual: regression weight = $1/[1 + \text{Abs(residuals)}]$. We then tested whether the growth rate differed between sexes by comparing male and female slopes on the log-log scale (ANCOVA-like procedure; for more details, see Festa-Bianchet et al., 1998).

Then the relationships between mother and offspring condition during fetal stage and weaning were investigated by regressing residuals of the linear growth equation against mother's condition, and by comparing mother and offspring phenotypic quality in autumn. We only considered the cases in which the calf-mother pair was identified with certainty because the pair either was standing alone or was outside a party. During the first year of life, the median mother-offspring distance is around 10 m (e.g., 8 m in Clutton-Brock et al., 1982a: 184), so we can confidently identify mother-calf associations. Simultaneous mother-calf shots also gave us the opportunity to gather information on two successive breeding attempts when uteruses were sampled. Calves provided information about the previous reproductive effort (either a male or a female), and extracted fetuses represented the current reproductive effort (pregnant versus nonpregnant and sex of fetuses).

On the use of harvesting data

The present work did not lead hunters to shoot additional deer, as annual quotas are set by provincial administration independently of our research program. In addition, since 1977 shooting rules in PPNR were aimed to prevent obtaining orphan calves as much as possible. Hunters were then directed to shoot the calf first and were allowed to shoot his mother from their own decision. Besides, before shooting a female, hunters have to check for the absence of a calf at heel. Therefore, we could get data on the mother and its calf from culled animals whenever hunters report the shooting of the whole calf-mother pair, but the latter were not specifically instructed for.

Extrapolating sex ratio at birth

Sex ratio in autumn matches with sex ratio at birth if males do not exhibit differential mortality during summer and autumn (Guinness et al., 1978) and/or if no selective harvest occurs on male calves (generally assumed to be fulfilled in red deer; see Boyce, 1989; Mysterud et al., 2000; Post et al., 1999). The mean shooting date was 15 November at the PPNR. By mid-November, in our study, male calves are only slightly heavier than females (8% here; see Bonenfant et al., 2002), and body mass range overlaps to a great extent between males and females because of within-sex variability (0.25 and 0.75 percentiles are 58–75 kg and 55–67 kg for males and females, respectively, in PPNR). Furthermore, the association between the mother and calf does not depend on the sex of the calf until the age of 1 year is reached (Clutton-Brock et al., 1982a: 183), so it seems unlikely that the harvest could be biased toward males based on body-size dimorphism or due to behavior. Comparisons of fetal and postcalving sex ratios were performed using chi-square tests (Sokal and Rohlf, 1981).

Analyses of sex ratio and maternal costs

To test prediction 1, we considered that the proportion of males among N fetuses or calves in each sample followed a binomial distribution in which p was the probability of being a male. Hence, p was tested against the null hypothesis that $p = .5$ (meaning that sex determination is a purely mendelian process) by using a binomial test (Conover, 1980) to check for deviation from parity. The effects of mass, age (two classes: yearling and older), density, and previous reproductive success on the proportion of males were investigated by using a generalized linear model (GLM) procedure. In our analyses, primiparity (defined as the first reproduction in a female lifetime) confounded with age-classes because most first-breeding hinds were yearlings. We thus fitted a logistic regression with calf sex as the binary-dependent variable, mass as covariate and density, and primiparity and the previous reproductive success as factors (ANCOVA-like procedure, see Festa-Bianchet et al., 1998).

We studied the occurrence of maternal expenditure by testing for a decrease in pregnancy rate and body mass with (prediction 2) and without (prediction 3) a sex-bias after controlling for density-dependent effects on the studied life traits of first-breeding hinds (in PPNR pregnancy and body mass were not affected by density for multiparous females, i.e., females who reproduced earlier in their lifetime; Bonenfant et al., 2002). The influence of offspring sex, previous reproductive effort, and primiparity on female pregnancy rate was modelled by using GLM models and a logistic link. The effects of these explanatory factors on maternal condition were considered by performing an ANOVA, with maternal body mass being the dependent variable, and with

Table 1

One-way ANCOVA of log-transformed fetus mass (variable) as a function of Julian date of shooting (covariable) and fetus sex (factor), and calf body mass corrected for Julian date (variable) as a function of calf's mother body mass (covariable) and calf sex (factor)

	Sum of squares	df	F	p	Coefficient
Ln (fetus mass)					
Ln (Julian day)	267.360	1	659.359	<.00001	3.097 ± 0.129
Sex	0.010	1	0.026	.871	0.731 ± 0.513
Ln (Julian day) × sex	0.857	1	2.115	.148	-0.187 ± 0.129
Residual	43.388	107	—	—	—
Calf body mass					
Mother body mass	475.041	1	10.630	.002	0.419 ± 0.140
Sex	190.003	1	4.254	.045	2.948 ± 8.301
Mother body mass × sex	16.328	1	0.365	.548	-0.084 ± 0.140
Residual	1875.783	42	—	—	—

offspring sex or the previous reproductive status being the factors.

In each case, the factors were tested with a likelihood-ratio test. To account for the unbalanced sampling design, we used a backward stepwise selection procedure, testing successively the interaction terms and then the main effects of factors against the most general model (Searle, 1971). We set the level of significance of a factor at $p = .05$. All calculations were performed by using S-plus Software (Venables and Ripley, 1994).

RESULTS

Relationships between mother and offspring condition

In contradiction with what would have been expected from a dimorphic species such as red deer, during the first 2 months of gestation, the growth rate did not statistically differ between sexes, despite a higher estimate for male fetuses (slope of 3.09 ± 0.12 versus 2.90 ± 0.78 for males [$n = 60$] and females [$n = 51$] respectively; $F_{1,107} = 2.11$, $p = .148$). In December, male calves were 8.6% heavier than female calves (dressed body mass = 33.4 ± 1.0 kg versus 30.5 ± 0.8 kg; Bonenfant et al., 2002). Our data suggest a weak but significant relationship between mother and fetus body mass, which is identical for both sexes (Table 1, $R^2 = .098$). Likewise, the relationship between maternal and calf body mass still occurred at weaning (Table 1, $R^2 = .193$), but it was not possible to differentiate between male and female calves (i.e., no interaction between sex and mother body mass; Table 1 and Figure 1) once size dimorphism was taken into account. The first assumption (i.e., the correlation between mother and calf quality) required for testing T&W's model was thus fulfilled.

Overall sex ratio in PPNR calves during weaning did not show any significant deviation from parity (mean = 0.45, $n = 389$, $p = .10$) and did not differ markedly from fetus sex ratio (0.45 versus 0.54, $\chi^2 = 2.06$, df = 1, $p = .15$), although the percentage of male offspring showed a slight decrease from conception to weaning.

The effects of the relative condition, primiparity, previous reproductive effort, and density on the offspring sex ratio and maternal condition

Our first prediction that females of higher than average condition should bias their offspring sex ratio toward males was not supported because maternal body mass did not

correlate with the sex of her calf (Table 2 and Figure 2). However, the six lightest hinds (less than 45 kg) produced daughters exclusively (binomial test, $p = .015$). Further, among the factors known to affect maternal condition, neither primiparity nor the previous reproductive effort had a conspicuous effect on the progeny sex ratio (Table 2). Changes in population density did not influence the body mass of adult females (Bonenfant et al., 2002). Calf sex did not depend on the sex of the previous weaned young because sex ratio after the weaning of a male calf was 0.83 versus 0.5 after a female calf, (Fisher's exact test, $p = .5$, $n = 10$). Although very few hinds were available to compare the offspring sex ratio in relation to the sex of the previously weaned calf, the observed trend was reversed compared with what was expected. Indeed, under the hypothesis that males are costlier to raise than females, we should have observed a higher sex ratio in females that had previously weaned a female. Likewise, the proportion of male fetuses produced by females whatever their physical condition did not change in relation to density (Table 2). Owing to the small sample size, we were not able to test for all interactions between density and other factors. Some effects may have thus been overlooked because they lay within these interaction terms.

Tests of our second prediction were all rejected as no sex-biased maternal costs were detected either for pregnancy rates (expressed as a mean number of fetuses per hind) or body mass. Adult females that had previously weaned a male calf were not more likely to be barren the next year than were mothers that had weaned a female calf (pregnancy rates of 0.73 ± 0.11 versus 0.77 ± 0.13 for females that weaned a male and a female calf, respectively; $\chi^2 = 0.059$, $p = .80$, $n = 24$), nor did they weigh significantly less (59.0 ± 3.1 versus 58.4 ± 2.8 kg, $t = 0.271$, $p = .78$, $n = 46$).

Contrary to our third expectation, red deer hinds did not show any evidence of costs of reproduction relative to their body mass (60.0 ± 1.7 kg versus 58.0 ± 1.9 kg for milk and yeld hinds, respectively; $t = 1.6$, $p = .11$, $n = 97$) (Figure 3) or pregnancy rate (0.83 ± 0.09 versus 0.91 ± 0.07 for milk and yeld hinds, respectively; $n = 157$, $\chi^2 = 2$, df = 1, $p = .15$). Mean pregnancy rates were 0.90 ± 0.06 for multiparous females and 0.63 ± 0.15 for first breeding females ($\pm 95\%$ CI, irrespective of body mass), and only the latter was density dependent (Bonenfant et al., 2002). The trade-off between growth and reproduction was marginally significant for primiparous females: females that did not reproduce as yearlings were 3.4 kg heavier than those that had weaned a calf (54.9 ± 3.3 kg versus 58.3 ± 3.9 kg; $n = 27$, $t = -1.26$, $p = .05$ one-tailed test) (Figure 3).

DISCUSSION

In the present study, all the three assumptions of T&W's model were likely to be fulfilled. Maternal phenotypic quality was positively correlated with offspring phenotypic quality (Figure 1). This first assumption relies on the reliability of body mass to assess phenotypic quality, a criterion that was satisfied in the present study because of the strong correlation between structural size and body mass (see Methods). Trivers and Willard (1973) predicted that sex ratio should vary with mother quality, reflecting her capacity to invest in her young. Inadequate or unreliable measures of mother "quality" are likely to lead to misleading conclusions. For instance, offspring sex ratio was correlated to mother quality at conception but not during gestation in feral horses (Cameron et al., 1999a), to mother's age in mountain goats (Côté and Festa-Bianchet, 2001) and caribou (*Rangifer tarandus ssp.*, Thomas et al., 1989), and to mother's social rank in red deer (Clutton-Brock et al., 1986, Kruuk et al., 1999a) and Barbary sheep (*Ammotragus lervia*, Cassinello, 1996). Evidence for the second assumption, the relationship between offspring quality at the end of the maternal care period and during adulthood, is more equivocal. Early body mass was positively related to reproductive success or adult quality in red deer (Kruuk et al., 1999b), bighorn sheep (Festa-Bianchet et al., 2000), and fallow deer (Birgersson and Ekvall, 1997), but was not in bison (Green and Rothstein, 1991) and roe deer (Gaillard et al., 1993). Lastly, as a general rule, males of polygynous ungulates compete intensively for mating so that their reproductive success is influenced by their phenotypic quality to a greater extent than are females (third assumption; Hewison and Gaillard, 1999; for support on red deer, see Clutton-Brock et al., 1986; Rose et al., 1998). Because red deer seem to meet all assumptions of T&W's model (Hewison and Gaillard, 1999), we would expect high-quality females to invest more in sons than in daughters provided that environmental conditions are good enough to allow such an additional investment (Kruuk et al., 1999a).

Accordingly, several studies have suggested that mothers do invest differentially in the sexes (for reviews, see Clutton-Brock, 1991; Trillmich, 1996). For example, male-biased maternal costs in terms of subsequent reproductive success (Albon et al., 1983; Clutton-Brock, 1991; Monard et al., 1997), especially for subordinate females (Gomendio et al., 1990), male-biased suckling rates or milk transfer (Birgersson et al., 1998; Clutton-Brock et al., 1986; but see Cameron et al., 1999b; Ono and Boness, 1996), and higher body mass and growth rate for males than for females (Clutton-Brock et al., 1981, 1986; Glucksmann, 1974), have been reported. The strength of selection pressure for sex-biased investment will thus depend on the regression slope of calf condition against mother quality (Hewison and Gaillard,1999), which is expected to be steeper for males than for females (Birgersson and Ekvall, 1997). In red deer at PPNR, the regression slope did not differ between sexes either during the fetal stage or at weaning. The coefficients of the regression found in this study (male: 0.42 ± 0.14; female: 0.34 ± 0.14) are similar to those reported for reindeer (male: 0.328; female: 0.514; Kojola, 1993) but higher than those found in fallow deer (male: 0.25; female: 0.21; Birgersson and Ekvall, 1997), bighorn sheep (0.12 in both sexes; Festa-Bianchet and Jorgenson, 1998), and feral sheep (0.08 estimated from the birth mass; Clutton-Brock et al., 1996). Those comparative data suggest that deer mothers invest more in their offspring than ovids (Festa-Bianchet and Jorgenson, 1998). Contrary to the expectation, red deer hinds of higher than average quality do not seem to allocate more energy to sons than to daughters, as shown by the absence of a decrease in reproduction or body mass after
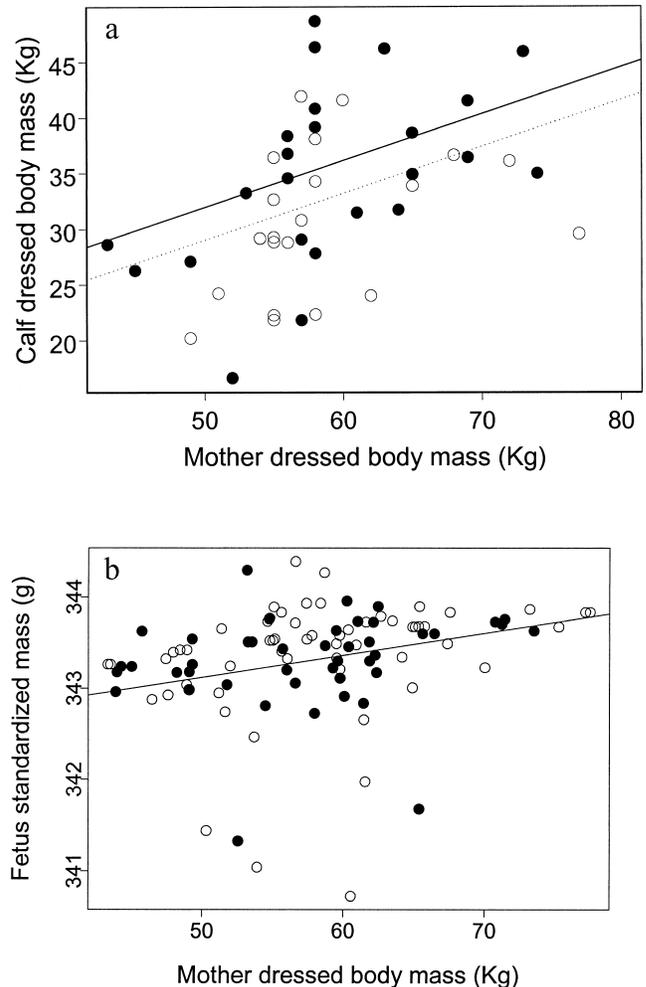

Figure 1
(a) Relationship between calf body mass at weaning and mother's body mass (males, filled circles; females, open circles). Calf body masses were standardized to 5 December (mean shooting date) to account for body growth that occurred during the hunting season ($F_{1,42} = 10.30$, $p = .002$, $R^2 = .19$). Straight and dotted lines are plots of the regression lines for male and female calves respectively. (b) Relationship between fetus mass (males, filled circles, $n = 51$; females, open circles, $n = 60$) and mother's body mass in autumn ($F_{1,107} = 659.35$, $p < .0001$, $R^2 = .85$). We standardized fetus masses by fitting the model: mass $= \alpha \times \text{age}^\beta$ with $\alpha = 0.0008$ and $\beta = 3.015$. We thus could remove the effect of gestation length. In both cases, calf sex did not influence the regression slope, meaning that good-quality hinds did not conceive or wean heavier male calves than did low-quality ones once maternal effect was taken into account.

rearing a son compared with a daughter. Similar results were found in other dimorphic species, including fallow deer (Birgersson, 1998), reindeer (Kojola, 1993), and mountain goat (Côté and Festa-Bianchet, 2001). Sex-specific differences in investment may depend on the absolute level of maternal investment (Birgersson, 1998; Byers and Moodie, 1990; but see Pélabon et al., 1995). In red deer that allocate a relatively low level of energy expenditure in reproduction (Pélabon et al., 1995), a higher investment in a son is expected under favorable conditions. However, unfavorable conditions could prevent females from providing an additional investment in their sons, leading to equal investment between sons and daughters.

We expected to find an effect of the previous reproductive

Table 2

Generalized linear model of fetal sex ratio according to mother's body mass, parity, the previous reproductive effort, and density

Models to be compared	Test for the effect of:	df	LRT	p
(1) MBM versus null model	Mother body mass	97	0.245	.62
(2) MBM × PRIM versus (3)	Interaction between body mass and primiparity	95	0.059	.80
(3) MBM + PRIM versus (1)	Main effect of primiparity	96	0.142	.70
(4) MBM × PRE versus (5)	Interaction between body mass and PRE	59	0.026	.60
(5) MBM + PRE versus (1)	Main effect of PRE	60	0.002	.96
(6) MBM × D versus (7)	Interaction between body mass and density	95	0.390	.53
(7) MBM + D versus (1)	Main effect of density	96	0.586	.44

Likelihood ratio test (LRT) corresponds to the difference in deviance between the two models to be compared. LRT follows a χ^2 distribution for which the df is calculated as the between model difference in the number of parameters. The null model corresponds to the simplest model with a constant fetal sex ratio. The final model selected is the constant model. MBM indicates mother's body mass (continuous); PRIM, parity (primiparous versus multiparous); PRE, the previous reproductive effort (yeld versus milk); and D, density (high versus low).

effort on fecundity or body mass (Albon et al., 1983 in red deer; Rutberg, 1986 in bison; Festa-Bianchet, 1989 in bighorn). We did not find such an effect for adult females. However, yearling females that did not reproduce were 3.6 kg heavier than those that did, illustrating the trade-off usually expected between growth and reproduction (Festa-Bianchet et al., 1995; Rutberg, 1986; Stearns, 1992). On the contrary, adult hinds were able to meet the high energy requirements of lactation (Sadleir, 1984), possibly by increasing foraging time (Watkins et al., 1991) or by selecting higher quality forage (Clutton-Brock et al., 1982b). The slightly poorer condition of nonlactating versus lactating females may only reflect the lower fertility of low phenotypic quality females (van Noordwijk and de Jong, 1986). Alternatively, the fitness costs of reproduction may not be limited to subsequent fecundity but may affect weaning success during the next breeding attempt (Bérubé et al., 1996).

On Rum, Kruuk et al. (1999a) suggested that the proportion of males produced by high-quality females decreased because of increasing losses of male fetuses with increasing nutritional stress resulting from high density or harsh climatic conditions. At PPNR, density did not influence female survival, and nearly all females gave birth to their first calf at 2 years of age (Bonenfant et al., 2002). On Rum, age at first calving was delayed by 2 or 3 years (Clutton-Brock et al., 1982a). Moreover, female calves and yearlings survived better at PPNR than on Rum (Bonenfant et al., 2002; Clutton-Brock et al., 1982a), suggesting higher resource availability and, hence, higher population performance at PPNR (Eberhardt, 1977). However, despite the marked change in density from 1983 onward, we did not find any relationship between sex ratio and mother quality at low population densities. Lastly, because body mass was not influenced by the mild climatic conditions of PPNR (Bonenfant et al., 2002) a higher rate of abortion of male fetuses, as reported in other red deer populations (Kruuk et al., 1999a; Mysterud et al., 2000), is unlikely to occur in the present study. We propose another explanation to account for the discrepancy between previous results and those reported from the present study. In the forest-dwelling red deer populations at PPNR, the magnitude
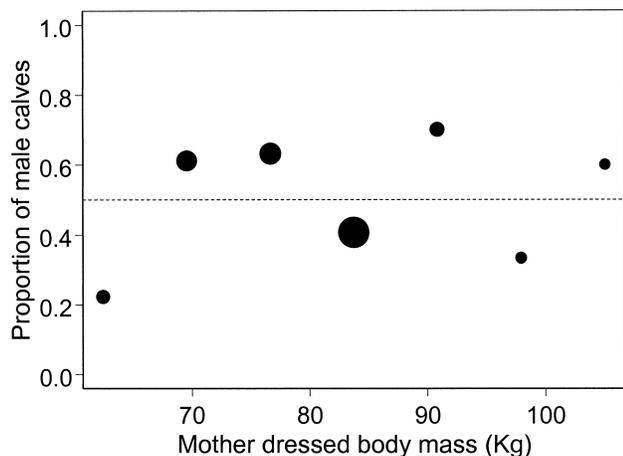

Figure 2
Relationship between fetal sex ratio (proportion of males) and mother's body mass during pregnancy in the Petite Pierre National Reserve, France ($n = 99$ hinds). The probability that a female conceived a male or a female calf did not vary with maternal body mass. Dot size is proportional to sample size. The straight line represents a sex ratio of 0.5.
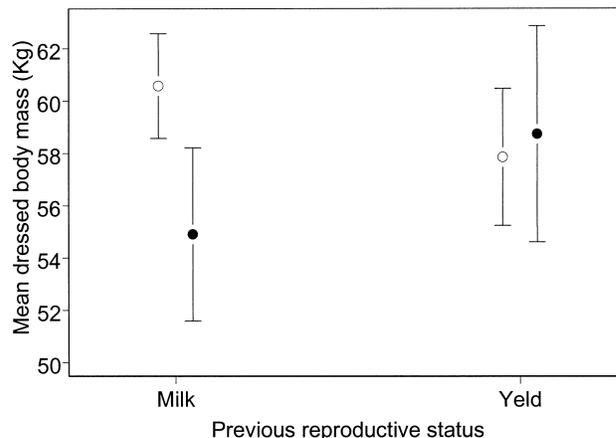
Figure 3
Effect of the previous reproductive status (milk versus yeld) on body mass for primiparous (filled circles) and multiparous (open circles) female red deer. Multiparous yeld hinds were not significantly heavier than milk ones, whereas primiparous yeld females (females that did not reproduce at 1.5 years) were 3.6 kg heavier than milk primiparous (females reproducing 1.5 years). Error bars show the 95% confidence interval of the observed mean body mass.

of sexual selection might be depressed because of the small party size occurring in such environments. In the present study, the median party size (defined as the number of deer aggregated in the same party in which no individual was more than 50 m from any other; see Clutton-Brock et al., 1982a) was 3.2 times lower than on Rum (two versus 6.4), meaning that access to reproductive females may be considerably enhanced in a forested area. Consequently, dominant males of high phenotypic quality cannot monopolize a large number of females and cannot exclude subordinate males from reproductive activities. Such a process could lead to a lower variance of male lifetime reproductive success (LRS). Hence, a high-quality son would not provide a higher fitness return than a high-quality female (Leimar, 1996), and bias in sex ratio would no longer be expected.

Even when support for adaptive variation in the sex ratio has been reported, the increase in the proportion of males with improving conditions is weak (Kruuk et al., 1999a; Mysterud et al., 2000). It is possible then that variation in sex ratio occurred at PPNR also but was too slight to be detected because of the small sample size. On the other hand, adaptive variations in sex ratio may not occur, and positive observed patterns might be the result of type I errors if all studies were to be considered (Festa-Bianchet, 1996; Palmer, 1999). Nonetheless, at the population level, our results are concordant with Fisher's (1930) theory, which predicts a sex ratio of 0.5 at the end of the parental investment if the fitness costs and return associated with the production of a male and a female offspring are the same(Maynard-Smith, 1980; for a similar conclusion on elephant seals, *Mirounga angustirostris*, see Le Boeuf et al., 1989).

REFERENCES

Albon SD, Mitchell B, Staines BW, 1983. Fertility and body weight in female red deer: a density-dependent relationship. J Anim Ecol 52:969–980.

Bérubé CH, Festa-Bianchet M., Jorgenson JT, 1996. Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. Behav Ecol 7:60–68.

Birgersson B, 1998. Adaptive adjustment of the sex ratio: more data and considerations from a fallow deer population. Behav Ecol 9:404–408.

Birgersson B, Ekvall K, 1997. Early growth in male and female fallow deer calves. Behav Ecol 8:493–499.

Birgersson B, Tillbom M, Ekvall K, 1998. Male-biased investment in fallow deer: an experimental study. Anim Behav 56:301–307.

Bonenfant C, Gaillard JM, Klein F, Loison A, 2002. Sex- and age-dependent effects of population density on life history traits of red deer (*Cervus elaphus*) in a temperate forest. Ecography 25:446–458.

Boyce MS, 1989. The Jackson elk herd. Cambridge: Cambridge University Press.

Brown GR, 2001. Sex-biased investment in nonhuman primates: can Trivers and Willard 's theory be tested? Anim Behav 61:683–694.

Byers JA, Moodie JD, 1990. Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. Behav Ecol Sociobiol 26:157–164.

Cameron EZ, Linklater WL, Stafford KJ, Veltman CJ, 1999a. Birth sex ratios relate to mare condition at conception in Kaimanawa horses. Behav Ecol 10:472–475.

Cameron EZ, Stafford KJ, Linklater WL, Veltman CJ, 1999b. Suckling behavior does not measure milk intake in horses, *Equus caballus*. Anim Behav 57:673–678.

Cassinello J, 1996. High-ranking females bias their investment in favour of male calves in captive *Ammotragus lervia*. Behav Ecol Evol 38:417–424.

Caughley G, 1977. Analysis of vertebrate populations. New York: Wiley.

Clutton-Brock TH, 1991. The evolution of parental care. Princeton, New Jersey: Princeton University Press.

Clutton-Brock TH, Albon SD, Guinness FE, 1981. Parental investment in male and female offspring in polygynous mammals. Nature 289:487–489

Clutton-Brock TH, Albon SD, Guinness FE, 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313:131–133.

Clutton-Brock TH, Albon SD, Guinness FE, 1986. Great expectations: dominance, breeding success and offspring sex ratios in red deer. Anim Behav 34:460–471.

Clutton-Brock TH, Guinness FE, Albon SD, 1982a. Red deer: behavior and ecology of two sexes. Chicago, Illinois: University of Chicago Press.

Clutton-Brock TH, Guinness FE, Albon SD, 1983. The costs of reproduction to red deer hinds. J Anim Ecol 52:367–383.

Clutton-Brock TH, Iason GR, 1986. Sex ratio variation in mammals. Q Rev Biol 61:339–374.

Clutton-Brock TH, Iason GR, Albon SD, Guinness FE, 1982b. Effects of lactation on feeding behaviour and habitat use in wild red deer hinds. J Zool 198:227–236.

Clutton-Brock TH, Sevenson IR, Marrow P, McColl AD, Houston AI, McNamara JM, 1996. Population fluctuations, reproductive costs and life history tactics in female soay sheep. J Anim Ecol 65:675–689.

Conover WJ, 1980. Practical nonparametric statistics, 2nd ed. New York: Wiley.

Côté SD, Festa-Bianchet M, 2001. Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*). Behav Ecol Sociobiol 49:260–265.

Eberhardt LL, 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environ Conserv 4:205–212.

Festa-Bianchet M, 1989. Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). J Anim Ecol 58:785–795.

Festa-Bianchet M, 1996. Offspring sex ratio studies of mammals: does publication depend upon the quality of the research or the direction of the results? Ecoscience 3:42–44.

Festa-Bianchet M, Gaillard JM, Jorgenson JT, 1998. Mass and density-dependent reproductive success and reproductive costs in a capital breeder. Am Nat 152:367–379.

Festa-Bianchet M, Jorgenson JT, 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behav Ecol 9:144–150.

Festa-Bianchet M, Jorgenson JT, Lucherini M, Wishart WD, 1995. Life history consequences of variation in age of primiparity in bighorns ewes. Ecology 76:871–881.

Festa-Bianchet M, Jorgenson JT, Réale D, 2000. Early development, adult mass, and reproductive success in bighorn sheep. Behav Ecol 11:633–639.

Fisher RA, 1930. The genetical theory of natural selection. Oxford: Oxford University Press.

Gaillard JM, Delorme D, Jullien JM, 1993. Croissance précoce et poids a l'entrée de l'hiver chez le faon de chevreuil (*Capreolus capreolus*). Mammalia 57:359–366.

Glucksmann A, 1974. Sexual dimorphism in mammals. Biol Rev Cambridge Phil Soc 49:423–475.

Gomendio M, Clutton-Brock TH, Albon SD, Guinness FE, Simpson MJ, 1990. Mammalian sex ratios and variation in costs of rearing sons and daughters. Nature 343:261–263.

Green WCH, Rothstein A, 1991. Trade-offs between growth and reproduction in female bison. Oecologia 86:521–527.

Guinness FE, Albon SD, Clutton-Brock TH, 1978. Factors affecting reproduction in red deer (*Cervus elaphus*) hinds on Rhum. J Reprod Fert 54:325–334.

Guinness FE, Lincoln GA, Short RV, 1971. The reproductive cycle of the female red deer (*Cervus elaphus*). J Reprod Fert 27:427–438.

Hamlin KL, Pac DF, Sime CA, Desimone RM, Dusek GL, 2000. Evaluating the accuracy of age obtained by two methods for Montana ungulates. J Wildl Manage 64:441–449.

Hardy ICW, 1997. Possible factors influencing vertebrate sex ratios: an introductory overview. App Anim Behav Sci 51:217–241.

Hewison AMJ, Andersen R, Gaillard JM, Linnell JDC, Delorme D, 1999. Contradictory findings in studies of sex ratio variation in roe deer (*Capreolus capreolus*). Behav Ecol Sociobiol 45:339–348.

Hewison MAJ, Gaillard JM, 1999. Successful sons or advantaged daughters? The Trivers-Willlard model and sex-biaised maternal investment in ungulates. Trend Ecol Evol 14:229–234.

Hiraiwa-Hasegawa M, 1993. Skewed birth sex ratios in primates: should high-ranking mothers have daughters or sons? Trend Ecol Evol 8:395–400.

James WH, 1998. Hypotheses on mammalian sex ratio variation at birth. J Theor Biol 192:113–116.

Jorgenson JT, Festa-Bianchet M, Lucherini M, Wishart WD, 1993. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. Can J Zool 71:2509–2517.

Kojola I, 1993. Early maternal investment and growth in reindeer. Can J Zool 71:753–758.

Kojola I, Eloranta E, 1989. Influences of maternal body weight, age, and parity on sex ratio in semi-domesticated reindeer. Evolution 43:1331–1336.

Kolman WA, 1960. The mechanism of natural selection for the sex ratio. Am Nat 94:373–377.

Krackow S, 1995. Potential mechanisms for sex ratio adjustment in mammals and birds. Biol Rev Camb Philos Soc 70:225–241.

Kruuk LEB, Clutton-Brock TH, Albon SD, Pemberton JM, Guinness FE, 1999a. Population density affects sex variation in red deer. Nature 399:459–461.

Kruuk LEB, Clutton-Brock TH, Rose KE, Guinness FE, 1999b. Early determinants of lifetime reproductive success differ between the sexes in red deer. Proc R Soc Lond Ser B 266:1655–1661.

Le Boeuf BJ, Condit R, Reiter J, 1989. Parental investment and the secondary sex ratio in northern elephant seals. Behav Ecol Evol 25:109–117.

Leimar O, 1996. Life-history analysis of the Trivers and Willard sex-ratio problem. Behav Ecol 7:316–325.

Lowe VPW, 1967. Teeth as indicator of age with special reference to red deer (*Cervus elaphus*) of known age from Rhum. J Zool 152: 137–153.

Martin P, 1984. The meaning of weaning. Anim Behav 32:1257–1258.

Maynard-Smith J, 1980. A new theory of sexual investment. Behav Ecol Sociobiol 7:247–251.

Mitchell B, Staines BW, Welch D, 1977. Ecology of red deer: a research relevant to their management. Cambridge: Institute of Terrestrial Ecology.

Monard AM, Duncan P, Fritz H, Feh C, 1997. Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. Behav Ecol Sociobiol 41:243–249.

Mysterud A, Yoccoz NG, Stenseth C, Langvatn R, 2000. Relationship between sex ratio, climate and density in red deer: the importance of spatial scale. J Anim Ecol 69:559–974.

Ono KA, Boness DJ, 1996. Sexual dimorphism in sea lion pups: differential maternal investment, or sex specific differences in energy allocation? Behav Ecol Evol 38:31–41.

Palmer RA, 1999. Detecting publication bias in meta-analyses: a case study of fluctuating asymmetry and sexual selection. Am Nat 154:220–233.

Pélabon C, Gaillard JM, Loison A, Portier C, 1995. Is sex-biased maternal care limited by total maternal expenditure in polygynous ungulates? Behav Ecol Sociobiol 37:311–319.

Post E, Forchhammer M, Stenseth NC, Langvatn R, 1999. Extrinsic modification of vertebrate sex ratios by climatic variation. Am Nat 154:194–204.

Reznick D, 1992. Measuring the costs of reproduction. Trends Ecol Evol 7:42–45.

Rose KE, Clutton-Brock TH, Guinness FE, 1998. Cohort variation in male survival and lifetime breeding success in red deer. J Anim Ecol 67:979–986.

Rutberg AT, 1986. Lactation and fetal sex ratios in American bison. Am Nat 127:89–94.

Sadleir RMFS, 1984. Ecological consequences of lactation. Acta Zool Fenn 171:179–182.

Searle SR, 1971. Linear models. New York: Wiley.

Seber GAF, 1982. Estimation for animal abundance and related parameters, 2nd ed. London: Griffin.

Skogland T, 1986. Sex ratio in relation to maternal condition and parental investment in wild reindeer *Rangifer t. tarandus*. Oikos 43:417–419.

Sokal RR, Rohlf FJ, 1981. Biometry, 2nd ed. San Francisco, California: Freeman.

Stearns SC, 1992. The evolution of life histories. New York: Oxford University Press.

Thomas DC, Barry SJ, Kiliaan HP, 1989. Fetal sex ratio in caribou: maternal age and condition effects. J Wildl Manage 53:885–891.

Trillmich F, 1996. Parental investment in pinnipeds. Adv Study Behav 25:533–577.

Trivers RL, Willard DE, 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 173:90–92.

van Noordwijk AJ, de Jong G, 1986. Acquisition and allocation of resources: their influences on variation in life history tactics. Am Nat 128:137–142.

Venables WN, Ripley BD, 1994. Modern applied statistics with S-PLUS. New York: Springer Verlag.

Watkins WG, Hudson RJ, Fargey LJ, 1991. Compensatory growth of wapiti (*Cervus elaphus*) on aspen parkland ranges. Can J Zool 69:1682–1688.

Wauters LA, De Crombrugghe SA, Nour N, Matthysen E, 1996. Do roe deer in good condition produce more sons than daughters? Behav Ecol Evol 37:189–193.

Williams CG, 1979. The question of adaptive sex ratio in outcrossed vertebrates. Proc R Soc Lond B 205:567–580.