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Title: Observational evidence of a risk sensitive reproductive allocation in a long-lived mammal

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Abstract: In a previous study we found that organisms can adopt a risk sensitive reproductive allocation when summer reproductive allocation competes with survival in the coming winter (Bårdsen et al. 2008). This trade off is present through autumn female body mass, which acts as an insurance against unpredictable winter environmental conditions. In the present study we tested this hypothesis on female reindeer in a population that has experienced a time-period of dramatic strong increase in abundance. Environmental conditions during winter were at the same time fairly stable (with the exception of one year). We conclude that the increased population abundance (perhaps in interaction with winter environmental conditions) represented a worsening of winter environmental conditions as both autumn offspring and spring female body mass decreased during the course of the study. Moreover, we found that the cost of reproduction was related to environmental conditions as: (1) autumn body mass was larger for barren than for lactating females, and this difference was temporally highly variable; (2) lactating females produced smaller offspring than barren ones in the following year; and (3), reproductive output (offspring size) decreased over time. We also found evidence of an individual quality difference as lactating females had a higher reproductive success in the following year. In sum, a worsening of winter conditions lead to (1) decreased reproductive output, (2) lowered autumn body mass for lactating and (3) increased body mass for barren females. Since female reduce their reproductive allocation as winter conditions becomes more unpredictable we conclude that reindeer have adopted a risk sensitive reproductive allocation.

Key words: cost of reproduction; environmental stochasticity; life history; phenotypic plasticity; *Rangifer tarandus*.

INTRODUCTION

A central issue in life-history theory is how individuals balance reproductive investments against their own chances to survive and reproduce in the future (Roff 1992; Stearns 1992). This trade-off between current reproduction and future survival is commonly referred to as the cost of reproduction (sensu Williams 1966), and this has been documented in a wide range of taxa: mammals (Clutton-Brock et al. 1989; Festa-Bianchet et al. 1998; Gittleman and Thompson 1988; Lambin and Yoccoz 2001; Sand 1996; Tavecchia et al. 2005) including humans *Homo sapiens* and other primates (Anderson 1983; Bronson 1995; Dufour and Sauther 2002; Ellison 2003; Lummaa and Clutton-Brock 2002), birds (Lindén and Møller 1989; Monaghan and Nager 1997; Moreno 1989; Zammuto 1986) and plants (Obeso 2002).

Long-lived organisms favour own survival over reproduction as reproductive output and juvenile survival are more variable than adult survival (Gaillard et al. 2000; Gaillard and Yoccoz 2003). However, the balance between reproduction and survival should depend on environmental conditions affecting the two traits (Bårdsen et al. 2008; Forchhammer et al. 2001; Gaillard and Yoccoz 2003; Sæther 1997). For long-lived species with several breeding attempts, such as northern large terrestrial herbivores, reproduction generally takes place during the favourable season (summer), whereas survival is particularly constrained in the unfavourable season (winter: Sæther 1997). In a variable environment where the amount of resources needed for survival during winter are difficult to predict, long-lived species should adopt a risk sensitive reproductive strategy (Bårdsen et al. 2008). Consequently, body size or mass (a proxy for condition or reserves) is an important trait affecting both survival and reproduction, and hence the cost of reproduction [e.g. humans (Lummaa and Clutton-Brock 2002), terrestrial large herbivores (Sæther 1997), birds (Hanssen et al. 2005; Parker and Holm 1990), fish (Hutchings 1994; van den Berghe 1992) and reptiles (Radder 2006; Shine 2005)]. Body mass, thus, acts as an important state variable (e.g.

Houston and McNamara 1999), which in this case is a currency that can be traded for reproduction *or* survival.

In northern and clearly seasonal environments, late winter conditions have profound effects on survival and reproduction (Coulson et al. 2001; Coulson et al. 2000; DelGiudice et al. 2002; Patterson and Messier 2000). Autumn body mass, which represents an insurance against winter starvation is then traded against the resources a female invest in her offspring during summer (Bårdsen et al. 2008; Clutton-Brock et al. 1996; Fauchald et al. 2004; Reimers 1972; Skogland 1985; Tveraa et al. 2003). Consequently, in a given summer a female have to choose how much resource to invest in somatic growth versus reproduction. If a female invest too much in reproduction this will lead to a lost opportunity for an increased autumn body mass (Bårdsen et al. 2008), and this will ultimately lower her chance for survival in harsh winters (Tveraa et al. 2003). Thus, the optimal reproductive strategy, which is defined by the amount of resources to invest in reproduction relative to somatic growth, will depend on the expected winter environmental conditions. How individuals optimize this trade-off is related to their body condition, i.e. their state, and the degree of risk imposed by the environment: an individual has no way of predicting the future so it has to trade somatic growth against reproductive allocation during summer based on an 'estimated' distribution of winter conditions (Bårdsen et al. 2008).

A changed distribution in winter environmental conditions can, thus, have important consequences for both reproductive output and survival. Individuals experiencing stable and benign winter conditions can afford a low autumn body mass and might therefore increase their fecundity by increased reproductive allocation. On the other hand, animals experiencing harsh and variable winter conditions should maximize their autumn body mass and should therefore be limited by a relatively low fecundity and reproductive allocation. Accordingly, northern large herbivores might have adopted a risk sensitive reproductive allocation in the sense that they adjust their reproductive allocation during summer according to the risk of starvation the following

winter (see Bårdsen et al. 2008 and references therein). Consequently, individuals can play different strategies where a *risk prone* reproductive strategy involves high reproductive allocation that will result in high reproductive reward during benign conditions but high survival cost during harsh conditions. A low reproductive allocation will, on the other hand, result in high winter survival but lower potential reproductive reward. Consequently, this represents a *risk averse* reproductive strategy. Such an asymmetric response in the costs and benefits relative to environmental harshness indicates that long-lived organisms should be on the *risk averse* side of the *risk prone-risk averse* continuum (Bårdsen et al. 2008).

Several experimental studies on female semi-domestic reindeer (*Rangifer tarandus*) have proved that reindeer make strategic decisions during summer and that they pay a delayed cost of reproduction during late winter. First, Tveraa et al. (2003) found that especially harsh winter conditions can greatly reduce adult survival and reproductive success the following spring and summer. Second, when late winter feeding conditions are improved adult females increase their late winter body mass relative to early winter body mass (Fauchald et al. 2004). This gain in body mass is, however, rapidly lost during the calving season as the above difference in body mass are not present in the summer (Bårdsen et al. 2008; Fauchald et al. 2004). It has, thus, been concluded that female reindeer regulate their body mass down to some minimum threshold during spring in order to take care of their newborns when the risk of starvation is low (Bårdsen et al. 2008; Fauchald et al. 2004). Third, Bårdsen et al. (2008) found that female reindeer have adopted a risk sensitive reproductive allocation: they found an asymmetric response to improved (no response) *vs.* reduced winter conditions where the latter resulted in a prompt reduction in reproductive allocation the following summer. In essence, additional winter body mass acts primarily as an insurance against periods of winter starvation, which means that there is a dynamic relationship between summer and winter as the importance of body mass as a state variable varies across seasons.

We use empirical data from a reindeer herding district in Finnmark, Norway to test predictions on risk sensitive reproductive allocation in relation to body mass development during summer and winter (S1). Reindeer abundance drastically increased over and peaked at a historical high-level in 2005 (Fig. 1a), whereas climatic conditions have been relatively stable, with the exception of one year during the period in which we have detailed individual-data (Fig. 1b-c). Negative interactions between population density and late winter weather conditions have been documented previously (e.g. Coulson et al. 2001; Coulson et al. 2000; Grenfell et al. 1998). Consequently, we will argue that the recent increased abundance, leading to increased competition over resources, had a drastic effect on the reindeer's perception of the environment they inhabit. This should again have changed the cost of reproduction and the optimal balance between how many resources female reindeer should invest in reproduction relative to somatic growth during summer in a risk sensitive manner. This is empirically supported as (1) autumn female body mass was unaffected by increased reindeer abundance, whereas (2) reproductive allocation decreased when reindeer abundance increased (Fig. 1d-f).

Based on this we predicted that: (1) If female reindeer invest in reproduction during summer we expected the summer gain in body mass to be higher for barren vs. lactating females, and that the difference for barren and lactating females to be sensitive to past environmental conditions. (2) We also expected smaller lactating females to loose less body mass in winter compared to barren ones due to a quality difference across the two groups. Moreover, the loss of body mass should be negatively related to population density and winter conditions. (3) If reproduction is costly we expected summer gain in body mass for offspring to be lower for females that raised offspring last year. This response, which measure reproductive allocation, should also be sensitive to past environmental conditions. (4) If reproduction is costly we also expected that only individuals of superior quality can afford to reproduce where reproductive success measure another component of reproductive allocation. Thus, reproductive success, i.e.

the probability of having a calf, was predicted to be positively related to maternal body mass and previous year reproductive status.

MATERIAL AND METHODS

Study population and study area

The present study was conducted on semi-domestic reindeer in Finnmark, Norway (Fig. 1-2). The study herds (Njarga and Mieron) is most of the time free-ranging. Both herds utilize the same winter pastures where they are kept together through the winter, but they utilize different summer pastures. None of the herds was given supplementary feeding. The winter pastures is situated 4-500 m above sea level (a.s.l.), and this area is characterized by stable and continental winter conditions (Tveraa et al. 2007). The herds are separated in April and they are then herded ~170 km to their respective summer pastures at the coast. The Njarga herd arrives at their summer pasture area about 2 weeks later than the Mieron herd as females in this herd give birth during the migration and not on the summer pastures (Fig. 2). The herds occupy neighbouring areas at the coast, and the summer pastures consist of rugged mountainous terrain with peaks reaching >1000 m a.s.l. Mixing between herds is practically non-existent as all animals have owner specific earmarks (if animal are mixed with neighbouring the owner will recognize them and collected by later on) and as the summer pasture areas are separated by fences and natural barriers such as e.g. fjords (Fig. 2). During the autumn migration, on the way back to the winter pastures, the two herds are again mixed and the annual migration cycle is ended.

Study protocol

A random selection of fifty prime-aged female (≥1.5 year) from each herd was individually marked in April 2002. Since then we have followed the lineages formed by these individuals: i.e. initially

marked females, their offspring, their offspring's offspring and so on. We record individual body mass and presence ('present' or 'absent') in the spring (23rd, 5th, 5th, 4th, 17th, 16th and 28th of April in 2002-2008) and in the autumn (29th, 29th and 30th of October, 3rd of November, 31st of October, and 11th of November in 2002-2007). Body mass was recorded to the nearest 0.2 kg using an electronic balance (Avery Berkel, Birmingham, UK). Multiple observations of females with a calf at foot were used to identify mother-calf relationships, i.e. whether a female was lactating or barren (see also Bårdsen et al. 2008). This design opens up for the possibility to quantify the relative effect of winter and summer conditions on individual body mass and reproduction. The dataset contains the following variables:

Year.-- A factor variable with each year from 2002-2008 acting as levels.

Herd.-- A factor variable with the name of each herd ('Mieron' & 'Njarga') as levels.

Previous female autumn body mass.-- Female body mass in late October or early November the year before.

Female spring body mass.-- Female body mass in April.

Reproductive status.-- A variable that either acts as a binary variable ('0' & '1') or as a factor variable ('negative' & 'positive'). Barren females, i.e. individuals registered without a calf, was labelled '0' (binary) or 'negative' (factor), whereas lactating females was labelled '1' (binary) or 'positive' (factor). This variable was measured in June and September.

Female autumn body mass.-- Female body mass in late October or early November.

Offspring autumn body mass.-- Offspring body mass late October or early November.

Previous reproductive status.-- This variable is similar to 'reproductive status' the preceding year.

Age.-- A group of adult females (> 1 year) were included when the study was initiated. In a recent study from the same study region, we found that age and body mass was highly correlated for young (≤4 year) reindeer, but not for prime-aged individuals (5-13 year: Bårdsen et al. in press). This finding is in accordance with Lenvik et al's (1988) studies well. They found that body mass was a more important predictor of reproduction than age within the prime-aged

segment. Thus we felt confident that our inability to correct for age did not affect our results and conclusions (see S1 for details).

Statistical analyses

An overview of the statistical analyses

Our predictions, which for all analyses of body mass focus on body mass development from one point in time to another, can statistically be tested by the following comparisons (S1): (1) Autumn female body mass as a function of spring body mass and reproductive status (*Summer body mass development*). (2) Spring female body mass as a function of previous autumn body mass and previous reproductive status (*Winter body mass development*). (3) Autumn offspring body mass as a function of spring maternal body mass and previous reproductive status (*Offspring summer body mass development*). (4) Reproductive success, i.e. probability of producing a calf, as a function of spring maternal body mass and previous reproductive status. (5) Reproductive success as a function of maternal body mass the previous autumn and previous reproductive status (analysis 4 and 5 are hereafter termed *Reproduction*). Covariates were included and excluded within the 'paradigm' of model selection (S1). Statistical analyses were carried out in *R* (R Development Core Team 2007), All tests were two-tailed and the null-hypothesis was rejected at an α-level of 0.05.

Body mass

Linear models, using the *lm* function in *R*, were used to analyze the effect of the predictors on body mass of both females and offspring. Our aim was to assess the relative importance of the cost of reproduction on body mass development across the summer versus winter season. Thus, it is important to make comparisons between initial body mass (centred in all analyses; subtracting the average value), i.e. spring or previous autumn condition, across reproductive status. Our study is, thus, based on planned comparisons, and the predictions can then be tested statistically by *estimating* the three key parameters (S1; Fig. S1.1): (1) the main effect of reproductive status, or

previous reproductive status; (2) the main effect of initial body mass; and (3) the two-way interaction between them. This will provide us with an estimate of the mean difference in body mass between the lactating and barren group at a constant initial body mass, and how the relationship between body mass and initial body mass is different for lactating and barren females. Consequently, we started with the full model containing all the above predictors and interactions based on *a priori* expectations. From this model, we formed a pool of candidate models where all covariates and interactions were removed sequentially, where we selected the model with the lowest second-order *Akaike's Information Criterion* (AICc) value (see S2). As this study consists of planned comparisons we used the *treatment contrast* comparing each level of a factor to its baseline level, and Wald statistics to test if contrasts were significantly different from zero.

Reproduction

Generalized linear models, applied using the *glm* function in *R*, with a binary response variable (0 = 'absent', 1 = 'present'), using a logit link function and a binomial distribution, were applied similarly as in the analyses of body mass in order to quantify female reproductive success (i.e. the probability that a female had a calf). We adopted the same model selection procedure as in the analyses of body mass (S3).

Mixed-models – an alternative statistical approach

It can be argued that linear mixed-effect models (Pinheiro and Bates 2000: *Body mass*) and generalized linear mixed-effect models (Venables and Ripley 2002: *Reproduction*), using individual as a random effect, represent more correct statistical approaches. Estimating statistical significance and model selection are, however, not straightforward for mixed models (e.g. Pinheiro and Bates 2000; Wood 2006). Consequently, we did not apply this approach, but we fitted the mixed-model version of the selected model in each analysis and that did not change results notably.

RESULTS

Body mass

Summer body mass development

Initially smaller females gained more body mass summer in than larger females (main effect of spring body mass; 0.531 kg), and as the reproductive status (RS) × spring body mass interaction was small and insignificant initial body mass was of equal importance for barren and lactating females (Table 1a & Fig. 3a). Lactating females was, however, in 2002 on average >4 kg smaller compared to barren ones (main effect of reproductive status; Table 1a & Fig. 3b). Moreover, the difference between barren and lactating females were larger in all the following years (negative year × RS interactions; Table 1a) except for 2007. This interaction was, however, only statistically significant in 2006; lactating females was now on average 9.63 kg smaller than barren females (Table 1a). The year-effect on female autumn body mass was positive in all years, which means that there has been a general upward trend in body mass for barren females (main effect of year; Table 1a). Finally, females in the Njarga herd gained more in body mass over the summer compared to females in Mieron (main effect of herd; Table 1a). This may indicate that summer feeding conditions might be better for Njarga compared to Mieron. To summarize, female reindeer pay a considerable cost of reproduction during summer, and this cost was temporally highly-variable.

Winter body mass development

Initially smaller and larger females followed a similar pattern of winter body mass development [main effect of previous autumn body mass; 1.162 kg (Table 1b & Fig. 3c)]. The relationship between autumn and spring body mass was, however, weaker for lactating than barren females [previous reproductive success (PRS) × previous autumn body mass interaction; -0.195 kg (Table 1b)]. This indicates that smaller lactating females had a more positive winter body mass

development compared to barren ones (Fig. 3c). For 2007, however, a negative year and previous autumn body mass interaction occurred; the importance of initial body mass was, thus, of less importance in this year. There was a small and negative, but not statistical significant, main effect of PRS on spring female body mass, and this shows that the difference between lactating and barren females was small in 2003 (Table 1b & Fig. 3d). However, a statistically significant and positive year × PRS interaction was evident for 2007 (Table 1b). In this year, lactating females were on average 2.35 kg larger than barren ones. Consequently, in some years barren females were on average smaller than lactating ones (even though not statistically significant), while in other years lactating females was on average larger than barren ones. Interestingly, the year effect on female spring body mass was negative and decreasing through time, which means that there was a downward trend in body mass for barren females (Table 1b). This trend is also evident for lactating females, even though they have not been equally affected by this downward temporal trend in spring body mass (positive year × PRS interaction; Table 1b). Finally, females in the Njarga herd was on average smaller compared to females in Mieron [main effect of herd; -2.347 kg (Table 1b)], indicating that Njarga females afforded to loose more body mass compared to Mieron females. Moreover, the relationship between autumn and spring body mass was weaker in Njarga compared to Mieron. To summarize, there was no indications of lactating females loosing more body reserves compared to barren ones during winter. In fact, in some years lactating females increased in body mass compared to barren females. Perhaps even more importantly, autumn body mass was a weaker predictor for spring body mass for lactating compared to barren females. Moreover, both the difference between barren and lactating females and the predicted relationship between autumn and spring body mass was temporally variable.

Offspring body mass development

Initially smaller females produced smaller offspring than larger females (main effect of maternal spring body mass; 0.476 kg), and as the PRS × spring body mass interaction was small and insignificant spring body mass was of equal importance for females being barren and lactating in

the previous year (Table 1c & Fig. 3e). This also means that even though smaller females produced larger offspring in an absolute sense, smaller females invested proportionally more in their offspring. Surprisingly, we found that previously barren females produced significantly larger offspring compared to previously lactating females [main effect of PRS; -2.450 kg (Table 1c)]. Moreover, we found a large temporal variation in offspring body mass as 2005 and 2006 were statistical significantly different from 2003 (main effect of year; Table 1c). To summarize, a lagged cost of reproduction with respect to offspring body mass was evident as offspring body mass was substantially lower for females that were lactating the previous years compared to those who were barren. Maternal spring body mass was an important predictor for offspring body mass, which were temporally highly-variable.

Reproduction

Initially larger females had a higher probability of producing an offspring than smaller females when previous maternal autumn body mass was as used a predictor (main effect of initial body mass; 0.069 on logit scale), but not when maternal spring body mass was used as a predictor (Table 2 & Fig. 4). Thus, previous autumn body mass, i.e. before winter had taken its toll, was a poorer predictor of reproductive success than spring body mass even though the latter relationship nearly reached statistical significance. Moreover, the effect of initial body mass was similar for females that were lactating the previous year compared to barren ones as the PRS × initial body mass interaction was small and insignificant in both analyses (Table 2). Females that successfully reproduced the previous year were more likely to reproduce again compared to females who were barren when previous maternal autumn body mass was used as a predictor [main effect of PRS; 0.774 (Table 2b)]. This was not the case in the analysis including maternal spring body mass as a predictor even though it was nearly statistical significant (Table 2a). Moreover, reproduction showed a high temporal variation in both analyses, and this temporal variability was fairly similar

across the analyses (Table 2). In sum, females that produced an offspring the year before tended to have a higher chance of reproducing, and reproductive success were temporally highly-variable.

DISCUSSION

The present study demonstrates that female reindeer have adopted a risk sensitive reproductive allocation strategy because: (1) We found a considerable cost of reproduction with respect to autumn body mass; barren females gained significantly less body mass during summer compared to lactating ones. Interestingly, the difference between barren and lactating females was largest the summer after the peak in reindeer abundance. Female reindeer, thus, promptly increased their allocation in somatic growth following a period of dramatic increase in resource competition. (2) The difference for barren vs. lactating females was smaller in the analysis of spring body mass, but this trend was temporally variable to such an extent that lactating females had a higher spring body mass compared to barren ones in some years. A negative interaction between reproductive status and previous autumn body mass did, however, indicate that spring body mass was larger for initially smaller lactating than for barren females. (3) Females that reproduced the year before invested fewer resources in reproduction. Moreover, maternal spring body mass was an important predictor of offspring body mass; larger females, thus, produced larger offspring relative to smaller females, but smaller females invested proportionally more in their offspring. (4) Maternal spring body mass was a significant predictor of reproductive success. When previous maternal autumn body mass was a predictor, females that lactated the previous year had a significantly higher reproduction compared to barren ones, which indicates that individual qualities are important. Reproduction and, thus reproductive allocation, was also sensitive to environmental conditions as both herd and year was important predictors in the analyses.

Autumn body mass was substantially lower for lactating than for barren females, and in some years this difference was considerably larger compared to others. Interestingly, we found the largest difference between barren and lactating females (9.6 kg) in the autumn 2006 (the year after the peaked in abundance). The upward temporal trend in autumn body mass for barren females showed that density did not limit the ability for females to gain mass during summer. This is further empirically supported by the fact that the largest average autumn female body mass occurred after the peak in reindeer abundance and just after the winter with abnormally high levels of precipitation (Fig. 1d). Consequently, late winter conditions, defined by both density and weather (e.g. Coulson et al. 2001), affected how much a female should invest in somatic growth vs. reproduction. Further, a lowered reproductive allocation was also evident from the lowered offspring body mass and proportion of females breeding over time (Fig. 1d,f). This trade-off between allocation in growth vs. reproduction, which occurs in summer, has been found previously for large herbivores (e.g. Clutton-Brock et al. 1996; Reimers 1972; Skogland 1985), and the increased allocation in somatic growth over reproduction following a harsh winter is predicted for a *risk averse* reproductive strategy (Bårdsen et al. 2008). If we measure the cost of reproduction as a lost opportunity for summer gain proportional to spring body mass, this cost was considerable for initially smaller relative to larger females. Moreover, smaller females gained more body mass over the summer than larger ones. In essence, we documented a large cost of reproduction with respect to autumn body mass, and this cost was related to past winter conditions. This finding can be explained by the fact that reindeer have adopted a *risk averse* reproductive allocation strategy.

For spring body mass we found that individuals were substantially larger in 2003 compared to all other years. We interpret this decrease in body mass to be an effect of increasing population abundance acting in concert with harsh winter weather conditions. This is in accordance with previous studies that have documented that late winter conditions have profound effects on survival and reproduction for temperate large herbivores (e.g. Coulson et al. 2001; Coulson et al.

2000; DelGiudice et al. 2002; Patterson and Messier 2000; Tveraa et al. 2003). Second, the

difference between lactating and barren females showed a high temporal variation. In fact, no

significant difference between lactating and barren females was found in most years. Nevertheless,

lactating females did have the highest spring body mass in 2007. This was perhaps due to an

interaction between density, which was stable from 2005, and climate as this year had abnormally

high winter precipitation levels (Fig. 1c). This might have increased resource competition during a

particularly harsh winter. Third, we did find a more positive relationship between previous autumn

and spring body mass for barren compared to lactating females, indicating that smaller lactating

outperformed smaller barren females. This effect was, thus, the opposite of that found in the

previous analysis (van Noordwijk and de Jong 1986 show how positive relationship between two

traits subject to trade-offs might occur). Autumn body mass may, thus, act differently for barren

and lactating females due to a quality difference between them. Social dominance, may, be a

mechanism explaining this relationship (Kojola 1989). However, female reindeer regulate their

body mass down to some minimum threshold during spring when the risk of starvation is low

(Bårdsen et al. 2008; Fauchald et al. 2004), which may also explain why we did not find a clear cost

of reproduction on female spring body mass. In conclusion, the difference in spring body mass for

lactating and barren females were not clearly present as lactating females can outperform barren

ones. In contrast to the previous analysis, we found a strong negative trend in spring body mass

related to an interaction between density dependence and winter conditions.

Maternal spring body mass was a positive predictor of offspring autumn body mass. Surprisingly,

we documented a lagged cost of reproduction on offspring body mass: females that were lactating

the previous year produced calves that were on average ~2.5 kg, i.e. ~6%, smaller compared to

barren ones. In the analysis of offspring body mass, as in the analysis of maternal spring body

mass, 2003 was a particularly favourable year as offspring body mass was lower for all following

years (Fig. 1e). This, in combination with the previous analyses, shows that the cost of

reproduction has two components; (1) a *direct cost* related to adult survival manifested as a lost opportunity for summer gain in body mass, and (2) a *lagged cost* related to reproductive success manifested as a reduction in offspring body mass in the next breeding season.

Previous studies on reindeer have revealed that body mass as a state variable have different interpretation depending on seasons: (1) Autumn body mass represents an insurance against winter severity (Bårdsen et al. 2008) and (2) female reindeer regulate their body mass down to a threshold value during the spring in order to take care of their newborns (Fauchald et al. 2004). Based on this we modelled reproductive success with two sets of initial female body masses as predictors. In both analyses, reproduction was positive related to previous reproductive success even though it was only barely statistically significant in the analysis of previous autumn body mass. The analysis of reproduction can, thus, be said to be non-consistent with the analysis of offspring body mass. We interpret the positive effect of successful reproduction the year before was as evidence of individual differences in quality. Alternatively, this may reflect that females are reproducing more or less continuously after reaching maturation, but this is not likely as the proportion of females reproducing each year was highly variable (range: 0.6-0.9). Maternal body mass was, then, a positive predictor of reproduction showing that larger females had a higher reproductive success compared to smaller ones. The weaker effect of previous autumn body mass on reproductive success may be explained by the fact that this represents another 'currency' compared to spring mass, which reflects individual states in the beginning of the breeding season. In conclusion, we found evidence of individual variation in quality as we documented a lagged positive effect of previous year's reproductive success

We demonstrate that female reindeer have adopted a risk sensitive reproductive strategy where they are on the *risk averse* side of the *risk prone-risk averse* continuum. We found that a dynamic interplay between the favourable summer season, which is a period of resources abundance, and

the severe winter season, which is a period where population density interacts with environmental conditions. The degree of winter severity is, thus, characterized by an interaction between winter weather, e.g. precipitation and icing events (e.g. Solberg et al. 2001), and density dependent competition over already scarce resources. We argue that summers are truly favourable as autumn body mass for barren females increased over time, which means that density during summer was not a limiting factor. Moreover, we found a substantial cost of reproduction with respect to a lost opportunity for summer gain in body mass, and we also found a decreased allocation in reproduction under high density as both offspring body mass and the proportions of females breeding was lowered as reindeer abundance increased (Fig. 1). Individuals', thus, invest in reproduction according to expected winter conditions as they reduced their reproductive allocation when the environment became more severe. On the other hand, spring body mass declined over time so population density and winter conditions was limiting factors. Based on this we conclude that the cost of reproduction for female reindeer has two components. First, a *direct* cost that manifested through a lost opportunity for somatic growth during summer. This lost opportunity for increased autumn body mass will ultimately cause a lowered survival probability, but this will only happen during especially harsh winters (Tveraa et al. 2003). Thus, the actual cost of reproduction will be related to expected winter environmental conditions: individuals have no way of predicting the future so they have to trade somatic growth against reproduction during summer based an 'estimated' distribution of winter conditions based on past experience (Bårdsen et al. 2008). Second, a *lagged* cost that manifested as a lowering of offspring body mass. As juvenile survival is more variable and more sensitive to environmental harshness than adult survival (Gaillard et al. 2000) lowered juvenile body mass will result in reduced reproductive output. Additionally, individual quality was an important predictor controlled for in all analyses as: (1) initial body mass can be said to be a true state variable as it was an important predictor in all analyses, and (2) females producing an offspring in one year showed an increased probability of producing an offspring in the year to come.

The substantial direct and lagged cost of reproduction as well as the evidence of variation in individual qualities documented here are in accordance with other studies (e.g. Clutton-Brock et al. 1989; Dufour and Sauther 2002; Newton 1989) and with the more finding that reproduction is costly: mammals (Festa-Bianchet et al. 1998; Lambin and Yoccoz 2001; Lummaa and Clutton-Brock 2002; Sand 1996; Tavecchia et al. 2005; Tveraa et al. 2003), birds (Lindén and Møller 1989; Monaghan and Nager 1997; Moreno 1989) and plants (Obeso 2002).

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Table 1. Estimates from linear models (*LM*) relating female autumn (a) and spring (b) body mass (kg) as well as offspring (c) body mass (kg) to a set of predictors. The intercept shows mean body mass for; (1) the level 2002 (a) or 2003 (b-c) for the factor 'year', (2) the barren level for the factor 'reproductive status' (a-b) or 'previous reproductive status' (c) and (3) the level Mieron for the factor 'herd'. The other coefficients are the estimated difference between the intercept, or the main effect for initial body mass, for each level of the other included factors.

Parameter	Value (95% CI)	*t*-value	*P*-value
(a) *Summer body mass development*			
Intercept	70.658 (68.797, 72.520)	74.581	<0.001
Spring body mass (BM)[a]	0.531 (0.447, 0.614)	12.453	<0.001
Reproductive status (RS)[b] [positive]	-4.054 (-6.167, -1.941)	-3.769	<0.001
Herd [Njarga]	1.124 (0.346, 1.902)	2.839	0.005
Year [2003]	1.118 (-1.956, 4.192)	0.714	0.475
Year [2004]	1.629 (-1.187, 4.445)	1.137	0.256
Year [2005]	3.012 (0.573, 5.451)	2.427	0.016
Year [2006]	2.977 (0.189, 5.765)	2.098	0.036
Year [2007]	4.405 (1.762, 7.049)	3.274	0.001
RS[b] [positive] × BM[a]	0.074 (-0.033, 0.181)	1.358	0.175
RS[b] [positive] × Year [2003]	-1.267 (-4.768, 2.234)	-0.711	0.477
RS[b] [positive] × Year [2004]	-2.507 (-5.630, 0.616)	-1.578	0.115
RS[b] [positive] × Year [2005]	-1.156 (-4.024, 1.713)	-0.791	0.429
RS[b] [positive] × Year [2006]	-5.572 (-8.738, -2.407)	-3.459	0.001
RS[b] [positive] × Year [2007]	0.480 (-2.808, 3.767)	0.287	0.774
$R^2 = 0.58$, $F_{14,480} = 48.10$, $P < 0.01$			

Table 1. Continued.

Parameter	Value (95% CI)	t-value	P-value
(b) *Winter body mass development*			
Intercept	71.551 (69.732, 73.37)	77.310	<0.001
Previous autumn body mass (BM)[c]	1.162 (0.997, 1.327)	13.830	<0.001
Previous reproductive status (PRS)[d] [positive]	-0.106 (-2.105, 1.893)	-0.100	0.917
Herd [Njarga]	-2.347 (-3.724, -0.970)	-3.350	0.001
Year [2004]	-5.821 (-8.694, -2.948)	-3.980	<0.001
Year [2005]	-5.617 (-7.977, -3.258)	-4.680	<0.001
Year [2006]	-6.141 (-8.158, -4.124)	-5.980	<0.001
Year [2007]	-7.848 (-9.957, -5.740)	-7.320	<0.001
Year [2008]	-7.284 (-9.531, -5.037)	-6.370	<0.001
BM[c] × PRS[d] [positive]	-0.195 (-0.307, -0.084)	-3.440	0.001
BM[c] × Herd [Njarga]	-0.138 (-0.242, -0.034)	-2.610	0.009
RS [positive] × Herd [Njarga]	1.902 (0.344, 3.460)	2.400	0.017
BM[c] × Year [2004]	0.012 (-0.204, 0.228)	0.110	0.913
BM[c] × Year [2005]	0.079 (-0.094, 0.251)	0.900	0.370
BM[c] × Year [2006]	0.029 (-0.151, 0.208)	0.310	0.754
BM[c] × Year [2007]	-0.196 (-0.359, -0.033)	-2.370	0.018
BM[c] × Year [2008]	0.013 (-0.185, 0.212)	0.130	0.895
PRS[d] [positive] × Year [2004]	1.185 (-1.736, 4.105)	0.800	0.426
PRS[d] [positive] × Year [2005]	0.335 (-2.240, 2.910)	0.260	0.798
PRS[d] [positive] × Year [2006]	1.143 (-1.141, 3.426)	0.980	0.326
PRS[d] [positive] × Year [2007]	2.455 (-0.031, 4.941)	1.940	0.053
PRS[d] [positive] × Year [2008]	0.622 (-2.036, 3.281)	0.460	0.646
$R^2 = 0.82$, $F_{21,417} = 87.90$, $P < 0.01$			

Table 1. Continued.

Parameter	Value (95% CI)		t-value	P-value
(c) Offspring summer body mass development				
Intercept	44.082	(41.578, 46.586)	34.980	<0.001
Maternal spring body mass (BM)[a]	0.476	(0.235, 0.717)	3.930	<0.001
Previous reproductive status (PRS)[d] [positive]	-2.450	(-4.668, -0.233)	-2.200	0.031
Year [2004]	-3.167	(-5.899, -0.436)	-2.300	0.024
Year [2005]	-3.567	(-6.278, -0.857)	-2.610	0.010
Year [2006]	-3.278	(-5.667, -0.889)	-2.730	0.008
Year [2007]	-0.828	(-3.673, 2.017)	-0.580	0.565
BM[a] × PRS [positive]	-0.081	(-0.358, 0.197)	-0.580	0.564
$R^2 = 0.48$, $F_{7,90} = 11.90$, $P < 0.01$				

[a]This variable was measured in April (just before snowmelt).

[b]RS refers to whether a females was barren (negative) or lactating (positive) during summer.

[c]This variable was measured in October or November the year before.

[d]PRS refers to whether a females was barren (negative) or lactating (positive) the year before.

Table 2. Generalized linear model relating offspring reproduction, i.e. the probability of producing a calf, as a binary response (i.e. a *GLM* with binomial family and a logit link function) to a set of predictors. The intercept shows the logit mean for (1) the level 2002 for the factor 'year' and (2) the barren level for the factor 'previous reproductive status'. The other coefficients are the estimated difference between the intercept, or the main effect for initial body mass, for each level of the other included factors.

Parameter	Value (95% CI)	z-value	*P*-value
(a) *Maternal spring body mass*			
Intercept	0.941 (0.039, 1.889)	2.000	0.045
Maternal spring body mass (BM)[a]	0.069 (0.008, 0.139)	2.100	0.036
Previous reproductive status (PRS)[b] [positive]	0.600 (-0.062, 1.252)	1.800	0.072
Herd [Njarga]	-1.071 (-1.715, -0.463)	-3.360	0.001
Year [2004]	2.289 (0.904, 4.201)	2.860	0.004
Year [2005]	0.457 (-0.408, 1.318)	1.040	0.297
Year [2006]	1.244 (0.293, 2.234)	2.530	0.011
Year [2007]	-0.097 (-1.014, 0.816)	-0.210	0.835
BM[a] × PRS[b] [positive]	0.003 (-0.081, 0.083)	0.080	0.935
Residual deviance = 345.75, df = 339			
Null deviance = 297.36, df = 331			

Table 2. Continued.

Parameter	Value (95% CI)		z-value	*P*-value
(b) *Previous maternal autumn body mass*				
Intercep	1.222	(0.308, 2.195)	2.550	0.011
Previous autumn maternal body mass (BM)[c]	0.061	(-0.004, 0.132)	1.790	0.074
Previous reproductive status (PRS)[b] [positive]	0.774	(0.091, 1.454)	2.240	0.025
Herd [Njarga]	-1.190	(-1.873, -0.548)	-3.540	<0.001
Year [2004]	1.875	(0.483, 3.788)	2.340	0.020
Year [2005]	0.003	(-0.855, 0.844)	0.010	0.995
Year [2006]	0.974	(0.0257, 1.959)	1.990	0.047
Year [2007]	-0.472	(-1.356, 0.390)	-1.070	0.287
BM[c] × PRS[b] [positive]	-0.002	(-0.093, 0.087)	-0.040	0.965
Residual deviance = 277.58, df = 310				
Null deviance = 322.56, df = 318				

[a]This variable was measured in April (just before snowmelt).

[b]PRS refers to whether a females was barren (negative) or lactating (positive) the year before.

[c]This variable was measured in October or November the year before.

Fig. 1. Time series (t ; years) of (a) reindeer abundance[5] (N_t), (b) winter and summer Arctic Oscillation Index[6] (AO_t) and (c) precipitation for two coastal[7] (blue) and three continental[7] meteorological station (red). The black horizontal line shows where we have detailed individual-based data (d-f). The reindeer population in this district increased from 2001 peaked at an historical high abundance in 2005 (arrow). In contrast, climatic conditions have been relatively stable during the same period. Winter AO_t was negative, with the exception of 2007, indicating that climatic conditions were generally better from 2002-2008 compared to the long-term average[6]. Nevertheless, December precipitation in 2006 where approximately double of the monthly normal values for all stations (arrow; c). Female autumn body mass show no apparent temporal trend (d), whereas autumn offspring body mass (d), female spring body mass (e) and the proportions of females giving birth (f; sample size are provided in the figure) decreased as reindeer abundance increased.

Fig. 2. Position of summer pastures at the cost and the continental winter pastures in Finnmark, Norway. Females in the Njarge herd (blue) give birth on their way out to the summer pasture area, whereas the Mieron herd (red) move to the summer pasture area before the calving season starts. Rectangles show the position of the meteorological stations (Fig. 1).

Fig. 3. A visualization of the models (re-fitted without centring initial body mass) presented in Table 1. The left panel show a subset of data from 2006 and the Mieron herd to exemplify data and the relationship involving initial body mass, RS or PRS and the interaction between them (Table 1). The right panel shows the temporal trend in estimated body masses for barren and

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[5] Reindeer abundance data for Silvetnjaraga extracted from official statistics 1981-2007 Anonymous (2007) Ressursregnskap for reindriftsnæringen. In. Reindriftsforvaltningen, Alta, Norway.

[6] Winter AO is the average for monthly values from December (t - 1) to April, whereas summer AO is the June-August average: http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/teleconnections.shtml.

[7] Monthly normal (1961-1990) December precipitation levels (in mm): Tromsø (106), Alta (36), Cuovddatmohkki (18), Dividalen (16) & Sihccajavri (16): http://www.eklima.no.

lactating females keeping initial body mass constant at population specific averages (68.45 kg for

spring and 66.01 kg for previous autumn body mass).

Fig. 4. A visualization of the models (re-fitted without centring initial body mass) presented in

Table 2. The left panel show a subset of data from 2007 and the Mieron herd to exemplify data

and the relationship involving initial body mass, PRS and the interaction between them (Table 2).

The right panel shows the temporal trend in estimated probabilities for barren and lactating

females keeping initial body mass constant (see Fig. 3 for details). Numbers in the right panel are

showing average body mass for reproducing females in each year.
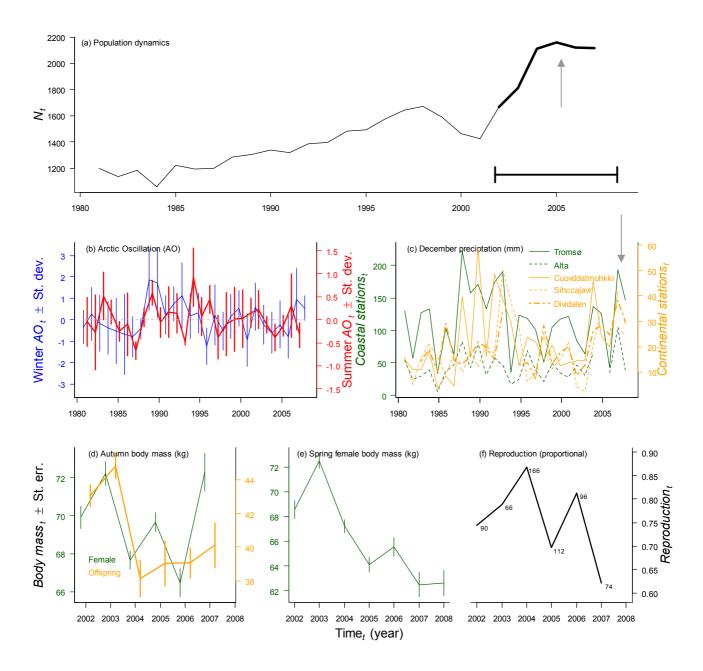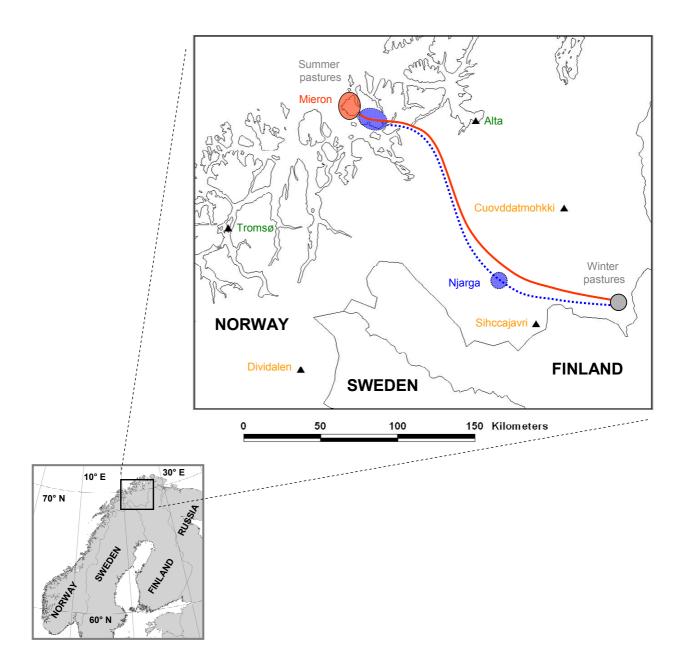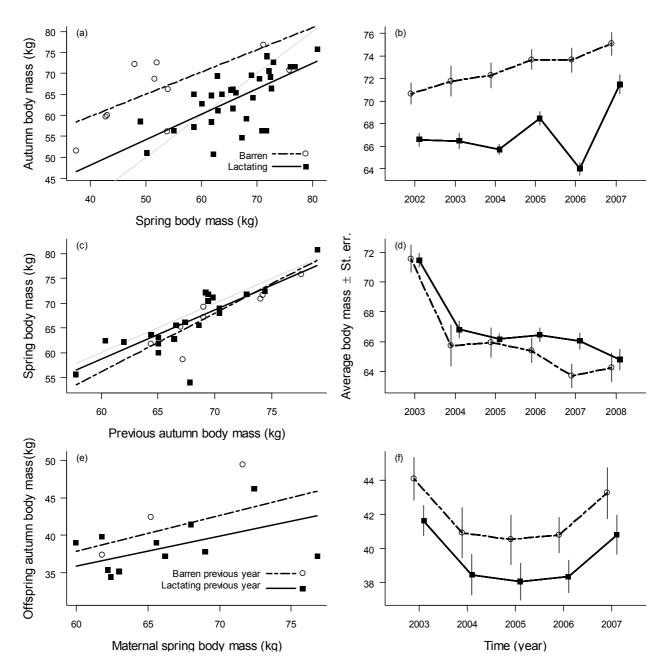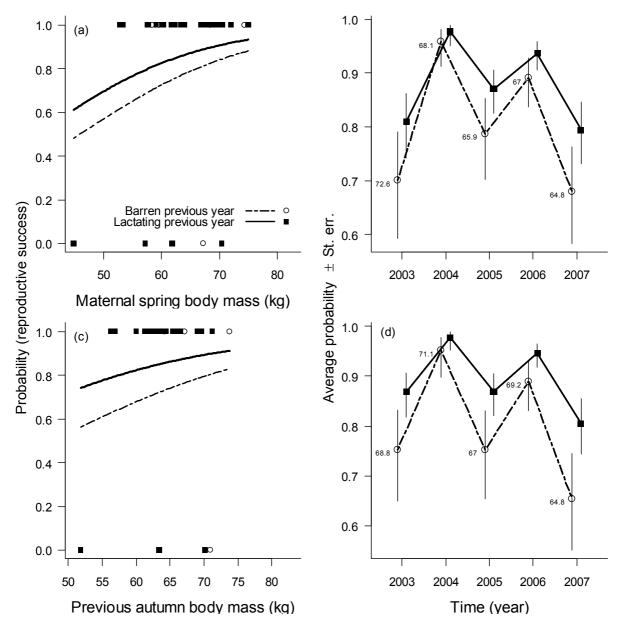
Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

S1: STATISTICAL ANALYSIS – PREDICTIONS, CONFOUNDING AND POSSIBLE SPURIOUS EFFECTS

As this is an observational study there are several confounding factors that can potentially induce bias in our analyses, but this problem is reduced to a minimum. First, we reduced the probability of pursuing spurious effects (Anderson *et al.*, 2001) as we had *a priori* expectations that formed the basis for the set of candidate models in which we selected the most parsimonious model (e.g. Anderson, Burnham & Thompson, 2000; Buckland, Burnham & Augustin, 1997; Burnham & Anderson, 2002). Second, we applied statistical control of initial body mass in order to assess temporal correlation in body mass, i.e. to 'reset our system to a given time' (Fig. S1.1). The biological rationale for this was that we assess *mass development* from one point in time to another. Moreover, by providing statistical control for initial body mass we also control for potential confounders like: (1) lagged and current reproductive success and reproductive allocation (Bårdsen *et al.*, 2008; Cameron *et al.*, 1993; Fauchald *et al.*, 2004; Kojola, 1993); (2) age (Kojola *et al.*, 1998; Reimers, Klein & Sorumgard, 1983; Rødven, 2003); (3) survival (Tveraa *et al.*, 2003); (4) parasitic infestation (Fauchald *et al.*, 2007); (5) social rank (Holand *et al.*, 2004; Kojola, 1989); and (6) population density and environmental conditions (Fauchald *et al.*, 2004; Kumpula, Colpaert & Nieminen, 1998; Tveraa *et al.*, 2007). We lack information on many of the above factors, but have information on age. Three age-classes, i.e. the juvenile, adult and senescent stage, has generally been identified for large-herbivores (Gaillard *et al.*, 2000: Fig. 1). As reindeer are harvested we do not have senescent individuals in our study. Juveniles (≤ 1 year) was smaller in the spring compared to the older classes (B.-J. Bårdsen, T. Tveraa, P. Fauchald & K. Langeland, unpublished results), and as they are not sexually mature we removed them from the data. Consequently, the analyses in the present study focus on the prime-aged segment of the adult stage. Third, even though we do not provide information about density or environmental conditions directly in the analyses these effects are at least partly controlled for by our inclusion of year and herd (Fig. 1-2). In essence, as

we based our analyses on *a priori* expectations and because we provided statistical control for initial

body mass, year and herd we are confident that our analyses are robust.

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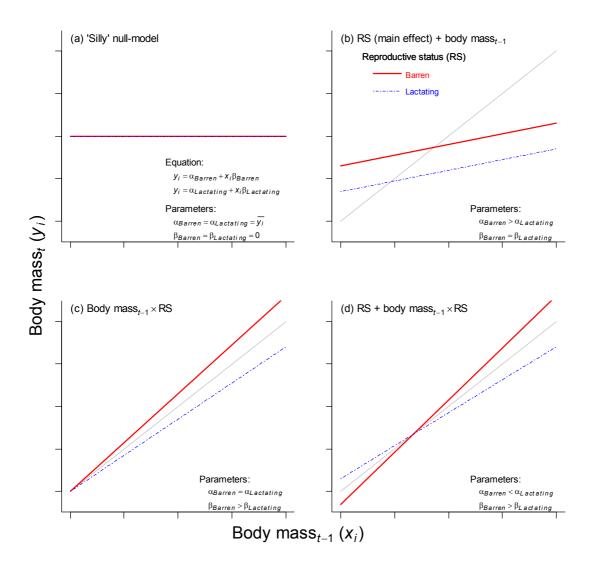
(a) 'Silly' null-model

Equation:
$$y_i = \alpha_{Barren} + x_i \beta_{Barren}$$
$$y_i = \alpha_{Lactating} + x_i \beta_{Lactating}$$
Parameters:
$$\alpha_{Barren} = \alpha_{Lactating} = \overline{y}_i$$
$$\beta_{Barren} = \beta_{Lactating} = 0$$

(b) RS (main effect) + body mass$_{t-1}$

Reproductive status (RS)
— Barren
·−· Lactating

Parameters:
$$\alpha_{Barren} > \alpha_{Lactating}$$
$$\beta_{Barren} = \beta_{Lactating}$$

(c) Body mass$_{t-1} \times$ RS

Parameters:
$$\alpha_{Barren} = \alpha_{Lactating}$$
$$\beta_{Barren} > \beta_{Lactating}$$

(d) RS + body mass$_{t-1} \times$ RS

Parameters:
$$\alpha_{Barren} < \alpha_{Lactating}$$
$$\beta_{Barren} > \beta_{Lactating}$$

Body mass$_t$ (y_i)

Body mass$_{t-1}$ (x_i)

Fig. S1.1. A graphical representation of possible predictions in the analyses of body mass. Body mass in any point in time (t) can be a function of body mass earlier ($t-1$; hereafter termed initial body mass) and reproductive status (hereafter RS; 'barren' versus 'lactating'). The two equations (a) show how separate models, defined by the parameters α and β, can be used to predict the relationship between y_i and x_i across the RS groups. (a) *The null-model*, where body mass is not explained by neither RS nor initial body mass; both the intercept (α), equaling the average of the predictor, and the slope (β), equaling zero, is similar across the RS groups. (b) *The main-effect model*, where mean body mass is different across the RS groups: α is now higher for barren compared to lactating females, but β is similar. The dotted grey line shows the predicted relationship for $\alpha = 0$ and $\beta = 1$, which indicates where $y_i = x_i$. Above this line individuals have gained body mass and below this line they have lost body mass between $t-1$ and t. (c) *The initial body mass × RS model*, where the relationship between initial body mass and body mass is different across the RS groups: α is equal across the groups, but β is higher for barren compared to lactating females. (d) *The main-effect and interaction model*, where both mean body mass and the relationship between initial body mass and body mass is different across the RS groups: α is higher for lactating compared to barren females whereas for β the difference is opposite.

S2: MODEL SELECTION & THE SET OF CANDIDATE MODELS IN THE ANALYSES OF BODY MASS

Selecting the models used for inference in the three analyses presented in Table 1 was performed within a model selection framework (e.g. Anderson et al. 2000; Buckland et al. 1997; Burnham and Anderson 2002): First, a pool of candidate models was defined. Defining the set of candidate models is an important but often underemphasized part of an statistical analysis: 'models without biological support should not be included in the set of candidate models' (Burnham and Anderson 2002). Thus, we kept initial body mass (either spring or autumn females body mass), reproductive status or previous reproductive status [factor with two levels: 'negative' (barren) or 'positive' (lactating) during either summer or last year], and the interaction between the two in all analyses based on our *a priori* expectations (see Table S1.1-3 for details). Second, in each analysis, rescaling and ranking models relative to the value of the model with the lowest second-order *Akaike's Information Criterion* (AICc[1]) value was performed (Burnham and Anderson 2002: Δi denotes this difference for model *i*).

LITTERATURE CITED

Anderson DR, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912-923

Buckland ST, Burnham KP, Augustin NH (1997) Model selection: an integral part of inference. Biometrics 53:603-618

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, Second edn. Springer, Inc., New York, USA.

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[1] AICc is often called a small sample size adjusted *Akaike's Information Criterion* (AIC). If the sample size (*n*) is large relative to the number of parameters (*K*), a model's AICc value will converge towards its AIC value (Burnham and Anderson2002).

Table S1.1. The relative evidence for each candidate model (*i*) in Table 1a based on differences in AICc values (Δ*i*). The model in <u>*underlined italics*</u> were selected and used for inference in each analysis as it was the simplest models with an $\Delta_i \leq 1.5$). The predictors included in the different models are marked with an 'x'.

i	Spring body mass (BM)[a]	Reproductive status (RS)[a]	BM × RS[a]	Herd (H)[a]	Year (Y)[a]	BM × H	RS × H	BM × Y	RS × Y	H × Y	BM × RS × H	BM × RS × Y	BM × H × Y	RS × H × Y	BM × RS × H × Y	*K*[b]	Δ_i
1.	**x**	**x**	**x**	x	x	x	x	x	x	x	x	x	x	x	x	48	36.52
2.	**x**	**x**	**x**	x	x	x	x	x	x	x	x	x	x	x		44	25.89
3.	**x**	**x**	**x**	x	x	x	x	x	x	x		x	x	x		43	23.75
4.	**x**	**x**	**x**	x	x	x	x	x	x	x		x	x			38	21.07
5.	**x**	**x**	**x**	x	x	x	x	x	x	x		x				33	17.92
6.	**x**	**x**	**x**	x	x	x	x	x	x	x						28	18.05
7.	**x**	**x**	**x**	x	x	x	x	x	x							23	14.10
8.	**x**	**x**	**x**	x	x			x	x	x						22	12.03
9.	**x**	**x**	**x**	x	x			x		x						17	2.02
<u>*10.*</u>	<u>**x**</u>	<u>**x**</u>	<u>**x**</u>	<u>x</u>	<u>x</u>				<u>x</u>							<u>*16*</u>	<u>*0.00*</u>
11.	**x**	**x**	**x**	x	x											11	7.17
12.	**x**	**x**	**x**		x											10	11.77
13.	**x**	**x**	**x**													5	71.93

[a]The predictors to the left in **bold** were kept in all models based on our *a priori* expectations.

[b]*K* denotes the number of parameters, whereas the number of observations (*n*) was 495 for all models.

Table S1.2. The relative evidence for each candidate model (*i*) in Table 1b based on differences in AICc values (Δ*i*). The model in <u>*underlined italics*</u> were selected and used for inference in each analysis as it was the simplest models with an $\Delta_i \leq 1.5$). The predictors included in the different models are marked with an 'x'.

i	Autumn body mass (BM)[a]	Previous autumn reproductive status (RS)[a]	BM × RS[a]	Herd (H)[a]	Year (Y)[a]	BM × H	RS × H	BM × Y	RS × Y	H × Y	BM × RS × H	BM × RS × Y	BM × H × Y	RS × H × Y	BM × RS × H × Y	K[b]	Δ_i
1.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	40	12.74
2.	x	x	x	x	x	x	x	x	x	x	x	x	x	x		37	7.89
3.	x	x	x	x	x	x	x	x	x	x		x	x	x		36	10.18
4.	x	x	x	x	x	x	x	x	x	x		x	x			32	13.24
5.	x	x	x	x	x	x	x	x	x	x		x				28	5.05
6.	x	x	x	x	x	x	x	x	x	x						24	0.00
7.	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*							*20*	*0.78*
8.	x	x	x	x	x		x	x	x							19	5.65
9.	x	x	x	x	x		x		x							15	10.74
10.	x	x	x	x	x				x							14	17.18
11.	x	x	x	x	x											10	14.63
12.	x	x	x		x											9	18.60
13.	x	x	x													5	167.075

[a]The predictors to the left in **bold** were kept in all models based on our *a priori* expectations.

[b]*K* denotes the number of parameters, whereas the number of observations (*n*) was 439 for all

models.

Table S1.3. The relative evidence for each candidate model (*i*) in Table 1c based on differences in AICc values (Δ*i*). The model in <u>*underlined italics*</u> were selected and used for inference in each analysis as it was the simplest models with an $\Delta_i \leq 1.5$). The predictors included in the different models are marked with an 'x'.

i	Maternal spring body mass (BM)[a]	Previous autumn reproductive status (RS)[a]	BM × RS[a]	Herd (H)[a]	Year (Y)[a]	BM × H	RS × H	BM × Y	RS × Y	H × Y	BM × RS × H	BM × RS × Y	BM × H × Y	RS × H × Y	BM × RS × H × Y	*K*[b]	Δ*i*
1.	**x**	**x**	**x**	x	x	x	x	x	x	x	x	x	x	x	x	30	90.30
2.	**x**	**x**	**x**	x	x	x	x	x	x	x	x	x	x	x		29	68.01
3.	**x**	**x**	**x**	x	x	x	x	x	x	x		x	x	x		28	62.87
4.	**x**	**x**	**x**	x	x	x	x	x	x	x			x	x		27	43.80
5.	**x**	**x**	**x**	x	x	x	x	x	x	x			x			24	29.52
6.	**x**	**x**	**x**	x	x	x	x	x	x	x						21	19.36
7.	**x**	**x**	**x**	x	x	x	x	x	x							18	9.75
8.	**x**	**x**	**x**	x	x			x	x	x						17	12.90
9.	**x**	**x**	**x**	x	x			x	x							14	4.77
10.	**x**	**x**	**x**	x	x				x							13	2.97
11.	**x**	**x**	**x**	x	x											10	1.48
12.	*x*	*x*	*x*		*x*											*9*	*0.00*
13.	**x**	**x**	**x**													5	3.48

[a]The predictors to the left in **bold** were kept in all models based on our *a priori* expectations.

[b]*K* denotes the number of parameters, whereas the number of observations (*n*) was 98 for all models.

S3: MODEL SELECTION & THE SET OF CANDIDATE MODELS IN THE ANALYSES OF OFFSPRING PRODUCTION

Table S3.1. The relative evidence for each candidate model (i) in Table 2a based on differences in AICc values (Δi; see S2 for details). The model in *underlined italics* were selected and used for inference in each analysis as it was the simplest models with an $\Delta_i \leq 1.5$). The predictors included in the different models are marked with an 'x'.

i	Maternal spring body mass (BM)[a]	Previous autumn reproductive status (RS)[a]	BM × RS[a]	Herd (H)[a]	Year (Y)[a]	BM × H	RS × H	BM × Y	RS × Y	H × Y	BM × RS × H	BM × RS × Y	BM × H × Y	RS × H × Y	BM × RS × H × Y	K[b]	Δ_i
1.	**x**	**x**	**x**	x	x	x	x	x	x	x	x	x	x	x	x	40	31.59
2.	**x**	**x**	**x**	x	x	x	x	x	x	x	x	x	x	x		36	24.77
3.	**x**	**x**	**x**	x	x	x	x	x	x	x		x	x	x		35	32.31
4.	**x**	**x**	**x**	x	x	x	x	x	x	x		x	x			31	27.42
5.	**x**	**x**	**x**	x	x	x	x	x	x	x		x				27	23.73
6.	**x**	**x**	**x**	x	x	x	x	x	x	x						23	17.57
7.	**x**	**x**	**x**	x	x	x	x	x	x							19	12.62
8.	**x**	**x**	**x**	x	x		x	x	x							18	10.91
9.	**x**	**x**	**x**	x	x		x		x							14	6.55
10.	**x**	**x**	**x**	x	x				x							13	4.44
11.	*x*	*x*	*x*	*x*	*x*											*9*	*0.00*
12.	**x**	**x**	**x**		x											8	10.13
13.	**x**	**x**	**x**													4	22.34

[a]The predictors to the left in **bold** were kept in all models based on our *a priori* expectations.

[b]K denotes the number of parameters, whereas the number of observations (n) was 319 for all models.

Table S3.2. The relative evidence for each candidate model (*i*) in Table 2b based on differences in AICc values (Δ*i*; see S2 for details). The model in <u>*underlined italics*</u> were selected and used for inference in each analysis as it was the simplest models with an Δ*i* ≤ 1.5). The predictors included in the different models are marked with an 'x'.

i	Maternal previous autumn body mass (BM)[a]	Previous autumn reproductive status (RS)[a]	**BM × RS**[a]	Herd (H)[a]	Year (Y)[a]	BM × H	RS × H	BM × Y	RS × Y	H × Y	BM × RS × H	BM × RS × Y	BM × H × Y	RS × H × Y	BM × RS × H × Y	*K*[b]	Δ*i*
1.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	39	41.46
2.	x	x	x	x	x	x	x	x	x	x	x	x	x	x		36	34.30
3.	x	x	x	x	x	x	x	x	x	x		x	x	x		35	36.43
4.	x	x	x	x	x	x	x	x	x	x		x	x			31	29.01
5.	x	x	x	x	x	x	x	x	x	x		x				27	28.17
6.	x	x	x	x	x	x	x	x	x	x						23	19.32
7.	x	x	x	x	x	x	x	x	x							19	13.55
8.	x	x	x	x	x			x	x	x						18	11.71
9.	x	x	x	x	x	x		x								14	7.22
10.	x	x	x	x	x				x							13	5.18
<u>*11.*</u>	<u>*x*</u>	<u>*x*</u>	<u>*x*</u>	<u>*x*</u>	<u>*x*</u>											<u>*9*</u>	<u>*0.00*</u>
12.	x	x	x		x											8	11.56
13.	x	x	x													4	21.64

[a]The predictors to the left in **bold** were kept in all models based on our *a priori* expectations.

[b]*K* denotes the number of parameters, whereas the number of observations (*n*) was 319 for all models.