Adaptive adjustment of offspring sex ratio and maternal reproductive effort in an iteroparous mammal

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Large mammals in seasonal environments have a pattern of high-reproductive synchrony in spring, but how the timing of reproduction affects resource allocation decisions at different stages of the reproductive cycle remains largely unexplored. By manipulating the timing of conception in reindeer (*Rangifer tarandus*), we tested how the timing of conception affected sex ratio, gestation length and weight development of mother and offspring. Females that conceived at their first ovulation within the rut had a 60.5% probability of producing a male; in contrast, females that conceived a cycle later had a 31.3% probability of producing a male. Late conceiving females had gestation times that were 10 days shorter and the calves were 0.6 kg (9.2%) lighter at birth and 7.4 kg (14.7%) lighter in autumn. Over the year, female weight changes was similar between the groups suggesting reindeer follow a bet-hedging strategy; reducing the quality of this year's offspring to ensure their own future reproduction and survival. Harvesting is often selective leading to skewed sex ratios and age structure, which may influence the timing of reproduction due to females hesitation to mate with young males. Whenever this hesitation is strong enough to increase the frequency of recycling, harvesting is likely to have profound life history consequences.

Keywords: bet-hedging strategy; gestation; seasonality; Trivers–Willard model; ungulates

1. INTRODUCTION

The Trivers–Willard model (TWM; Trivers & Willard 1973) of optimal sex ratio adjustment predicts that, in polygynous species, mothers in poor condition should produce offspring sex ratios biased towards females, with the converse true for mothers in good condition (review in Hewison & Gaillard 1999). Because large mothers produce large offspring (Weladji *et al.* 2003; Loison *et al.* 2004), in species where mass is a measure of condition, large mothers should produce more males than females. Factors other than mother's condition, however, can influence offspring size: the timing of conception and birth in ungulates is associated with offspring condition (Bunnell 1982; Festa-Bianchet 1988; Côté & Festa-Bianchet 2001). These differences at birth can persist throughout life (review in Lindström 1999), with late-born offspring typically smaller in autumn than those born earlier in the year (Eloranta & Nieminen 1986; Holand *et al.* 2003). Consequently, the TWM can be used to predict that females conceiving late should produce more females, as in highly dimorphic and polygynous species,

birth size is less correlated with fitness in females than in males (Kruuk *et al.* 1999).

Among placental mammals a widely accepted theory is that gestation lengths vary little intra-specifically (Kiltie 1982, 1988), and that the timing and synchrony of births occurs by adjustment of the timing of ovulation (Langvatn *et al.* 2004). Late ovulation is, therefore, expected to provide the next year's offspring with a poor start in life, as late-born offspring are smaller in autumn and thus more likely to die during their first winter (Hogg *et al.* 1992; Langvatn *et al.* 2004). Mothers allocating extra resources to offspring that then achieve large body sizes typically increase their offspring's chances of surviving harsh winters (review in Gaillard *et al.* 2000). However, prolonging offspring investment too much into the autumn may lower the mother's own performance and hence her ability to ovulate sufficiently early during the next reproductive cycle (Hogg *et al.* 1992).

All deer species except roe deer *Capreolus capreolus* (Sempere *et al.* 1998) have repeated oestrus within a breeding season with a mean interval between two consecutive oestruses of about 18 days (Guinness *et al.* 1971; Putman 1988). However, the life history

consequences of late conception in synchronously breeding species has not to date been investigated using an experimental approach. Using a research herd of semi-domestic reindeer—the species used by Trivers & Willard (1973) to illustrate their adaptive sex ratio theory—we experimentally manipulated conception date. Fertile adult males were introduced to one-half of the herd, while the other half of the herd was exposed to males that had undergone vasectomies. Mating then occurred. The two classes were then reunited and females that had not conceived had an opportunity to conceive in a later cycle. We tested the consequences of this manipulation of the timing of conception on sex ratio, gestation length and weight development of mother and offspring over the reproductive cycle.

2. MATERIAL AND METHODS
(a) *Study area and research herd of reindeer*
The study was carried out at the Kaamanen Experimental Reindeer Station in Finland (69° N, 27° E; Holand *et al.* 2003; Mysterud *et al.* 2003). The total area of 43.8 km² is fenced and sub-divided into several smaller enclosures. This study was conducted in the northwest (Lauluvaara, 13.8 km²) and southeast section (Sinioivi, 15 km²). Birch (*Betula* spp.) and pine (*Pinus sylvéstris*) forests with numerous lakes and bogs dominate the habitat in these areas. The habitat composition is similar in the two enclosures. The experimental herd is given supplementary feeding during winter only (Holand *et al.* 2003).

(b) *Experimental design*
During the rut of 2003, we manipulated the timing of conception by exposing half of the female herd ($n=51$) to four vasectomized males (one 1.5 year old male, one 2.5 year old male and two 3.5 years old) kept in the Lauluvaara enclosure, while keeping four intact males (one 1.5 year old male, one 2.5 year old male and two 3.5 years old) together with the other half of the female herd ($n=49$) in the Sinioivi enclosure. The female segment was kept similar with respect to age and weight structure between treatments. After the first ovulation cycle, the female herds were joined in Sinioivi together with the four intact males. Thus, the females reovulating were inseminated by the same males that fertilized half of the female herd in first ovulation. We confirmed this with paternity analyses (details on methodology in Røed *et al.* 2002). During the rut, we followed the herd by direct observation to determine date of copulation. As this is very difficult in the large enclosures, sample sizes involving copulation dates are smaller than the number of females present.

Females are all aged and individually marked and were weighed (to the nearest kilogram) before (11 September) and after (7 November) the rutting season of 2003. Additionally, individuals were weighed every month throughout the winter, the last time before calving being 7 April 2004 when they were confined to a calving paddock (about 50 ha). The calving area was searched every morning and evening and newborn calves were caught by hand after the mother had licked them dry, weighed with a steelyard to the nearest 0.1 kg, ear-marked with numbered ear-tags and sexed. All animals, both calves and their mothers, were weighted on the 11th June before being released into their larger summer enclosure.

The animals were again rounded up on 13 September 2004 and weighed.

DNA marker analysis revealed that 13 females were fertilized by two of the assumed vasectomized males in Lauluvaara during first ovulation. This failure in the sterilization procedure led to 13 calves of the 'late conceiving' herd actually conceiving in the early conception period, all of which we excluded from analyses (explaining the slightly smaller sample size of the late conceiving herd).

(c) *Statistical analyses*
We used a combination of generalized linear models (GLM, McCullagh & Nelder 1989), generalized linear mixed-effects models (LME and GLMM, Crawley 2003), and generalized additive models (GAM, Hastie & Tibshirani 1990) to estimate the effect of conception period (early versus late) on variation in performance of reindeer. To all models, we added both female age and weight to avoid possible bias, as these factors have been reported to be important for female performance in other studies of deer (e.g. Langvatn *et al.* 2004). For the sex ratio analysis, we tried both female weights before rut and close to the time of conception (i.e. using weight at a later date for late conceiving females). The effect of female age on reproduction is typically nonlinear (peaking at prime-age, Gaillard *et al.* 1998), and we tried both a second and a third order term for age. However, the way female age was modelled did not affect the factor of interest (conception period). Whenever we considered repeated measurement of the same individual, we used LME with female identity as a random factor to account for non-independency of observations. In the model of sex ratio variation, the first alternative would be to assume a binomial distribution. Any violation of the assumption of independence will lead to unaccounted heterogeneity, what is termed overdispersion indicating a poor model fit. Overdispersion is assessed by statistical significance of the residual deviance (i.e. the goodness-of-fit statistic) of the fitted model. As we found evidence of overdispersion in initial modelling attempts assuming a binomial error distribution, we turned to a quasi-likelihood test that need not correspond to any particular distribution, and which can be used to combine any available link and variance function (Venables & Ripley 1994). There was no evidence of overdispersion when using a quasi-likelihood link ($\chi^2_{64}=65.129$, $p=0.437$), i.e. the model fitted the data appropriately. We also ran a GLMM fitting male ID as a random term (using library 'MASS' in R) to control for the possibility of individual males consistently produced biased sex ratio.

3. RESULTS
As predicted, conception date had a strong influence on offspring sex ratio. Females that conceived at their first ovulation within the rut had a 60.5% probability of producing a male, while females that conceived a cycle later had a 31.3% probability of producing a male (tables 1*b* and 2). There was only a tendency for heavy mothers (weighed before rut; on 11 September) to produce more males (table 1), this result was similar when using weight closer to time of conception: 11 September for early breeders; 22 October for late breeders). Females were on average in poorer condition during the second ovulation cycle (80.0 kg on 11 September versus 77.9 kg on 7 November LME,

Table 1. Results from analysis on how date of copulation affected (*a*) gestation length (days), and how conception period (late versus early) affected (*b*) offspring sex ratio (proportion of males), (*c*) weight (kg) of offspring at birth and (*d*) during autumn (11 September 2003) and (*e*) female weight (kg) variation over the entire reproductive period (autumn year 2003 via spring year 2004 to autumn year 2004. (Thus, the interaction term for 'conception period (early versus late) × time (sp04 versus au03)' indicate that weights are different during spring. For analysis (*e*), female identity was fitted as a random factor in a linear mixed-effects model. Exact dates for weighing in autumn 2003 it was 11 September, for spring 2004 it was 11 June and for autumn 2004 it was 13 September.)

parameter	l.s. mean	standard error	d.f.	T	p
(a) gestation length					
intercept	339.6	20.7	13	16.382	<0.001
Julian date of conception	−0.41	0.062	13	−6.718	<0.001
calf sex	22.53	10.02	13	2.247	0.043
female weight (autumn 2003)	−0.015	0.12	13	−0.127	0.901
(b) sex ratio					
intercept	−1.04	3.66	65	−0.285	0.777
late versus early conceiving	−1.21	0.55	65	−2.194	0.032
female weight (autumn 2003)	0.020	0.048	65	0.415	0.680
female age	−0.026	0.104	65	−0.254	0.800
(c) calf weight—birth					
intercept	1.03	0.21	58	4.873	<0.001
calf sex (male versus female)	0.036	0.029	58	1.212	0.230
age	0.19	0.081	58	2.334	0.023
$(age)^2$	−0.0259	0.0122	58	−2.126	0.038
$(age)^3$	0.0011	0.0006	58	1.945	0.057
female weight (autumn 2003)	0.0050	0.0025	58	1.958	0.055
conception period (late versus early)	−0.096	0.029	58	−3.294	0.002
(d) calf weight—autumn 2004					
intercept	3.20	0.18	51	17.919	<0.001
calf sex (male versus female)	0.082	0.022	51	3.802	<0.001
age	0.23	0.088	51	2.667	0.010
$(age)^2$	−0.033	0.015	51	−2.226	0.031
$(age)^3$	0.0014	0.0007	51	1.885	0.065
female weight (autumn 2003)	0.0022	0.0019	51	1.209	0.232
conception period (late versus early)	−0.16	0.023	51	−7.058	<0.001
(e) female weight					
intercept	4.25	0.035	142	120.745	<0.001
age	0.035	0.012	73	2.800	0.007
$(age)^2$	−0.0017	0.00096	73	−1.719	0.090
conception period (late versus early)	−0.014	0.017	73	−0.846	0.401
time (spring 2004 versus autumn 2003)	−0.061	0.0091	142	−6.695	<0.001
time (autumn 2004 versus autumn 2003)	0.052	0.0093	142	5.592	<0.001
conception period (late versus early) × time (spring 2004 versus autumn 2003)	0.051	0.014	142	3.583	0.001
conception period (late versus early) × time (autumn 2004 versus autumn 2003)	0.019	0.014	142	1.294	0.198

$p < 0.001$; no difference between early and late breeders; $p = 0.30$; and no interaction between 'weight' and 'conception period', $p = 0.78$). The interaction between female age and conception period ($T = 1.231$, $p = 0.222$) was far from significant when added to the sex ratio model. An overview of male paternities in the first and second conception period is given in table 3. One younger male was more involved in the last rut and produced a very female-biased sex ratio. When including father ID as a random term, the effect of conception period on sex ratios was still significant (GLMM; $Z = -2.233$, $p = 0.029$), but not when adding also father age as a fixed effect ($Z = -0.883$, $p = 0.381$).

Female reindeer conceiving late shortened their gestation by approximately 10 days (figure 1*a*, $n = 18$, $r^2 = 0.85$). Mean date of birth for early and late breeders was, respectively, 19 May and 30 May, and thus more synchronous than expected from conception times.

Late conceiving females produced lighter offspring (figure 1*b*, tables 1*c* and 2, $n = 67$, $r^2 = 0.41$). Average weight of offspring born from early conceiving females was 6.4 kg (for a 5 yr old female weighing 80 kg), as compared to offspring of late conceiving females that weighed only 5.8 kg (table 1*c*, no interaction 'sex' and 'time of breeding'; $p = 0.65$). This means that on a given date in early summer (11 June 2004, figure 1*c*), the weight difference was considerable: calves from early and late breeders weighing, respectively, 15.6 versus 10.37 kg (a 34% difference).

Late conceiving females lost less weight from September to June (mainly gestation period, early lactation period for early breeders). However, late breeders increased reproductive effort during late summer (post natal period, mainly lactation period). Even with this increased energy expenditure, the absolute difference in the weight of calves between early and late conceiving females was similar during autumn (13 September 2004; 50.4 kg versus

Table 2. An overview of life history consequences of early and late conception for reindeer in Kaamanen, Finland, based on predicted values from models in table 1.

parameter	early conception		late conception		difference	
	mean	s.e.	mean	s.e.	absolute (early–late conception)	relative (%)
sex ratio (prop. of males)	0.60	0.08	0.31	0.10	0.29	48.24
offspring birth weight (kg)	6.42	1.03	5.83	1.03	0.59	9.18
offspring autumn weight (kg)	50.40	1.03	42.97	1.02	7.43	14.70
female weight (kg)—autumn 2003	80.13	1.13	78.98	1.15	1.14	1.43
female weight (kg)—spring 2004	75.38	1.14	78.19	1.18	-2.81	3.73
female weight (kg)—autumn 2004	84.40	1.14	84.75	1.18	-0.36	0.42

Table 3. An overview of paternities and offspring sex ratios per individual males in early and late conception period for reindeer in Kaamanen, Finland. (The numbers in the female and male columns represent the numbers of each sex born to each male.)

male identity	age	1st conception period			2nd conception period		
		female	male	sex ratio	female	male	sex ratio
RC-06	3.5	7	9	56.25	1	1	50.00
RC-10	3.5	10	14	58.33	5	4	44.44
RC-08	2.5	1	1	50.00	5	3	37.50
RC-02	1.5				7	1	12.50
total		18	24	57.14	18	9	33.33

43.0 kg, tables 1*e* and 2, $n = 60$, $r^2 = 0.59$). Over the year, female weight change was similar (tables 1*e* and 2) in both early and late breeders.

The tactic of not breeding or failure to breed was rare among adult females; 1 out of 45 in the early breeding enclosure and 2 out of 31 in the late breeding enclosure did not breed.

4. DISCUSSION

Our study provides the first evidence based on an experimental manipulation that the cycle in which conception occurs influences the life history of an iteroparous mammal.

Late conceiving females produced a more female-biased offspring sex ratio, as may be expected from theoretical arguments (see §1). Recent evidence based on meta-analyses suggests that studies using female condition at conception often report sex ratio variation consistent with the TWM (Cameron 2004; Sheldon & West 2004). Females, through an unknown mechanism (see discussion in Cameron 2004) are, therefore, presumably able to assess their own condition and the consequences of conceiving at different times. Females were indeed on average in poorer condition during the second ovulation cycle, but individual female weight was not a significant predictor of offspring sex (though the estimate was in the predicted direction). It has also been suggested that if individual males produce biased X- or Y-chromosome ejaculates, this may lead to biased sex ratios (DeYoung *et al.* 2004). In white-tailed deer (*Odocoileus virginianus*), individual males did not produce biased ejaculates nor did ratio of X- and Y-sperm differ depending on collection period (DeYoung *et al.* 2004). However, several studies indicate that younger males are

more active during the later part of the rut (Prothero *et al.* 1979; Noyes *et al.* 1996), and thus that male age may potentially affect sex ratio if young males produce more X-sperm or via sperm selection in the uteri. In moose (*Alces alces*), male age was found to be a significant predictor of offspring sex ratio, with prime-aged males siring more male offspring (Sæther *et al.* 2004). Our data was not decisive in this respect; as there was a tendency for younger males to be more involved in the last rut and siring more female offspring (table 3). Clearly, further replication is required before the generality of this result can be determined with confidence.

While the exact physiological mechanisms involved in sex ratio variation remain elusive, evolutionary models such as the TWM are intended to assess the pattern of variation in sex ratio rather than the mechanism. Thus, the selection pressure is the more important for the TWM and other evolutionary-based models. A common weakness with much of the work on sex ratios is indeed the failure to link patterns of variation with selection. The critical issue of understanding the direction of the shift depends on knowledge of which sex gains relatively more by being large (Charnov *et al.* 1981; Leimar 1996), and in our case equivalent to being born early (table 2). There is considerable evidence that birth size is more important for future survival (Loison *et al.* 1999*b*) and reproductive success of males than females (Clutton-Brock *et al.* 1988). For red deer on Rum

> birthweight was a significant determinant of total lifetime reproductive success in males, with heavier-born males being more successful than lighter ones. In contrast, birthweight did not affect female reproductive success
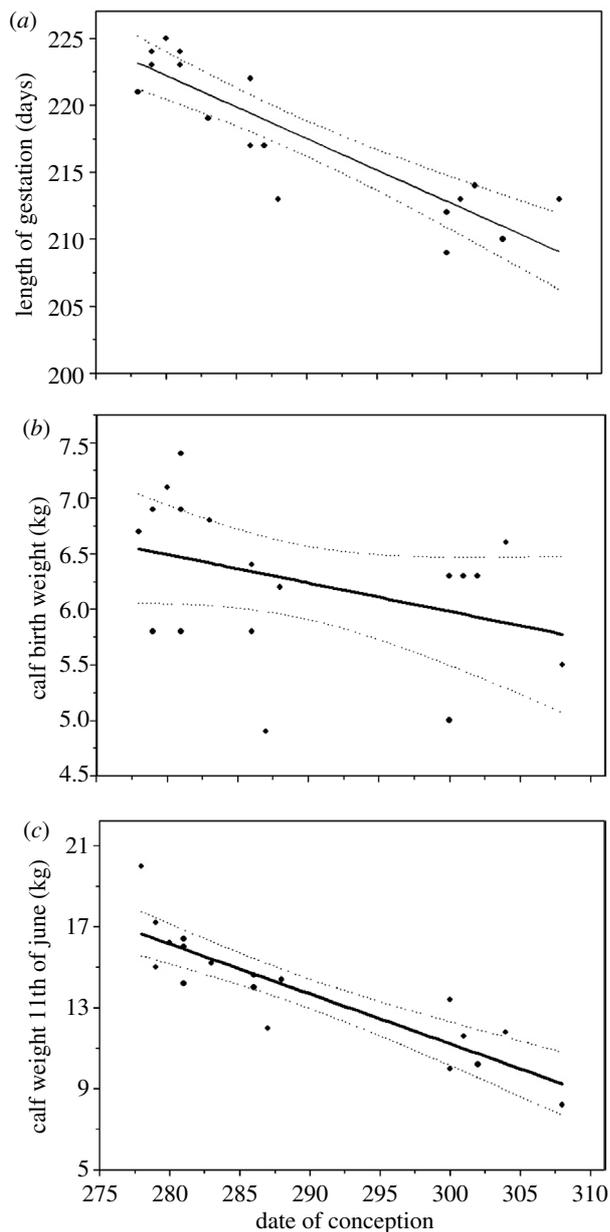>
> (Kruuk *et al.* 1999 p. 1655).

Figure 1. The relationship between conception date (Julian date) and (*a*) gestation length (days), (*b*) birth weight and (*c*) offspring weight on 11 June 2004 for reindeer in Kaamanen, Finland. Data are from a smaller sub-sample of females for which date of copulation was observed.

Reindeer and red deer have a similar life history and a similar degree of sexual body size dimorphism (Weckerly 1998; Loison *et al.* 1999*a*), and both species have been shown to fulfill the underlying assumptions of the TWM (Hewison & Gaillard 1999). There is thus ample evidence that males benefit more from being born early than females in highly polygynous, sexually dimorphic ungulates (Hewison & Gaillard 1999), and thus that the selection pressure behind the observed sex ratio variation is as expected in reindeer. Therefore, a beneficial strategy for females may be to reduce the reproductive costs of late conception by producing a female calf rather than a male calf.

Our study provides new insight into how iteroparous mammals in seasonal environments solve the trade-off between investment in current year offspring versus future reproduction and survival. Comparative studies indicate

that adult survival in mammals varies little between years while juvenile survival can vary substantially (Gaillard & Yoccoz 2003). The contrasting responses of juvenile and prime-age survival to environmental variation in ungulates is considered to originate from the way females partition resources between offspring production and self maintenance, and could be viewed as a bet-hedging strategy (Gaillard & Yoccoz 2003). Our results provide support for this because female weight changes over the year were similar between the groups (table 2), while quality of offspring differed between female groups (table 2). Reindeer thus follow a bet-hedging strategy, and can both reduce the quality (weight) and potential cost (sex) of this year's offspring to ensure their own future reproduction and survival.

Our manipulation further revealed phenotypic plasticity in gestation length. Female reindeer conceiving late increased their probabilities of gaining sufficient condition to breed next year by shortening their gestation by approximately 10 days (figure 1*a*). That females can reduce gestation length by up to ~6 days has previously been shown for bison (*Bison bison*) cows in good condition (Berger 1992). Following dry summers, pronghorn antelope (*Antilocapra americana*) also prolonged gestation with between one and 10 days depending on age (Byers & Hogg 1995). Lactation is the most energy demanding part of reproduction (Clutton-Brock *et al.* 1989), and it is regarded as very important to have high plant quality available during this stage. It is, thus, likely that the reduction in gestation length was also a way to ensure better use of plant quality during periods of intense lactation. Nevertheless, there was a penalty of such short gestation length in terms of lighter offspring (table 2, figure 1*b,c*). Late born offspring also experienced a shorter growth period before winter, attained a lower body mass at the onset of winter and, therefore, had a decreased expectation of survival compared to early born calves (Festa-Bianchet *et al.* 1997). As argued above, this effect is typically stronger in males than females in sexually size dimorphic species (Kruuk *et al.* 1999; Loison *et al.* 1999*b*). Late conceiving females lost less weight from September to June (mainly gestation), probably because early breeders had experienced a longer period of lactation at this time. However, late breeders increased reproductive effort (as evidenced from weight changes) during late summer (post natal period), when they were also lactating. Even with this increased energy expenditure, the absolute difference in the weight of calves between early and late conceiving females was similar during autumn.

Virtually all populations of large herbivorous mammals in the temperate and sub-arctic zones are exposed to human manipulation through harvesting and poaching. Further, harvesting is usually sex- and/or age-biased affecting the remaining age and sex structure of the population (Langvatn & Loison 1999). Such a change influences the dynamics of the rut, since females will not mate with a young male if a larger, more dominant male is available (Komers *et al.* 1999, review in Mysterud *et al.* 2002). A skew in sex ratio and/or in the male age structure may thus result in delayed and less synchronous conception reflected in the calving season (Mysterud *et al.* 2002; Holand *et al.* 2003; Sæther *et al.* 2003), although we found that the females may try to compensate through shortening gestation length. Under natural

conditions in our reindeer population (i.e. in the years before the experiment), only 4.5% of the females recycled (Holand *et al.* 2003). We still lack good quantification of if and how much harvesting increases recycling rates. A key question is whether the hesitation to mate with young males is strong enough to increase the frequency of recycling. If recycling becomes more frequent due to harvesting, there may be opposing selection on the sex ratio to balance the overall population sex ratio. Our study underlines the potential strong effect on the life history if sex ratios become as skewed as that currently is observed in heavily harvested populations.

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