

Maternal age and offspring sex ratio variation in reindeer (*Rangifer tarandus*)

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Different evolutionary hypotheses have been proposed to explain variation in offspring sex ratios among mammalian populations. The Trivers and Willard and local resource competition hypotheses, which are based on adaptive modification by maternal investment, are two opposing hypotheses commonly used for ungulates, but empirical patterns often do not fit either hypotheses' expectations. We investigated sex ratio variation in 1658 reindeer (*Rangifer tarandus*) calves in relation to their mothers' mass and age, while accounting for potential density-independent factors such as climate. The most parsimonious model included only the effect of maternal age, the proportion of males increasing with increasing maternal age. Similar models in terms of parsimony included (in addition to maternal age) the winter temperature or the North Atlantic Oscillation (NAO) index when the mothers were *in utero*, indicating that climatic conditions experienced by mothers in their year of birth, have the potential to influence variation in a cohort's offspring sex ratio. Thus, a combination of both density-dependent and density-independent factors may influence sex ratio variation in reindeer and perhaps in other ungulates. We suggest that, if an adaptive maternal strategy is present, it may be induced and/or inhibited by, or interact with other factors such as climate.

Introduction

Fisher (1930) argued that sex ratios are self-adjusting through frequency-dependent selection, which should favour one-to-one sex ratios if the fitness costs of producing males and females are equal. Since then, several studies have reported variation in ungulates' sex ratios (reviews in Clutton-Brock & Iason 1986, Festa-Bianchet 1996, Hewison & Gaillard 1999), most

of them reporting contrasting results (Hewison & Gaillard 1999). Generally, two adaptive modifications of maternal investment have been proposed to explain the variation in offspring sex ratios among ungulates, the Trivers and Willard (1973) and the local resource competition (Clark 1978) hypotheses. Trivers and Willard (1973) used caribou/reindeer (*Rangifer tarandus*) as an example of a polygynous species in which one could expect females to manipulate their

investment in sons and daughters based on their physical condition, mothers in good condition producing more sons. The local resource competition hypothesis (Clark 1978), however, predicts that females in poor condition will produce more sons, because sons will emigrate and therefore are less likely than daughters to compete for resources in the mother's home range.

Reindeer is a polygynous and sexually dimorphic species in which males' fighting ability is closely related to body mass (Kojola 1989), age (Kojola 1989, Skogland 1989) and antler development (Hirotani 1990), and largely determines their access to receptive females (Hirotani 1994). Male fitness is therefore highly variable and related to early growth rates; and hence the mothers' ability to invest in reproduction, since body size correlates with early growth rates and tends to endure into adulthood (Reimers 1997). Both Trivers and Willard's (1973), and the local resource competition hypotheses (Clark 1978) have triggered an array of empirical studies that produced contradictory findings not only in reindeer and caribou (*see* Reimers 1999 for examples), but also in other ungulates (*see* Hewison & Gaillard 1999 for examples). Reviews of sex ratio variations and maternal investment in mammals emphasised this inconsistency (Clutton-Brock & Iason 1986, Frank 1990, Hewison & Gaillard 1999), and several explanations may be suggested for this inconsistency, including the role of climate.

Climate variables have been demonstrated to affect offspring or calf sex ratios in red deer *Cervus elaphus* (Kruuk *et al.* 1999, Post *et al.* 1999, Mysterud *et al.* 2000) and reindeer (Weladji & Holand 2003). Moreover, because life history predicts that reproductive effort is age-related in reindeer (Weladji *et al.* 2002b) and other ungulates (*see e.g.* Mysterud *et al.* 2001), the importance of maternal age (*e.g.* Côté & Festa-Bianchet 2001) and lifetime reproductive success (Gaillard *et al.* 2000) has been increasingly considered. More recently, Saltz (2001) suggested that maternal age is the predominant determinant (more than, for example, environmental conditions) of progeny sex ratio among ungulates. He argued that prime-age mothers produced predominantly male offspring while young and old mothers produced an excess of females and that this can be explained by a modification

of the Trivers and Willard hypothesis. In a reply to Saltz, Hewison *et al.* (2002) demonstrated that maternal age is not a predominant determinant (but rather a correlate) of progeny sex ratio variation in ungulates. It is thus of interest to examine the relationship between sex ratio variation and maternal mass and age while accounting for environmental variables (*e.g.* Kruuk *et al.* 1999).

In this paper, we consider recent advances regarding density-independent climatic effects on sex ratio variation in reindeer (Weladji & Holand 2003), by controlling for mother's cohort-weather related effect in our analyses. We used a relatively large data set and adequate analytical tools to investigate whether female body mass and age, as indicators of physical condition and social status, affect calf sex ratio within a population of semi-domestic reindeer.

Methods

Reindeer data

We used data from a study on one semi-domestic reindeer population from Riast/Hylling grazing district, south-central Norway (Lenvik *et al.* 1988), where no supplemental feeding is applied. Body mass of 1969 females of known age was recorded in March 1984. Based on 1658 known mother-calf relationships in mid-July, the sex and body mass of calves were determined. The sex ratio, defined as percentage of male calves for each mother's cohort, was then established. The age of the females were known exactly because all animals from the herd had been tagged as calves. In this paper, the correct female age in March is around 2 months less than the actual stated age, because reindeer are generally born in May. Reindeer is monotocous, giving birth normally to one offspring. The mother-calf relationship was established based on which female the calf was following.

The social status of reindeer has a major effect on access to winter food resources that are distributed in patches (Skogland 1989, Hirotani 1990) and abortions occur mainly when reindeer are under severe nutritional stress (Tyler 1987). However, the calving success (percent of females with calf as measured in June during

the calf-marking) in this population was above 90%, due to the good condition of the range (D. Lenvik pers. comm.). Kojola and Eloranta (1989) found no indices of selective abortion in the supplementary fed Kaamanen herd. We therefore suggest that given the rather good range condition of the Riast/Hylling grazing district (Reindrifftsforvaltningen 2001), there cannot be large selective foetal mortality, indicating that the sex ratios observed in mid-July are closely related to the primary sex ratios.

Climatic data

After identifying the winter area of the studied population, we obtained climatic records from the nearest weather stations, namely Røros and Drevsjø. Based on previous work relating weather to northern ungulates phenotypic traits (review in Weladji *et al.* 2002a), we selected total precipitation, average temperature and maximum snow depth for the period December–March to characterize winter weather patterns. Local weather data were obtained from the Norwegian Meteorological Institute, Oslo. Additionally, we used Hurrell's winter (December to March) North Atlantic Oscillation (NAO) index, as a large-scale measure of global winter weather (<http://www.cgd.ucar.edu/~jhurrell/nao.html>) (Hurrell 1995), because this has been shown to influence offspring sex ratio in both reindeer (Weladji & Holand 2003) and red deer (Post *et al.* 1999, Mysterud *et al.* 2000). Detailed description of the NAO index and its influence on phenotypic and demographic traits for ungulates can be found in Post and Stenseth (1999), Mysterud *et al.* (2000) and Weladji *et al.* (2002a). All weather variables (local and global) are for the mother's year of birth because variable environmental conditions around birth have the potential to create fitness differences among cohorts and this advantage/disadvantage can persist into adulthood among ungulates (*see e.g.* Reimers 1997, Forchhammer *et al.* 2001). In the 20 years period including this study (1971–1990), winter temperature variation was closely correlated in space ($r_{\text{Drevsjø,Røros}} = 0.99$), but not winter precipitation ($r = 0.19$) or winter snow depth ($r = 0.31$). Reflecting this pattern, the

winter NAO index was positively correlated to temperature ($r = 0.68$ for Drevsjø and Røros), but weakly correlated to precipitation (Drevsjø: $r = 0.08$; Røros: $r = 0.31$) and snow depth (Drevsjø: $r = -0.23$; Røros: $r = 0.06$). Maximum snow depth and winter precipitation were more closely correlated (Drevsjø: $r = 0.58$; Røros: $r = 0.76$) than snow depth and winter precipitation were (Drevsjø: $r = -0.33$; Røros: $r = -0.26$). We therefore incorporated winter temperature, maximum snow depth at both stations and the winter NAO index in our analyses.

Statistical analyses

We used logistic regression to investigate how calf sex ratio depended on climatic variables, maternal age and maternal body mass. The best model was selected on the basis of the Akaike's Information Criterion (AIC; Akaike 1973, Burnham & Anderson 1998), the best model being the one with the smallest value for AIC (the sample size being large, we did not use the small sample size correction). Effect of body mass was assessed by using either body mass or the residuals of a non-parametric (lowess) regression of body mass on age (Venables & Ripley 1999), as body mass depends non-linearly on age (Weladji *et al.* 2002b). We investigated the existence of non-linear relationships by using additive generalised models (Hastie & Tibshirani 1990; *see e.g.* Mysterud *et al.* 2001). We assessed the goodness of fit of the models by considering frequency data of sex ratio by age (*i.e.*, not the individual observations of calf sex ratio), as goodness of fit is difficult to assess for 0/1 observations. We also provided the AIC weights, which are measures of the relative likelihood of the different models (Burnham & Anderson 1998, 2001). We performed Likelihood Ratio Test for testing the effect of single variables in the most parsimonious model. We used the statistical package S-plus (Venables & Ripley 1999) for all analyses.

Results

The best model to predict calf sex ratio was a model including maternal age only (Table 1). The

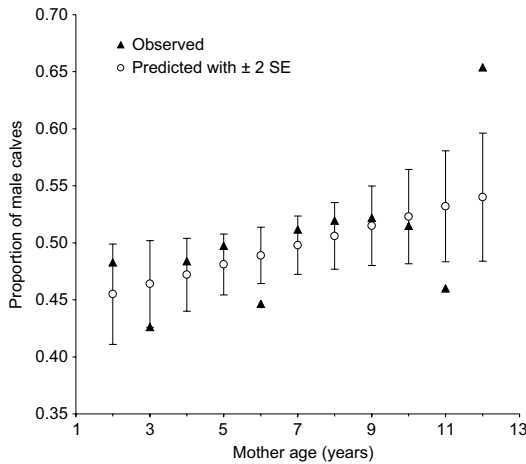


Fig 1. Relationship between proportion of male calves and maternal age with approximate (predicted) 95% confidence intervals.

proportion of male calves increased with increasing maternal age (estimate = 0.034, SE = 0.018, see Fig. 1). The model including maternal age has a relative likelihood as estimated using the AIC weight three times higher than the model including maternal weight, and more than twice

the likelihood of the constant model (see Table 1). Moreover, the three first best models based on AIC values all include maternal age. Indeed, the second and third best models are a model including maternal age and the winter temperature ($\Delta\text{AIC} = 0.15$, see Table 1) and a model including the winter NAO index when the mothers were *in utero* ($\Delta\text{AIC} = 1.0$, see Table 1). Including maternal weight in the most parsimonious model (i.e. the model including maternal weight and maternal age), did not significantly affect the parameter estimate for the variable maternal age ($\hat{\beta}_{\text{MA}} = 0.031$, SE = 0.018). Similarly, including the winter NAO index when the mothers were *in utero* in the most parsimonious model did not significantly affect the parameter estimate for the variable maternal age ($\hat{\beta}_{\text{MA}} = 0.039$, SE = 0.018). The model including winter temperature in addition to maternal age gave a stronger effect of maternal age ($\hat{\beta}_{\text{MA}} = 0.067$, SE = 0.030), but this was due to a strong negative correlation between winter temperature and age for the period considered ($r = -0.77$). *P*-values based on the Likelihood Ratio Statistic for the null hypothesis $\beta_{\text{MA}} = 0$ varied from 0.026 to 0.054

Table 1. Logistic regression models for sex ratio variation. The deviance, the number of parameters (N_{par}) and the Akaike Information Criterion (AIC) are given for each model. In addition, difference between AIC values as compared to the best AIC-based model (ΔAIC) and the AIC weights are provided. AIC weights indicate the relative likelihood of the models (Burnham & Anderson, 1998). The three best AIC-based models are shown in boldface. MA = maternal age, MW = maternal weight, T = winter temperature for Røros, and WSD = winter snow depth. All weather variables are for the winter when the mothers were *in utero*.

Model	Deviance	N_{par}	AIC	ΔAIC	AIC weights
MA	2294.22	2	2298.22	0.00	0.15
MW	2296.50	2	2300.50	2.28	0.05
NAO	2297.70	2	2301.70	3.48	0.03
T	2297.33	2	2301.33	3.11	0.03
WSD Røros	2297.78	2	2301.78	3.56	0.02
WSD Drevsjø	2297.09	2	2301.09	2.87	0.04
WSD (Røros + Drevsjø)	2297.32	2	2301.32	3.10	0.03
MA + T	2292.37	3	2298.37	0.15	0.14
MA + NAO	2293.21	3	2299.21	0.99	0.09
MA + MW	2293.66	3	2299.66	1.44	0.07
MA + WSD Drevsjø	2294.22	3	2300.22	2.00	0.05
MA + WSD Røros	2294.22	3	2300.22	2.00	0.05
MW + NAO	2296.36	3	2302.36	4.14	0.02
MA + WSD Drevsjø + T	2292.11	4	2300.11	1.89	0.06
MA + MW + NAO	2292.87	4	2300.87	2.65	0.04
MA + MA ²	2294.12	3	2300.12	1.90	0.06
MW + MW ²	2296.42	3	2302.42	4.20	0.02
Constant	2297.93	1	2299.93	1.71	0.06

depending on which model was used. The effect of winter temperature was positive ($\hat{\beta}_{WT} = 0.044$, SE = 0.033), as was the effect of NAO ($\hat{\beta}_{NAO} = 0.063$, SE = 0.063), but confidence intervals were wide. Effect of maternal weight was weakly negative ($\hat{\beta}_{MW} = -0.0059$, SE = 0.0079). For the last three estimates, maternal age was included in the model as it led to better models.

Snow depths ($\Delta AIC > 2.9$; see Table 1) in Røros and Drevsjo resulted in substantially poorer models. Including non-linear effects of age, either by using polynomials (Weladji *et al.* 2002b) or additive generalised models, did not improve the fit ($\Delta AIC > 1.8$). Similar patterns of non-significant effects were found for maternal body mass (see Table 1). Considering the frequency data of sex ratio by age, the model fit the data well (residual deviance = 5.82, df = 9, $P = 0.76$), that is, there was no indication of residual variability in sex ratio besides maternal age.

Discussion

Our study shows that maternal age was the best AIC-based predictor of calf sex ratio variation in this semi-domestic reindeer herd. The second and third best models (and close in terms of relative likelihoods) however also included the winter temperature and NAO index when the mother was *in utero* respectively, indicating that climatic conditions experienced by females in their year of birth have the potential to influence variation in cohorts' offspring sex ratio. This suggests that a combination of both density-dependent and density-independent factors may influence sex-ratio variation in reindeer (e.g. Weladji & Holand 2003) and perhaps in other ungulates (e.g. red deer: Kruuk *et al.* 1999, Post *et al.* 1999, Mysterud *et al.* 2000). Weladji and Holand (2003) found that the proportion of male reindeer calves decreased with an increasing NAO index when calves were *in utero*, the effect being associated with nutritional stress caused to the mother before and/or during pregnancy.

An increase in maternal age resulted in increasingly male-biased sex ratio in this reindeer population. However, maternal age relationship to progeny sex ratio is inconsistent among

ungulates. Indeed, as summarized by Hewison *et al.* (2002: table 1) several studies reported an age effect (e.g. *Rangifer tarandus*: Thomas *et al.* 1989, *Oreamnos americanus*: Côté & Festa-Bianchet 2001) whereas many others did not (e.g. *Rangifer tarandus*: Kojola & Eloranta 1989 and Reimers & Lenvik 1997, *Cervus elaphus*: Kruuk *et al.* 1999). Thomas *et al.* (1989) reported that young (1 to 4 years) mothers of barren-ground (*Rangifer tarandus groenlandicus*) and Peary caribou (*Rangifer tarandus pearyi*) produced an excess of female fetuses, whereas older (> 10 years) barren-ground females produce an excess of male fetuses. However, both Reimers and Lenvik (1997) and Reimers (1999) did not find female age to affect variation in foetal sex ratio from different age groups. Similarly, Kojola and Eloranta (1989) did not find any significant age effect in a twelve-year dataset of the Kaamanen herd comprising 1087 newborn calves.

When considering primary sex ratio, females' condition during rut is probably critical (Krackow 1995), as large-bodied females have a better capacity to maintain their physical condition throughout winter than small-bodied females (Kojola 1989, Skogland 1990). The mother's mass in spring correlated with calf mass in this population (Weladji *et al.* 2002b). The body mass measurements in March should therefore roughly reflect females' body mass and hence condition, during rut. However, we did not find that mother mass affected calf sex ratio. This result is consistent with studies by Kojola and Helle (1994), Reimers and Lenvik (1997), and Reimers (1999). Thomas *et al.* (1989) also found no female weight effect on sex ratio in both barren-ground caribou and Peary caribou. However, our results differ from Skogland's (1986) findings that reported a large proportion of males in food-limited conditions in wild reindeer, and Kojola and Eloranta's (1989) findings of a maternal body mass effect on newborns' sex ratio of semi-domestic reindeer, owing to an excess of female calves born to the smallest females. That female weight did not affect offspring sex ratio certainly does not fit predictions by both the Trivers and Willard (1973) and the local resource competition hypotheses (Clark 1978).

Contrary to Kojola's (1989) suggestion that age usually had smaller effect than body mass,

the proportion of males tended to increase with increasing maternal age (Fig. 1). There was no systematic evidence of social status deterioration with body mass in this population, but the relationship between female body mass and age was quadratic (cf. Lenvik *et al.* 1988). This may be due to the selection regime practiced in the herd in combination with good winter ranges, thereby explaining the significant age effect and the lack of a body mass effect in relation to sex ratio. The adaptive significance of sex ratio deviation is therefore not clear. This is in part attributed to the absence of evidence of the potential physiological mechanism that could cause such variations and that selection may act upon. As the cost of manipulation depends on the nature of these mechanisms, no claim of the adaptive value of sex ratio adjustment can be made (Frank 1990).

Several reviews of sex ratio variation have revealed inconsistency in the effect of both age and body mass, both of which are based on adaptive modification by maternal investment (Clutton-Brock & Iason 1986, Frank 1990, Hewison & Gaillard 1999). In this study, maternal age seems to better correlate with offspring sex ratio than e.g. female's body mass and mother's cohort climatic effects, its effect being positive. Our findings however do not support Saltz's (2001) argument of a bell-shaped relationship between maternal age and progeny sex ratio. The controversial debate about the adaptive, maternal modification of offspring sex ratios therefore remains. We suggest that, if an adaptive maternal strategy is present, it may be induced and/or inhibited by, or interact with other factors such as density and/or climate. Within a population, favored strategy may depend on the "individual's" potential to cope with the existing stress.

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