Risk sensitive reproductive strategies

The effect of environmental unpredictability

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ABSTRACT

A crucial task in ecology is to quantify trade offs between competing demographic processes for experienced by individuals that inhabit unpredictable environments. Perhaps the most widely studied trade off is that between current reproduction and future survival (‘the cost of reproduction’). While experimental studies have been widely used to quantify life history strategies in birds, virtually no experimental studies have been carried out on large and free ranging mammals. This thesis quantifies how female reindeer *Rangifer tarandus* subject to variability in food availability, trade their resources between reproduction and body mass to ensure own survival. By combining two experiments, one observational study and one theoretical model, this thesis show that: (1) Individuals subject to reduced food availability in one winter feeding promptly reduced their reproductive allocation the following summer to increased their autumn body mass. On the other hand, short-term improved conditions did not result in increased reproductive allocation. (2) Long-term improved winter feeding conditions did, however, result in increased reproductive allocation. (3) Reproduction was costly, especially for smaller females, as occasional harsh winters and high population density resulted in reduced reproduction and lowered female body mass. Moreover, a successfully reproducing female produced a smaller offspring in the coming year relative to a barren one. Reindeer also differ in their intrinsic quality as successfully reproducing females’ showed an increased probability of reproducing also in the following year. (4) In harsh and unpredictable winter conditions, the optimal reproductive strategy involved a low reproductive allocation per unit female spring body mass. Under such conditions females increased their autumn body mass to enhance their own survival. Conversely, the optimal reproductive strategy in benign and predictable conditions involved a higher reproductive allocation. (5) Reproductive strategies and environmental conditions had significant effects on population dynamics. Female reindeer do not to jeopardize their own survival and adjust their reproductive allocation in order to buffer periods of low food availability in a risk sensitive manner.

Key words: cost of reproduction; evolution; environmental stochasticity; phenotypic plasticity; *Rangifer tarandus*; risk sensitive life histories.

PAPERS INCLUDED IN THE THESIS

Paper 1

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz and R. A. Ims. 2008. *Experimental evidence for a risk sensitive life history allocation in a long-lived mammal.* **Ecology** 89:829-837. (doi: 10.1890/07-0414.1)

Paper 2

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland and M. Nieminen. in press. *Experimental evidence of cost of lactation in a low risk environment for a long-lived mammal.* **Oikos**. (doi: 10.1111/j.1600-0706.2008.17414.x)

Paper 3

Bårdsen, B.-J., T. Tveraa, P. Fauchald and K. Langeland. manuscript. *Observational evidence of a risk sensitive reproductive allocation in a long-lived mammal.*

Paper 4

Bårdsen, B.-J., J.-A. Henden, P. Fauchald, T. Tveraa and A. Stien. manuscript. *Plastic reproductive allocation as a buffer against environmental unpredictability – linking life history and population dynamics to climate.*

PREFACE

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INTRODUCTION

Biologists, anthropologists and psychologists have for a long time recognized that the theory of economic allocation of a limited budget can be useful in studies of optimal behaviour (e.g. Real and Caraco 1986, Stephens and Krebs 1986 ch. 6, Mace and Houston 1989, Mace 1990, 1993, Winterhalder et al. 1999). Risk sensitivity and related concepts have its roots within economical theory, but in biology risk sensitivity has its basis in studies of optimal foraging. The definition of risk used both in this thesis and its associated articles is similar to the definition used in risk sensitive foraging (reviewed in e.g. Real and Caraco 1986, Kacelnik and Bateson 1996): risk is defined as unpredictable variation in the outcome of behaviour, with consequences for an organism's fitness (the ultimate currency in evolutionary biology), utility (an economic currency) or value[1] (a synonym for both currencies: sensu Winterhalder et al. 1999, Winterhalder 2007). It is important to keep in mind that the probability distribution of outcomes can be known to the organism based on past experience, but stochasticity makes it impossible for organisms to predict with certainty any particular future outcome (Kacelnik and Bateson 1996). Risk is not the same as uncertainty, i.e. incomplete information, as risk cannot be overcome simply by acquiring more information (Kacelnik and Bateson 1996, Winterhalder et al. 1999, Winterhalder 2007). Risk sensitivity analysis is relevant for a wide range of different behaviours, such as reproductive behaviour (e.g. Bednekoff 1996, Winterhalder and Leslie 2002), as risk sensitivity should be presumed important whenever: (i) the fitness function is nonlinear, and (ii) one or more of the behavioural alternatives is characterized by unpredictable fitness outcomes (e.g. Stephens and Krebs 1986, Kacelnik and Bateson 1996, Winterhalder et al. 1999, Winterhalder 2007).

The fitness function (deduced from utility theory) makes an explicit assumption that organisms make consistent and rational choices based on the information they have at hand (Stephens and Krebs 1986). Specifically, organisms facing stochastic environments should solve two distinct problems: (i) the organisms must learn the fitness associated with different behaviours ('a problem of information'); (ii) then, the organism must select a strategy for exploiting those distributions ('a problem of risk') (Real and Caraco 1986). First, individuals that successfully track environmental fluctuations will have a selective advantage over poor trackers (Boyce and Daley 1980). Second, the relationship between reward[2] and fitness must be nonlinear if organisms are said to be risk sensitive (linear relationships imply risk neutrality: e.g. Stephens and Krebs 1986, Kuznar 2001, Kuznar 2002, Kuznar and Frederick 2003). If the fitness function is: (i) concave-down, i.e. negatively accelerating, individuals are said to be risk averse as the rate of increase in fitness decreases as the amount of reward increases ('the law of marginal diminishing returns'); and (ii) concave-up, i.e. positively accelerating, individuals are said to be risk prone as each unit of additions reward is valued more than the previous (Stephens and Krebs 1986: Fig. 6.1-2). Risk sensitivity can, thus, be used to understand under what circumstances individuals are willing to

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[1] 'Fitness' is used instead of 'utility' or 'value' through the rest of this study. Utility measures 'the level of satisfaction' associated with a specific good or decision (Kuznar 2001) and this is the basic organizing principle that individuals subject to certain constraints seek to maximize (e.g. Real and Caraco 1986). This can be illustrated using an example from economy: winning a price of 100 € makes a substantial contribution to the utility of a poor person, whereas the same prize makes an insignificant contribution to the utility of a multi-millionaire.

[2] 'Reward' can be used synonymously to 'wealth' or 'good', which is typically the same as 'individual state' (e.g. Houston and McNamara 1999).

accept or avoid gambling: being risk neutral[3] means that the cost of loosing is similar to the benefit of winning; being risk averse[3] means that the cost of loosing is large compared to the benefit of winning; whereas being risk prone[3] means the potential cost is minor relative to the benefit.

A central issue in life-history theory is how individuals allocate resources between current reproduction and future survival, a trade-off known as the cost of reproduction (e.g. Roff 1992, Stearns 1992). How environmental stochasticity affects life-history evolution is poorly understood except that long-lived organisms generally favor own survival over reproduction (e.g. Lindén and Møller 1989, Erikstad et al. 1998, Gaillard et al. 1998, Gaillard et al. 2000, Ellison 2003, Gaillard and Yoccoz 2003). Many organisms inhabit fluctuating environments, where fluctuations usually consist of a predictable seasonal component and a more unpredictable stochastic variation around this seasonal trend (**Paper 4**). Organisms inhabiting this type of environments have to make behavioural decisions without full knowledge about future environmental conditions (e.g. McNamara et al. 1995). Reproduction typically takes place during the favourable season (summer), whereas survival is particularly constrained in the unfavourable season (winter: Sæther 1997). In this type of environments, late winter conditions can have profound effects on both survival and reproduction (Coulson et al. 2000, Patterson and Messier 2000, Coulson et al. 2001, DelGiudice et al. 2002). Autumn body mass, which represents an insurance against winter starvation, is then traded against the resources a female can allocate to her offspring during summer as accumulation of fat reserves during summer might compete with lactation (Clutton-Brock et al. 1989, Clutton-Brock et al. 1996, Fauchald et al. 2004, Festa-Bianchet and Jorgenson 1998, Reimers 1972, Skogland 1985, Tveraa et al. 2003, **Paper 1-2**). Body mass is a proxy for condition or reserves, and an important trait affecting both survival and reproduction[4]. Consequently, in a given summer a female has to choose how many resources to allocate to somatic growth vs. reproduction: if a female allocates too much in reproduction this will reduce her ability to build an insurance against winter starvation (**Paper 1-4**).

Risk sensitivity in the context of the present thesis can be understood as a combination of the probability of encountering an extreme winter and the consequences such winters have on fitness (**Paper 1-4**). First, the outcome of a given reproductive allocation on survival is unpredictable due to the stochastic nature of winter climatic conditions (**Paper 4**): even though females might have 'estimated' this statistical distribution based on previous experience, environmental stochasticity makes any reliable forecasting of climatic events practically impossible[5]. Second, the relationship between winter weather conditions and fitness is nonlinear as: (i) the combination of an extremely harsh winter and low body reserves is not only fatal for reproductive success (e.g. juvenile and

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[3] In the 'standard design of risk sensitive foraging experiments' (reviewed by Stephens and Krebs 1986, Kacelnik and Bateson 1996) risk prone and risk averse have been defined as: "Given a choice between two equal means, an organism is said to be risk-prone if it prefers the more variable option and risk-averse if it prefers the less variable option" (Houston 1991). Conversely, an individual is risk neutral if it shows no preference.

[4] Body mass acts as a state variable (e.g. Houston and McNamara 1999), which is a currency that can be traded for reproduction or survival.

[5] Since meteorologists do only produce reliable predictions of weather phenomena for more than perhaps a few days into the future it is unlikely that wild herbivores can predict weather ~7 month into the future. Meteorologists have an advanced knowledge about weather systems (high level of information), but the stochastic nature of these systems makes accurate predictions far into the future impossible. The *Norwegian Meteorological Institute*, for example, does not forecast more than three months into the future (http://retro.met.no/sesongvarsler/introduksjon.html).

neonatal survival) but it can even greatly reduce adult survival (Skogland 1985, Clutton-Brock et al. 1992, Clutton-Brock et al. 1996, Aanes et al. 2000, Aanes et al. 2002, Tveraa et al. 2003); whereas (ii) extremely benign winters do not represent bonanzas as survival and reproduction are not boosted way above that of an average winter (Fauchald et al. 2004, **Paper 1**-**3**). Using terms from risk sensitivity, such an asymmetric response in the costs and benefits relative to environmental unpredictability indicates that long-lived organisms should be risk averse as they should be unwilling to expect the coming winter to be a benign one (**Paper 1**). It is important to keep in mind that organisms cannot manipulate the probability of encountering a harsh winter, but they can buffer the adverse consequences of such winters by reducing their summer reproductive allocation in order to increase their own autumn body reserves (Adams 2005, **Paper 1**). Organisms inhabiting such systems should not prepare for an average winter, but for extreme events that might happen from time to time (**Paper 2**).

The optimal reproductive strategy will, thus, depend on the expected winter environmental conditions. A changed distribution in winter conditions can have important consequences for both reproduction and survival. Individuals experiencing stable and benign winter conditions can afford a low autumn body mass and might therefore increase their reproductive allocation. On the other hand, animals experiencing harsh and variable winter conditions should maximize their autumn body mass by lowering their reproductive allocation. Accordingly, organisms experiencing unpredictable environments should adopt a *risk sensitive reproductive strategy* by adjusting their reproductive allocation during summer according to the chance of starvation the following winter (**Paper 1**-**4**). For a given body mass and distribution of environmental conditions, individuals can play different strategies (**Paper 4**). 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 a low reproductive reward and represents a *risk averse reproductive strategy*. Moreover, when benign conditions appear for many years, individuals should increase their reproductive allocation as the amount of autumn body reserves that is needed for insurance against winter starvation will be lowered under such conditions. Population density, which in interaction with winter climate, can have profound negative effects on survival and reproduction (e.g. Grenfell et al. 1998, Coulson et al. 2000), are confounded with environmental conditions as harsh conditions generally supports lower densities than benign conditions (e.g. Morris and Doak 2002). Thus, density may also affect the optimal reproductive allocation strategy (**Paper 3**-**4**). For example, increased densities of reindeer *Rangifer tarandus* have direct effects on the individuals through increased competition for resources (Tveraa et al. 2007), and indirect effects through long-term effects on the pastures (Bråthen et al. 2007, Tveraa et al., *unpublished results*). In sum, environmental conditions and density have effects on how organisms should allocate resources between reproduction and somatic growth (**Paper 1**-**4**).

A *risk sensitive reproductive strategy* is one of several factors that can be of importance for population dynamics (**Paper 4**). Populations of large terrestrial mammalian herbivores (with an adult mass ≥ 10 kg: Gaillard et al. 2000 hereafter referred to as 'large herbivores') in northern and seasonal environments show different population dynamics. How individuals allocate resources into reproduction may provide an explanation for this. The Soay sheep *Ovis aries* on Hirta, Scotland has, for example, a high population growth rate due to a high fecundity, low age at first reproduction and early lambing (Clutton-Brock et al. 1996, Clutton-Brock and Coulson 2002, Clutton-Brock and Pemberton 2004). Over-compensatory density dependence combined with harsh environmental conditions results in more or less regular events of mass starvation and population crashes during winter (Clutton-Brock et al. 1996, Grenfell et al. 1998, Coulson et al. 2001). In contrast, red deer *Cervus elaphus* on Isle of May, Scotland has a much lower population growth rate (Clutton-Brock et al. 1987). The population is regulated through a low fecundity, late age at maturity, late calving and direct density dependent juvenile mortality resulting in relatively stable populations (Clutton-Brock and Coulson 2002). In semi-domestic reindeer, Norway differences in productivity, due to differences in reproductive allocation as an adaptation to buffer winter climate severity (**Paper 1**-**3**), can have profound effects on population dynamics as: a combination of climate severity, harvest and foraging conditions has a profound impact on average population densities, individual body masses, and population dynamics (Tveraa et al. 2007). In sum, differences in reproductive strategies might have important consequences on the cost of reproduction and on population dynamics (Clutton-Brock et al. 1996, Clutton-Brock and Coulson 2002, **Paper 4**).

Apart from the assumptions underlying risk sensitivity, a few more assumptions should be fulfilled for defining *risk sensitive reproductive strategies*. First, organisms must be fitness maximizing, which is not an assumption specific for this study as it is a general assumption for evolutionary biology as a discipline (e.g. McNamara 2000, Coulson et al. 2006). Second, the organism of interest should be iteroparous (i.e. long-lived with many potential breeding attempts per lifetime: Schaffer 1974, Stearns 1992). This assures that an organism can spread the cost of breeding across several attempts. Third, the organism should experience unpredictable costs of reproduction. If no cost of reproduction does occur or if this cost is predictable there is no reason for spreading the potential negative consequences of reproduction over several breeding attempts. Fourth, the organism should be able to build energy reserves functioning as insurance against adverse environmental conditions. Fifth, the environment inhabited by the organism should be characterized by either strong seasonality (a favourable breeding season and an unfavourable non-breeding season) or at least by periods of favourable and unfavourable conditions. During the favourable season, organisms trade resources to reproduction against resources for building body reserves. The overall objective of this thesis was to investigate how environmental conditions affect reproductive strategies, and to investigate how interactions between optimal reproductive strategies and the environment can shape population dynamics. This thesis uses reindeer as a biological model as this species fulfils the above assumptions. The following research questions were addressed:

(1) How do improved and reduced winter feeding conditions on a short-term basis affect how individuals allocate their resources between reproduction and gain in body mass during summer (**Paper 1**-**3**)?
(2) How do long-term changed winter feeding conditions affect summer reproductive allocation (**Paper 1**-**2**)?
(3) How does the cost of reproduction vary according to individual quality, and factors extrinsic to the individuals like winter climatic conditions and population density (**Paper 1**-**4**)?
(4) How do winter climatic conditions affect the optimal reproductive strategy (**Paper 4**)?
(5) How do plastic life histories and climate affect population dynamics (**Paper 4**)?

METHODS

Study species and area

Reindeer belongs to the family Cervidae and the order Cetartiodactyla (Price et al. 2005). Cetartiodactyla is a relatively new order that includes the two former orders: Artiodactyla ('even-toed hoofed mammals') and Cetacea (whales & dolphins) (Price et al. 2005). Reindeer is a sexually dimorphic species where females are smaller than males (e.g. Reimers 1983, Reimers et al. 1983), and during most of the year the sexes are separated. The rut and conception happens in the autumn (e.g. Skogland 1994), and calving usually takes place in May (Reimers et al. 1983, Flydal and Reimers 2002). Reindeer are group living and highly migratory as they move between distinct summer and winter pastures (e.g. Folstad et al. 1991, Skogland 1994, Fauchald et al. 2007).

The thesis is based on empirical data from two semi-domesticated herds in Northern Norway (**Paper 1** & **Paper 3**) and one in Northern Finland (**Paper 2**). The number of semi-domestic reindeer in Norway increased towards the late 1980's (e.g. **Paper 3**:Fig. 1a). This trend was particularly strong in the northernmost part of Norway, where the peak in reindeer numbers was followed by a population decrease that continued throughout the 1990's (Tveraa et al. 2007: Fig. 1). The herds are organized in herding districts that are separated by fences and natural boarders. Since all animals are ear marked according to owner, virtually no effective movement between different populations exist (Tveraa et al. 2007). Our data source in Finland is from the research herd in Kaamanen, which consist of ~80 females with known life histories (**Paper 2**).

Scientific approach

Research on large herbivores has generally been performed using descriptive long-term observational studies and lack of experimental manipulations (Caughley 1981, Gaillard et al. 1998). Experiments on wild animals can be difficult to perform for practical reasons, especially for long-lived species that covers large geographical area, as experiments can be time consuming, expensive and impracticable (Turchin 1995). Consequently, there is still a need for long-term studies of marked individuals and with experimental designs that allow the relationship between population parameters and variables such as climate and density to be estimated (Festa-Bianchet et al. 1998, Gaillard et al. 1998). Semi-domestic reindeer provides a unique opportunity in this context because: (i) herds are gathered at least once each year for marking and slaughtering (e.g. **Paper 1** & **Paper 3**); (ii) they are managed within and exposed to the same natural environment as wild reindeer used a long time ago (Parks et al. 2002); (iii) it is easier to identify the mechanisms causing demographic changes in larger compared to smaller organisms (Sæther 1997); and (iv) it is possible, within a reasonable time frame, to generate knowledge of importance to researchers, authorities, as well as reindeer herders.

Ecological questions should be assessed with an analytical approach that combines statistical analyses of observational data, experiments, and mathematical models (Turchin 1995). The present thesis tests a common scientific hypothesis using these three approaches: an experimental protocol (**Paper 1** & **Paper 2**); an observational protocol (**Paper 3**); and a theoretical model (**Paper 4**). The three approaches have different advantages and disadvantages. First, well-designed experiments[6] have an advantage compared to the other approaches as this type of studies can make so-called 'design-based inference', which is called 'strong inference' due to its ability to reveal evidence of causation (e.g. Quinn and Keogh 2002, Crawley 2003, Yoccoz and Ims 2008). A critical issue in ecological experiments, however, is whether the applied treatment is relevant for addressing the research question of interest and if the level of treatment is realistic with respect to a natural setting (discussed in **Paper 1** & **Paper 2**). Second, observational studies, which do not include the design properties of experiments, have the advantages of assessing research questions in a natural setting. This advantage, however, comes with the cost of possible confounding (discussed in **Paper 3**:S1). As observational protocols can only reveal 'model-based inference' they are often said to reveal 'weak inference' (e.g. Quinn and Keogh 2002, Crawley 2003, Yoccoz and Ims 2008). Third, models are useful tools in assessing mechanisms that might occur in nature. Numerous definitions exists of what models are and what they can be used for, but as there exist many different types of models developed for a wide range of different topics I will not enter such a general discussion. In the context of the present thesis it might, however, be useful to think of a model as an idealized, or simplified, representation of reality. These sorts of 'conceptual models' can be viewed as tools for testing arguments in a formal mathematical setting, where models can be used to test if specific patterns emerge from known processes and mechanisms given a set of more or less realistic assumptions (e.g. Kokko 2007).

Study design

Manipulation of winter conditions: supplementary feeding vs. natural pastures (**Paper 1**)

In both experiments in this study, which was performed in Northern Norway, females were included and allocated to different experimental groups according to the order in which they appeared in the corral. This was done under the assumption that this represented a sufficient randomization. We tested the design with respect to initial female body mass, a potentially confounding covariate (see *Introduction*), and as this state variable was equally distributed within the experimental groups we concluded that the study was sufficiently randomized. We used one herd where females had received supplementary feeding for years, and another herd where females utilized only natural pastures (see **Paper 1**:Fig. 1 for details). Manipulation of winter feeding conditions on a short-term basis was performed by moving individuals from one herd to the other: (i) translocation of individuals from the herd utilizing natural pastures to the herd receiving supplementary feeding ('improved winter conditions'); and (ii) translocation of individuals from the herd receiving supplementary feeding to the herd utilizing natural pastures ('reduced winter conditions'). Additionally, the control groups from the two experiments were used in an analysis of the effects of long-term supplementary feeding. Individual body mass as a response was recorded during summer, autumn and the coming winter. Multiple observations of females with a calf at foot were used to identify mother-calf relationships or whether a female was barren within a given year. The experiments were replicated in two different years (2003 & 2004) using a new set of individuals, and individuals were followed from January (initiation) to the next January (finalization).

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[6] The following assumptions are often discussed: manipulation (including controls), randomization, replication, realism and representation.

Manipulation of winter conditions and reproduction: supplementary feeding and reproduction (**Paper 2**)

This experiment was performed in Northern Finland during 2007-2008. Only initially pregnant females were included in this experiment, and a stratified-randomized design ensured that initial female body mass, and consequently also initial age, had the same distribution in the experimental groups (**Paper 2**). Individuals were assigned to one of two experimental manipulations: (i) environmental manipulation, which consisted of control females on natural pastures and a group of females receiving supplementary feeding; and (ii) reproductive manipulation, which consisted of control females that were lactating and a group where the offspring was removed 0-2 days after parturition (see **Paper 2**:Fig. 1 for details). Individual body mass, as a response, was recorded during winter, spring, summer, autumn, and the coming spring. Newborns were caught by hand and individually marked, and body mass, date of birth as well as offspring sex were also recorded. Individuals were followed from January (initiation) to April next year (finalization).

Increased population abundance and varying winter conditions: following two herds for six years (**Paper 3**)

This observational study was initiated by the marking of fifty prime-aged females (≥1 year) in each of two herds in Northern Norway. Both herds utilize the same winter pastures where they are kept together through the winter, but utilize different summer pastures. None of the herds were given supplementary feeding. The herds are separated on the winter pastures in the spring, and they are then herded to their respective summer pastures at the coast (**Paper 3**: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. Individual body mass was recorded during spring and autumn, whereas calf production, mother-calf relationships and whether a female was barren or not were assessed similar as in the first study (**Paper 1**). Individuals were followed from April 2002 (initiation) to April 2008 (finalization). During this period population size increased dramatically.

Manipulating winter climate: changing the distribution of winter environmental conditions (**Paper 4**)

This simulation model, which is a follow-up to the previous empirical studies (e.g. **Paper 1**-**3**), used a state-dependent individual-based model (IBM) to investigate how females should optimize their reproductive investment in a stochastic environment that contains density dependent processes. The model excludes males as the aim was to assess female life-histories and because important parameters were widely available for females but not for males. Each time step was discrete (equalling one year) and divided in two distinct seasons: (i) summer where density dependent competition among individuals over a shared food resource occurred; and (ii) winter where temporal variability in environmental conditions affected individual survival and body mass losses. Individuals did not know the state of the coming winter conditions at the time when reproduction took place (summer). Winter environmental conditions were simulated assuming a normal distribution with three different average winter conditions (‘control’, ‘improved’ and ‘reduced’) and a gradient the distribution’s standard deviation to mimic a gradient in environmental unpredictability.

RESULTS

Short-term changes in winter feeding conditions (Paper 1-2)

An asymmetric response to short-term improved vs. reduced winter conditions was present. When food availability was reduced, females immediately reduced their reproductive allocation the following summer (**Paper 1** & **Paper 2**), presumably in order to not compromise their own body mass at the onset of the next winter. On the contrary, when winter conditions were improved females were reluctant to increase their reproductive allocation (**Paper 1**). A small positive effect of short-term improved winter conditions was, however, found on offspring birth mass of initially smaller females in one study (**Paper 2**).

Long-term changed winter feeding conditions (Paper 1-3)

In contrast to short-term improved conditions, females that had been provided additional winter forage over several years allocated more in summer reproduction indicating that reindeer can track consistent changes in winter conditions (**Paper 1**). Moreover, winter feeding conditions for the Finnish herd, which has received supplementary feeding for years, were superior to most other Fennoscandian herds (**Paper 2**). This has probably resulted in an increased reproductive allocation by females in this herd as both reproductive success and offspring body masses were particularly high in this herd compared to the two other empirical studies (**Paper 1** & **Paper 3**). Female body mass was, however, also on average higher in the Finnish herd compared to the two Norwegian herds. This could be used as evidence against an increased reproductive allocation, but this might also indicate that these females have reached an upper threshold for which additional body mass does not translate into larger offspring or increased reproductive success. This can be explained by the fact that female reindeer are normally constrained to producing only one offspring per year so the consequence of allocating too many resources into reproduction during gestation can at best lead to giving birth to one very obese offspring.

The cost of reproduction and environmental conditions (Paper 1-4)

Winter conditions were unpredictable even though the degree of environmental stochasticity was varying across study areas (**Paper 2** vs. **Paper 1** & **Paper 3**); and extremely harsh and benign winters have asymmetric, or nonlinear, negative and positive consequences for the cost of reproduction (**Paper 2** & **Paper 4**). Lactating females gained less body mass during summer compared to barren ones (**Paper 2**-**3**). Additionally, this difference was negatively related to population density and winter climate indicating that a higher competition for resources had a more profound negative effect of reproducing compared to barren females (**Paper 3**). Moreover, successfully reproducing females allocated fewer resources into future reproduction by producing smaller offspring in the coming year (**Paper 3**). Individual quality was also of importance as: female body mass was a positive predictor of offspring body size within a period of ~9 months from birth (**Paper 1**-**3**); and successfully reproducing females experienced an enhanced probability of giving birth the next year (**Paper 3**).

Environmental conditions and optimal reproductive strategies (Paper 4)

The model (**Paper 4**), which synthesizes our understanding of the empirical results, showed that winter climatic conditions had a large effect on the amount of resources that reindeer should allocate to reproduction vs. somatic growth during summer. This study generally confirmed the finding in the empirical studies (**Paper 1**-**3**). This study, however, also went a bit further as it showed that plastic reproductive strategies were superior compared to fixed strategies in all types of environments (**Paper 4**). For adults following a plastic strategy, reproductive allocation was estimated and updated each year according to the individuals' spring body mass. This ensured that females in poor body condition during spring either skipped reproduction or reduced their reproductive allocation in order to enhance their body reserves during summer. A fixed strategy, on the other hand, implied that females always allocated a constant proportion of its spring body mass to reproduction (**Paper 4**:A1). This severely limited females following this strategy from buffering periods of reduced forage availability.

Plastic strategies with a low reproductive allocation per unit female spring body mass did win in the most unpredictable environments (**Paper 4**:Fig. 3). This relationship was, however, weakest for improved environmental average. Similarly, strategies involving a higher reproductive allocation per unit spring body mass did win in more predictable environments for all environmental averages except for the improved one. The latter was more an effect of population density, which was confounded with environmental conditions (**Paper 4**:Fig. 5). Moreover, the realized average reproductive allocation interacted with environmental average and stochasticity, and average population density: the lowest reproductive allocation was found in harsh and unpredictable winter conditions and during high density (**Paper 4**:Fig. 4).

Environmental conditions, reproductive allocation and population dynamics **(Paper 4)**

Populations inhabiting benign and predictable winter conditions were most sensitive to climatic perturbation. These populations supported the highest population densities, which in interaction with climate limited the possibility for individuals to buffer adverse climatic effects. Negative density dependence had a strong negative effect on offspring body mass and consequently on reproductive success: the combination of high density, which resulted in lowered offspring autumn body mass, and an extremely harsh winter had dramatic negative effects on offspring survival. A high reproductive allocation also resulted in lowered female autumn body mass in these good environments, which gave the potential for very low adult survival rates in the rare occasions of an extremely harsh winter.

Populations subject to poor winter conditions were, on the other hand, characterized by low density, and these populations were least sensitive to climate. A low reproductive allocation resulted in increased female autumn body mass, and a consequently high adult survival in these environments. This model did not include any predation or harvest, but harsh winters apparently 'harvested' these populations by removing especially younger individuals. This released these populations from negative density dependence, and this had a positive effect on reproduction as females received a higher reproductive reward (for a given allocation value) during low compared to high density (**Paper 4**:A1).

DISCUSSION

Female reindeer, which are long-lived with many potential breeding attempts during a lifespan, do not want to jeopardize their own survival over reproduction. Consequently, females have adopted a *risk sensitive reproductive strategy* where they trade reproduction against the amount of autumn body reserves needed for survival insurance during the coming winter (**Paper 1**-**4**). Being risk sensitive implies that individuals to some degree are either risk prone or risk averse, where female reindeer are risk averse because: (i) during the summer they cannot predict with certainty the coming winter; and (ii) extremely harsh and benign winters have asymmetric fitness consequences (mainly through their effects on adult survival). Female reindeer are, thus, not willing to gamble that a coming winter will be a benign one, because the cost of preparing for a benign winter but meeting a harsh one is dramatically higher than the benefit of preparing for a benign winter and actually get one. Consequently, female reindeer optimized their allocation in reproduction vs. somatic growth according to expected winter conditions, but individuals do not prepare for an average winter, but for extreme winters (relative to past experience) that might happen from time to time. Such effects of environmental conditions on life histories have important consequences for both individual survival and reproduction, and hence also on population dynamics.

Many of the assumptions for a risk sensitive reproductive investment are, at least partly, fulfilled for many long-lived organisms as they experience a temporally varying cost of reproduction, they build body reserves during periods of favourable environmental conditions and they use these reserves as a buffer against unpredictable environmental variability during periods of non-favourable conditions [e.g. humans (Bronson 1995, Lummaa and Clutton-Brock 2002), large herbivores (Sæther 1997, Gaillard and Yoccoz 2003), birds (Lindén and Møller 1989, Parker and Holm 1990, Hanssen et al. 2005), fish (van den Berghe 1992, Hutchings 1994, Klemetsen et al. 2003) and reptiles (Shine 2005, Radder 2006)].

The ability for individual's to buffer negative climatic effects by adopting a *risk averse reproductive strategy* has important consequences for how the impacts of future climate change will be. These changes will most likely result in a shift towards more frequent extreme precipitation events (e.g. Wilby and Wigley 2002, Semmler and Jacob 2004, Tebaldi et al. 2006, Benestad 2007, Sun et al. 2007). Moreover, many of these climatic scenarios are expected to happen both sooner and more pronounced in the northern hemisphere (e.g. Tebaldi et al. 2006, Benestad 2007), which is why current efforts to understand the impacts of future climate change should focus on these systems. Hanssen-Bauer et al. (2005), for example, review several studies predicting how future climate change will affect Fennoscandia. The most important finding of this, and other studies, is a predicted shift between warm and cold periods during winter coupled with a year-round increased intensity of precipitation. Such shifts will lead to an increased frequency of wet weather, deep snow and ice crust formation that has negative consequences for large herbivores (e.g. Solberg et al. 2001).

Many recent analyses of climatic effect signatures in population time series have been used to infer the likely consequences of future climate change (Stenseth et al. 2002). The impact of future climate change commonly invokes more frequent population collapses (e.g. Post 2005). Such inferences are based on an underlying assumption that animals have non-plastic life history strategies that are not adequately adaptive to new climate regimes. The studies in the present thesis, however, suggest that these changes will more likely result in a change towards more risk averse life histories that have the potential of buffering negative effects of climate up to a certain point where extinction is inevitable. I, thus, propose that future studies should focus more on how long-lived organisms may adjust their life histories to counteract climate changes.

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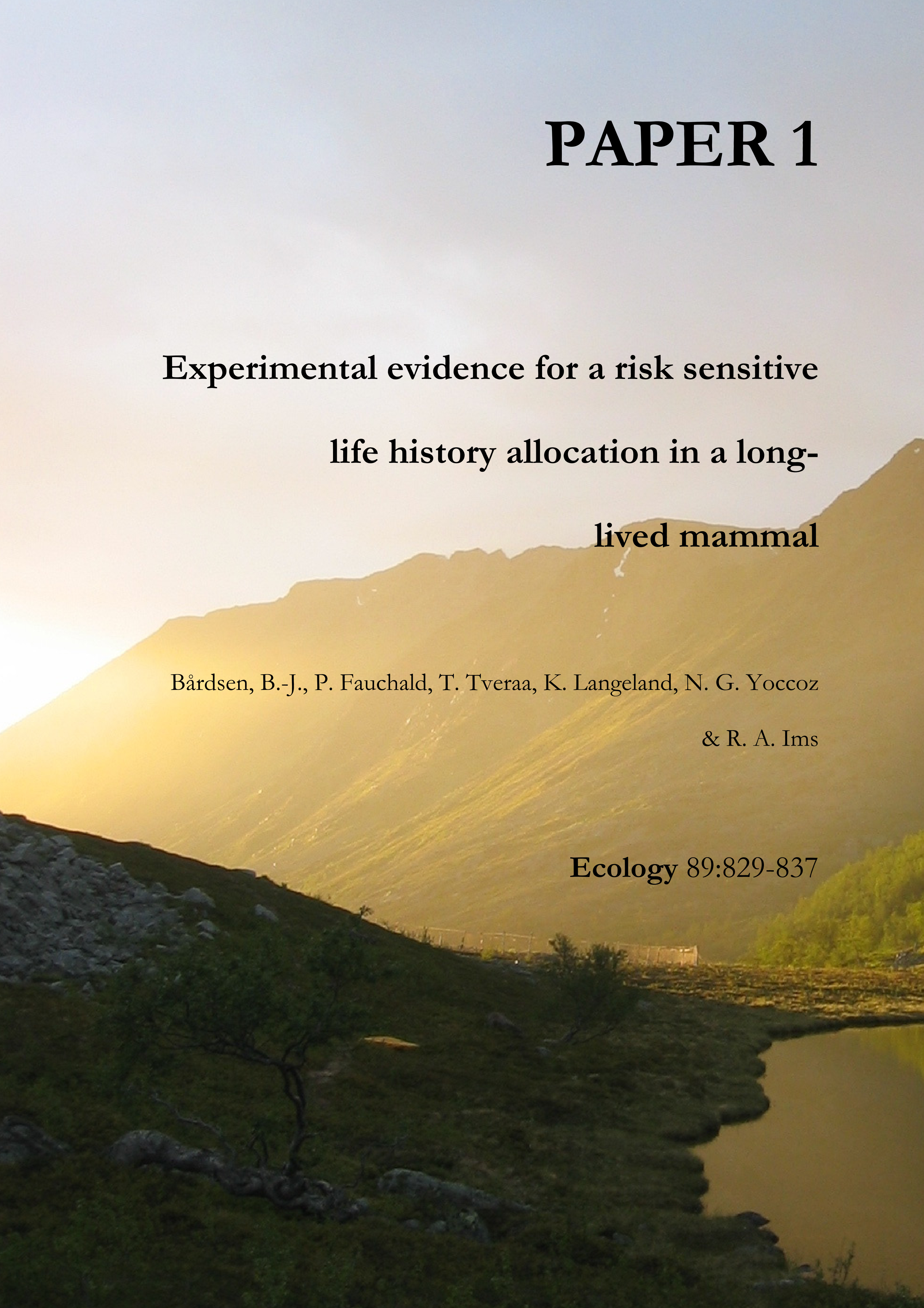

PAPER 1

Experimental evidence for a risk sensitive life history allocation in a long-lived mammal

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EXPERIMENTAL EVIDENCE OF A RISK-SENSITIVE REPRODUCTIVE ALLOCATION IN A LONG-LIVED MAMMAL

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Abstract. When reproduction competes with the amount of resources available for survival during an unpredictable nonbreeding season, individuals should adopt a risk-sensitive regulation of their reproductive allocation. We tested this hypothesis on female reindeer (*Rangifer tarandus*), which face a trade-off between reproduction and acquisition of body reserves during spring and summer, with autumn body mass functioning as insurance against stochastic winter climatic severity. The study was conducted in a population consisting of two herds: one that received supplementary winter feeding for four years while the other utilized natural pastures. The females receiving additional forage allocated more to their calves. Experimental translocation of females between the herds was conducted to simulate two contrasting rapid alterations of winter conditions. When females receiving supplementary feeding were moved to natural pastures, they promptly reduced their reproductive allocation the following summer. However, when winter conditions were improved, females were reluctant to increase their reproductive allocation. This asymmetric response to improved vs. reduced winter conditions is consistent with a risk-averse adjustment in reproductive allocation. The ability of individuals to track their environment and the concordant risk-sensitive adjustment of reproductive allocation may render subarctic reindeer more resilient to climate change than previously supposed.

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

Introduction

A central issue in life history theory is how individuals allocate resources between current reproduction and future survival (e.g., Roff 1992, Stearns 1992). In large mammals and birds, these demographic parameters are highly correlated with body mass (e.g., Sæther 1997, Lummaa and Clutton-Brock 2002). In reindeer (*Rangifer tarandus*), for example, both survival and successful reproduction are positively related to size; larger females are more likely to reproduce and produce larger calves than are small females (Kojola 1993, 1997, Tveraa et al. 2003).

In mammalian herbivores with long life spans, individuals favor their own survival over reproduction. Hence, reproductive output and juvenile survival are more variable than adult survival (Gaillard et al. 1998, 2000, Gaillard and Yoccoz 2003). However, the balance between reproduction and survival should depend on environmental conditions affecting the two traits (see, e.g., Sæther 1997, Forchhammer et al. 2001, Gaillard and Yoccoz 2003). This trade-off is especially important in northern temperate environments where reproduction takes place during the favorable season, whereas survival is particularly constrained in the unfavorable season (Sæther 1997). If, for example, winter conditions are improved, fewer resources are needed for survival and more resources should be allocated to reproduction. In a variable environment where the resources needed for survival during winter are difficult to predict, long-lived species should adopt a conservative reproductive strategy in which individuals should retain sufficient body reserves to ensure survival during especially harsh winters (see Erikstad et al. 1998). In the present study, we translocated reindeer between two herds experiencing different winter but similar summer conditions. Specifically, we experimentally improved and reduced winter conditions for the two herds.

For large herbivores in northern and clearly seasonal environments, late-winter conditions have profound effects on survival and reproduction (e.g., Coulson et al. 2000, 2001, Patterson and Messier 2000, DelGiudice et al. 2002). Accordingly, Tveraa et al. (2003) found that harsh winter conditions greatly reduced adult survival and fecundity in reindeer the following summer. To disentangle the impact of late-winter and spring conditions in reindeer, Fauchald et al. (2004) performed an experiment in which feeding conditions were improved during late winter and the calving season. Reindeer given additional winter forage greatly in-

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creased their body mass in the late winter relative to early-winter body mass. However, during the calving season, females given additional winter forage rapidly lost their additional body mass. After calving, there were no effects of winter feeding on either body mass or survival of females and calves. Consequently, Fauchald et al. (2004) suggested that female reindeer regulate their body mass down to some minimum threshold during spring, when the risk of starvation is low, in order to take care of their newborn calves. Hence, additional winter body mass acts primarily as an insurance against periods of winter starvation. However, autumn body mass, and hence the insurance against winter starvation, is traded against the resources that a female allocates to her calf during summer (Reimers 1972, Skogland 1985, Clutton-Brock et al. 1996, Tveraa et al. 2003, Fauchald et al. 2004). This trade-off implies that prevailing winter conditions, in terms of severity and predictability, might have profound effects on reproductive allocation for northern large herbivores (Tveraa et al. 2007). Animals experiencing stable and benign winter conditions can afford a low autumn body mass and might therefore increase their fecundity and 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 strategy in the sense that they adjust their reproductive allocation during summer according to the risk of starvation in the following winter (see Stephens and Krebs [1986] and Kacelnik and Bateson [1996] for a discussion of the concept of risk sensitivity). Risk sensitivity rests on the assumption that individuals are capable of tracking environmental variability (Stephens and Krebs 1986). Individuals that successfully track environmental fluctuations, e.g., by limiting their reproductive effort and increasing somatic growth when resource availability is low, will possess a selective advantage over poor trackers (Boyce and Daley 1980).

Experimental manipulations of reproduction in free-ranging large mammals are difficult (e.g., Festa-Bianchet et al. 1998). Here, we set up two experiments in subarctic Norway designed to test predictions about risk-sensitive reproductive allocation in reindeer. Semidomestic reindeer in Fennoscandia offer a unique opportunity to experiment on a wide-ranging large herbivore (e.g., Tveraa et al. 2003, Fauchald et al. 2004, Holand et al. 2007, Røed et al. 2007). Most herds are kept free-ranging on the same natural pastures in which wild reindeer roamed about three centuries ago (e.g., Parks et al. 2002). In modern times the reindeer husbandry has adopted alternative herding strategies, including additional winter feeding on natural pastures (e.g., Parks et al. 2002). We utilized this setting by studying two herds within one interbreeding population. The ecology of the two herds differed only in that one of the herds had received additional winter forage since 2000, whereas the other herd had access solely to natural pastures. In January 2003, we translocated females between the two herds, resulting in two experiments in which one herd faced reduced winter conditions while the other faced improved winter conditions. The experiments were repeated in 2004.

For a given distribution of winter conditions, a "risk-prone" reproductive strategy involves high reproductive allocation that will result in high reproductive reward during benign winters, but high survival cost during harsh winters. A low reproductive allocation will, on the other hand, result in stable winter survival, but lower potential reproductive reward. Consequently, this represents a "risk-averse" reproductive strategy. Because subarctic reindeer are long-lived, large mammals living in a strongly seasonal environment with severe winters that can even compromise the survival of adults (Tveraa et al. 2003), we expected them to be on the risk-averse side of the risk-prone–risk-averse continuum. However, when benign winter conditions appear over several years, even risk-averse animals should increase their reproductive allocation during summer if they are able to perceive the improved predictability of their environment (Gaillard and Yoccoz 2003). Accordingly, we investigated whether there was an increase in reproductive allocation due to a long-term feeding manipulation. On the other hand, improved winter conditions over just one season, according to a risk-averse reproductive allocation, should not provide a sufficiently strong cue to induce an altered reproductive allocation. We thus predicted that there would be no pronounced change in reproductive allocation in the short-term translocation experiment where winter conditions were improved. However, according to a risk-averse reproductive allocation, reindeer should be sensitive to a reduction in winter conditions. Thus, we expected an immediate response to experimentally reduced winter conditions in the sense that females should favor gain in own body mass over calf production.

METHODS

Study population and long-term feeding manipulation

The present study was conducted in East Finnmark [69°15′–70°03′ N; 24°30′–24°58′ E], Northern Norway. The study population, which includes more than the two herds in the present study, is free-ranging most of the time, utilizing a summer pasture area of $\sim$400 km^2. Since the harsh winter of 2000 (Tveraa et al. 2003), one herd was kept in a separate subarea from February/March until post-calving in late May, during which period the reindeer were given commercial reindeer pellets at $\sim$800 g·individual^{-1}·d^{-1} (Poron-Herkku, Raisio, Finland). Additional forage was provided using several feeding dispensers to ensure that subordinate individuals also had access to food. The other herd was free-ranging on natural pastures in all seasons. From late May the two herds were mixed, and they utilized the

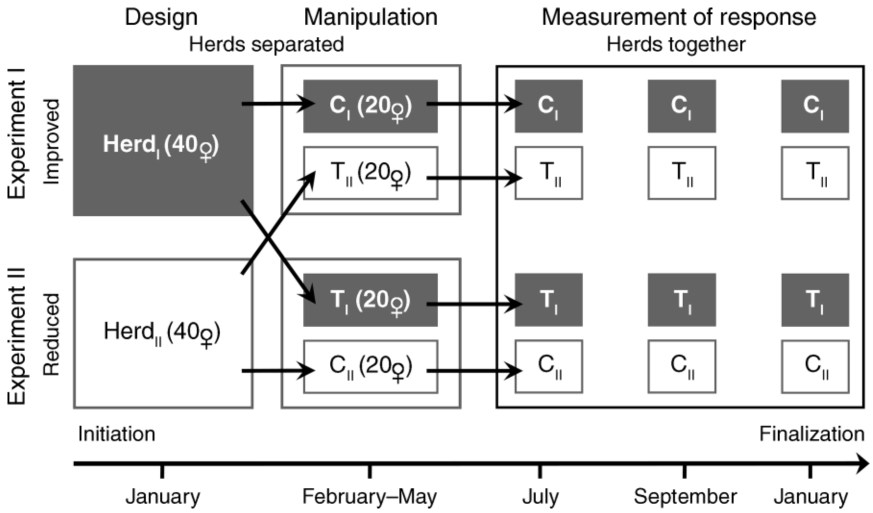

FIG. 1. The study was designed with respect to initial body mass (measured at the initiation of the experiments), which was used to assign 20 females (♀) to the control (C) and treatment (T) group, used as contrasts in Experiment I (improved; C_I vs. T_I) and Experiment II (reduced; C_{II} vs. T_{II}), respectively (Tables 2b, c and 3a, b). Manipulation of winter feeding conditions was performed in late winter by moving individuals from one herd to the other (the herds are represented by the parallel horizontal lines of boxes). The experiments were replicated in two different years, i.e., a new set of individuals was followed from January (initiation) to the next January (finalization). The two experiments represent not only two different sets of current winter conditions, but also different prevailing winter conditions, as supplementary feeding has been carried out for several years in one of the herds. Consequently, the control groups from the two experiments were used in an analysis of the effects of long-term feeding manipulation (C_{II} contrasted on C_I; Tables 1 and 2a).

same pastures until they were separated again in the following January.

Protocol of the translocation experiments

On 11 January 2003 and 3 January 2004, animals from the two herds were gathered. Each year a subsample of 40 females (>1.5 years old) from each herd was assigned to either of two experimental groups: (1) a control kept in the original herd and (2) a treatment moved to the other herd (Fig. 1). The females were selected in the order in which they appeared in the corral. Thus, the subsample of females does not represent a random sample from the entire herd, but each individual from the subsample was randomly allocated to one of the different experimental groups. The females and their calves were then followed until the next January. Individual body mass and presence (“present” or “absent”) was recorded on gatherings on 2 and 4 July, on 19 and 18 September, and on 11 and 3 January in 2003 and 2004, respectively. Individual body mass was recorded to the nearest 0.2 kg using an electronic balance (Avery Berke1, Birmingham, UK). Multiple observations of females with a calf at foot were used to identify mother–calf relationships or whether a female was barren. We updated positive calf sightings backward; a calf not observed in September but present in January (as we recorded its body mass) was assumed present in September. Consequently, we used updated calf presence in September as a proxy for production because the herd gathering in January only provided us information about calf presence based on recorded body masses.

Based on this design, we did the following comparisons (Fig. 1): (1) control (natural pastures) vs. control (supplementary feeding) to quantify possible effects of long-term improved winter conditions (hereafter termed “long-term feeding manipulation”); (2) control (natural pastures) vs. improved winter conditions (experimental translocation to the herd receiving supplementary feeding) to quantify possible effects of short-term improved winter conditions (Experiment I: hereafter termed “improved winter conditions”); (3) control (supplementary feeding) vs. reduced conditions (experimental translocation to the herd utilizing natural pastures only) to quantify possible effects of short-term reduced conditions (Experiment II: hereafter termed “reduced winter conditions”).

Statistical analyses

Missing values and initial female body mass.—There were some missing values of body mass due to individuals that eluded body mass recording or were missing during gathering. The effect of missing values on initial female body mass, a potentially confounding covariate (e.g., Kojola 1993, Clutton-Brock et al. 1996, Festa-Bianchet et al. 1998, Kojola et al. 1998, Tveraa et al. 2003, Adams 2005) controlled for in the experimental design, was examined in a two-way ANOVA with year included as an additional factor. In total, six and 13 individuals were missing at least once in the “improved winter conditions” during 2003 and 2004, respectively, whereas this number was seven and 13 in the "reduced winter conditions." There was no evidence for differences in mean initial body mass between the two groups of animals: individuals present at all times vs. individuals absent at least once. The difference between the groups was −0.37 kg (95% confidence limits [−3.05, 2.32], $df_{model} = 3, 77$) in the "improved winter conditions" and −0.05 kg ([−2.75, 2.65], $df_{model} = 3, 77$) in the "reduced winter conditions" after controlling for the effect of year. All statistical analyses were carried out in R (R Development Core Team 2006).

Body mass and reproductive success.—Linear mixed-effect models (LME) applied using the NLME package (Pinheiro and Bates 2000, Pinheiro et al. 2006) were used to analyze the effect of the predictors on body mass of the females and their calves. Experimental manipulation (control and treatment; reduced and improved winter conditions in each experiment, respectively), year (2003 and 2004), initial female body mass (January prior to manipulation), and season (July, September, and January) were applied as fixed effects (Fig. 1), whereas individual was included as a random effect (Pinheiro and Bates 2000). All mixed-effect models in the present study were fitted with random intercepts only. In order to assess whether reindeer have adopted a risk-sensitive reproductive allocation, it is important to make comparisons between maternal and offspring body masses across the experiments and the long-term feeding manipulation. Our study is based on planned comparisons, and the predictions can then be tested statistically by estimating two effects: (1) the main effect of experimental manipulation (i.e., July body mass for control vs. treatment), and (2) the two-way interaction between manipulation and season (e.g., the increase in body mass from July to September for control vs. treatment; Fig. 1). Consequently, manipulation and its interaction with season were kept in all candidate models based on our a priori expectations (see e.g., Anderson et al. [2001], Burnham and Anderson [2002] for extensive reviews of the theory behind the model selection philosophy adopted in the present study). Thus, we started with a model containing all of the predictors and two-way interactions between experimental manipulation and the other predictors. From this model, we formed a pool of candidate models in which all covariates and interactions were removed sequentially (Appendix: Table A1). From this pool of models, we selected the model with the lowest Akaike's Information Criterion (AIC) value (e.g., Burnham and Anderson 2002). Following Pinheiro and Bates (2000), maximum likelihood fitted models were used when models were compared to each other (Appendix: Table A1), whereas a restricted maximum likelihood fitted model was used for parameter estimation. Because this study consists of planned comparisons with well-defined control groups, we used the treatment contrast, comparing treatment to control, and Wald statistics to test the hypothesis that the contrasts were not significantly different from zero (see Pinheiro and Bates [2000] for details). All statistical tests in this study were two-tailed, and the null hypothesis was rejected at $\alpha = 0.05$.

Generalized linear models (GLM) with a binary response variable (0 = absent, 1 = present), using a logit link function and a binomial distribution, were applied in order to quantify female reproductive success (i.e., the probability that a female had calf present in the autumn) as a function of experimental manipulation, year, and initial body mass (Crawley 2003). A dog intruded the calf paddock in 2004, killing at least two of the calves in the manipulation group in the long-term feeding manipulation and in the improved winter conditions treatment. Hence, we excluded data from 2004 in the analyses of calf production in the two analyses. We adopted the same model selection procedure as in the analyses of body mass, except that season and its interaction with manipulation were not included as predictors in these analyses (Appendix: Table A2).

RESULTS

Long-term feeding manipulation

Improved winter feeding conditions did not have any large effect on female body mass the following July, September, and January (Table 1a). In contrast, we did find a significant positive effect of improved feeding conditions on calf body mass (Table 1b). Mean body mass was lower in 2004 compared to 2003 for both females and calves, and the effect of year was quite pervasive in all of the analyses presented. Interestingly, the year effect on body mass in calves was larger than that of females (Table 1). The main effect of initial body mass on female body mass was positive and statistically significant (Table 1a). The effect of initial maternal body mass on calf body mass was small and statistically insignificant in the control group. However, we found a positive interaction between long-term feeding and initial maternal body mass on calf body mass (Table 1b), indicating that larger females allocated more to their calves compared to smaller females in the long-term feeding group only. Long-term feeding did have a small, statistically insignificant effect on calf production (Table 2a), even though the direction of this estimate was positive as expected. Nevertheless, the estimated proportion of females with a calf was high across the two groups (the herd utilizing natural pastures had the lowest estimate; probability 0.72). To summarize, females experiencing long-term improved winter conditions increased their reproductive allocation in regard to calf body mass, which means that they adopted a risk-sensitive reproductive allocation, and this increased allocation appeared to be especially pronounced in initially large females.

Improved winter conditions (Experiment I)

Although females and calves tended to be larger after one winter with improved conditions, the estimated differences were small and nonsignificant after adjusting for covariates (year, season, and initial female body

Table 1. Estimates from linear mixed-effect models (LME) relating (a) female and (b) calf body mass to long-term feeding manipulation, season (July, September, and January), and year (2003 and 2004).

	a) Female body mass and long-term feeding				b) Calf body mass and long-term feeding			
Parameter	Value	95% CL	df	*P*	Value	95% CL	df	*P*
Fixed effects								
Intercept	63.50	62.15, 64.85	105		22.62	21.21, 24.03	69	
Manipulation (improved)	1.19	−0.50, 2.87	73	0.17	3.12	1.31, 4.94	55	<0.01
Year (2004)	−2.30	−3.68, −0.93	73	<0.01	−4.97	−6.44, −3.49	55	<0.01
Season (September)	11.73	10.50, 12.95	105	<0.01	22.09	20.78, 23.41	69	<0.01
Season (January)	8.79	7.62, 9.96	105	<0.01	21.28	20.01, 22.55	69	<0.01
Initial body mass†,‡	0.70	0.59, 0.82	73	<0.01	0.08	−0.08, 0.25	55	0.33
Manipulation (imp.) × Season (Sep)‡	−0.07	−1.86, 1.72	105	0.94	0.26	−1.81, 2.33	69	0.80
Manipulation (imp.) × Season (Jan)‡	−1.06	−2.77, 0.65	105	0.22	−0.27	−2.29, 1.75	69	0.79
Manipulation (imp.) × Initial body mass†,‡	. . .	. . .	. . .	. . .	0.28	0.02, 0.54	55	0.04
Random effects: female§								
Among-females standard deviation	2.55	2.03, 3.20			2.26	1.69, 3.01		
Within-females standard deviation (residuals)	2.35	2.05, 2.68			2.21	1.87, 2.61		

Notes: The long-term feeding manipulation (improved) consisted of supplementary feeding in winter. The intercept shows the July 2003 body mass for control females (i.e., females utilizing natural pastures), whereas the other coefficients are the estimated difference between the intercept and the mean body mass for each level of the other included factors. To make the intercept biologically meaningful, initial body mass was centered (subtracting the average body mass). Body mass of females and calves was measured in kilograms. Estimated parameters are for a model selected from a pool of candidate models (see Appendix and *Methods: Statistical analyses* for details on the model selection procedure applied). Ellipses indicate that the term was removed because it did not improve the model fit using AIC for model selection.

† Maternal body mass in January (i.e., before onset of manipulation) in both years.

‡ Removal of nonstatistically significant interactions did not affect the remaining coefficients.

§ Female random terms involved only the constant term (i.e., random intercepts fitted per female). For female body mass (a), among-females $n_{\mathrm{Obs}} = 186$; within-females $n_{\mathrm{Ind}} = 77$. For calf body mass (b), among-females $n_{\mathrm{Obs}} = 133$; within-females $n_{\mathrm{Ind}} = 60$, where n_{Obs} is the number of observations and n_{Ind} is the number of individuals observed.

mass; Table 3, Fig. 2a). Initial body mass had a positive effect on female body mass (Table 3a), but initial maternal body mass did not have a strong effect on calf body mass (Table 3b). This lack of an effect on calf body mass indicated either that reproductive allocation was higher for smaller relative to larger females (as calf body mass was independent of initial maternal body mass), or that winter body mass was a poor predictor of reproductive performance. Experimental feeding did not have a statistically significant effect on calf production (Table 2b), even though the direction of this estimate was positive as expected. In summary, these results agreed with the risk-averse reproductive allocation hypothesis: females are unwilling to increase their reproductive allocation during summer as a response to occasionally good winter conditions.

Table 2. Generalized linear model relating calf production to experimental manipulation (improved in the long-term feeding manipulation and in Experiment I, and reduced in Experiment II) and year (2003 and 2004).

	Calf production and manipulation			
Parameter	Value	95% CL	df	*P*
a) Long-term feeding manipulation†				
Intercept	0.96	−0.02, 2.09		
Manipulation (improved)	1.53	−0.47, 4.56	29	0.19
Residual deviance	28.32		29	
b) Improved winter conditions† (Experiment I)				
Intercept	0.96	−0.02, 2.09		
Manipulation (treatment)	0.51	−1.09, 2.25	32	0.54
Residual deviance	36.71		32	
c) Reduced winter conditions (Experiment II)				
Intercept	1.96	0.78, 3.42		
Manipulation (treatment)	−0.38	−1.69, 0.90	54	0.57
Year (2004)	−0.98	−2.42, 0.30	53	0.15
Residual deviance	58.24		53	

Notes: The intercept is the logit estimate for the control group in 2003. Calf production is the probability of producing a calf, as a binary response (i.e., a GLM with binomial family and a logit link function). See Appendix and *Methods: Statistical analyses* for details on the model selection procedure applied.

† Data from the year 2004 were removed from these analyses because a dog invaded the calf paddock, killing at least two calves in one of the experimental groups.

Table 3. Linear mixed-effect models (LME) relating (a) female and (b) calf body mass to experimental translocation of individuals between the two herds, to seasons (July, September, and January), and to years (2003 and 2004).

	Improved winter conditions (Experiment I)				Reduced winter conditions (Experiment II)			
Parameter	Value	95% CL	df	*P*	Value	95% CL	df	*P*
a) Female body mass (kg)								
Fixed effects								
Intercept	64.42	62.96, 65.88	106		64.32	62.92, 65.71	99	
Manipulation (treatment)	1.39	−0.42, 3.19	70	0.13	−1.71	−3.50, 0.08	69	0.06
Year (2004)	−3.01	−4.59, −1.43	70	<0.01	−1.43	−2.91, 0.06	69	0.06
Season (September)	11.76	10.56, 12.96	106	<0.01	11.58	10.21, 12.96	99	<0.01
Season (January)	8.81	7.66, 9.95	106	<0.01	7.64	6.33, 8.96	99	<0.01
Initial body mass†	0.60	0.46, 0.74	70	<0.01	0.77	0.60, 0.95	69	<0.01
Manipulation (treat.) × Season (Sep)‡	0.22	−1.58, 2.02	106	0.81	2.15	0.21, 4.08	99	0.03
Manipulation (treat.) × Season (Jan)‡	−0.94	−2.58, 0.70	106	0.26	1.79	−0.06, 3.63	99	0.06
Manipulation (treat.) × Initial body mass†	...	...	...	...	−0.30	−0.55, −0.05	69	0.02
Random effects: female§								
Among-females standard deviation	2.91	2.36, 3.60			2.58	2.04, 3.27		
Within-females standard deviation (residuals)	2.29	2.01, 2.62			2.48	2.16, 2.84		
b) Calf body mass (kg)								
Fixed effects								
Intercept	22.51	20.88, 24.14	75		25.97	24.23, 27.72	52	
Manipulation (treatment)	0.73	−1.39, 2.86	50	0.49	−4.14	−6.28, −2.01	49	<0.01
Year (2004)	−4.60	−6.41, −2.79	50	<0.01	−5.19	−7.08, −3.31	49	<0.01
Season (September)	22.13	20.77, 23.50	75	<0.01	22.44	20.91, 23.98	52	<0.01
Season (January)	21.28	19.97, 22.59	75	<0.01	21.06	19.55, 22.57	52	<0.01
Initial body mass†	0.16	−0.01, 0.32	50	0.06	0.36	0.13, 0.59	49	<0.01
Manipulation (treat.) × Season (Sep)‡	1.41	−0.66, 3.48	75	0.18	0.41	−1.73, 2.55	52	0.70
Manipulation (treat.) × Season (Jan)‡	0.49	−1.49, 2.47	75	0.63	0.71	−1.50, 2.91	52	0.52
Manipulation (treat.) × Initial body mass†,‡	...	...	...	...	−0.11	−0.43, 0.20	49	0.47
Random effects: female§								
Among-females standard deviation	2.79	2.12, 3.58			2.89	2.23, 3.75		
Within-females standard deviation (residuals)	2.27	1.93, 2.66			2.06	1.70, 2.49		

Notes: Winter conditions were experimentally manipulated (improved in Experiment I and reduced in Experiment II) on a short-tem basis. The intercept shows the July 2003 body mass for control females, whereas the other coefficients are the estimated difference between the intercept and the mean body mass for each level of the other included factors. To make the intercept biologically meaningful, initial body mass was centered (subtracting the average body mass). See Appendix and *Methods: Statistical analyses* for details on the model selection procedure applied. Ellipses indicate that the term was removed because it did not improve the model fit using AIC for model selection.

† Maternal body mass in January (i.e., before onset of manipulation) in both years.

‡ Removal of nonstatistically significant interactions did not affect the remaining coefficients.

§ Female random terms involved only the constant term (i.e., random intercepts fitted per female). For (a), among-females $n_{\mathrm{Obs}} =$ 184 for "improved" and 177 for "reduced"; within-females $n_{\mathrm{Ind}} = 74$ for both treatments. For (b), among-females $n_{\mathrm{Obs}} = 133$ for "improved" and 110 for "reduced"; within-females $n_{\mathrm{Ind}} = 54$ for both treatments.

Reduced winter conditions (Experiment II)

Experimentally reduced winter conditions had a negative, nearly statistically significant effect on female body mass in the following summer after controlling for the effects of year and initial female body mass (Table 3a, Fig. 2b). Moreover, there was a significant positive interaction between manipulation and season because females experiencing a reduction in winter conditions allocated more resources in somatic growth over the summer than did control females (interaction term manipulation × September season in Table 3a, Fig. 2b). There was a large effect of experimental manipulation on calf body mass; the mothers that experienced reduced winter condition gave birth to calves that were, on average, ~4 kg smaller in July compared to mothers that received supplementary feeding (Table 3b, Fig. 2b). As no interaction between manipulation and season was evident in the analysis of calf body mass, the calves of the mothers that experienced reduced winter conditions were smaller than the calves in the control group the following September and January (Table 3b, Fig. 2b). In contrast to the improved winter condition experiment, initial maternal body mass did have a relatively strong positive effect on calf body mass (Table 3b). Experimental reduction in winter conditions and year had a small, negative, and nonsignificant effect on calf production (Table 2c). In summary, these results were also in accordance with the risk-averse reproductive allocation hypothesis: females reduced their subsequent reproductive allocation as a response to reduced winter feeding conditions.

DISCUSSION

In the present study we demonstrate that reindeer adjusted their reproductive allocation during summer according to winter feeding conditions. When winter conditions were reduced, females immediately reduced their reproductive allocation the following summer, presumably in order to not compromise their own body mass at the onset of the next winter. In contrast, when winter conditions were improved, females were reluctant to increase their reproductive allocation. However, females that had been provided additional winter forage over several years allocated more in calves during summer, indicating that reindeer can assess the predictability of continuous winter conditions.

Critical issues in ecological experiments are whether the applied treatment is relevant for addressing the focal question, and if the level of treatment is realistic with respect to that found in a natural setting. In our study it is important that additional winter forage actually improved winter conditions. Because females on natural pastures were free-ranging during the winter, we were unable to quantify the direct impact of additional forage on female winter body mass. However, Fauchald et al. (2004) showed that females given winter forage gained ~12 kg during winter, compared to their control animals. Similar to Fauchald et al. (2004), the fed females in this study were observed daily to ensure that all individuals ingested forage and were in good health. Although there was a difference between the two years of the present study in terms of female and calf body mass, indicating that the natural conditions in summer differed, both winters were relatively benign, due to shallow snow layers and no ice (Tveraa et al. 2007). Thus, we could not expect a strong response to additional winter feeding, especially in terms of calf production, which is likely to be less sensitive than calf body mass (Tveraa et al. 2003: Table 2). In the study by Fauchald et al. (2004), female reindeer did not increase their reproductive performance, despite the significantly increased gain in body mass during winter. The improved winter condition experiment replicates and supports the findings of Fauchald et al. (2004) that female reindeer regulate their body mass down to some minimum threshold during spring when the risk of starvation is low. Because responses to both long-term improvement and short-term reduction of winter forage availability were demonstrated in the present study, we are confident that the manipulation applied in the present study worked as we intended.

The herd receiving additional winter forage for several years had larger calves. Interestingly, female body masses did not differ between herds. In addition to increased reproductive allocation, additional winter feeding is also supposed to increase the growth of subadults, which may greatly affect adult performance and induce a cohort effect (Rose et al. 1998, Lindström 1999, Coulson et al. 2001, Forchhammer et al. 2001, Lummaa and Clutton-Brock 2002, Gaillard et al. 2003). Indeed, the females in the herd receiving the long-term additional winter forage grow faster and reach maturity earlier (T. Tveraa, P. Fauchald, K. Langeland, and B.-J. Bårdsen, *unpublished data*). Improved winter conditions thus act to increase reproductive allocation at all ages while body mass is kept constant. Generally, larger females seem to outperform smaller females, which is reflected in the general positive relationships between initial female body mass and later maternal and offspring body mass. The positive relationship between maternal and offspring body mass can be used to support the hypothesis that initially larger females have a more risk-prone reproductive allocation relative to smaller females. However, this interpretation is inaccurate because even though initially larger females produced larger calves, they also had a larger autumn body mass compared to smaller females (van Noordwijk and de Jong [1986] discuss how positive relationship between two traits subject to trade-offs might occur).

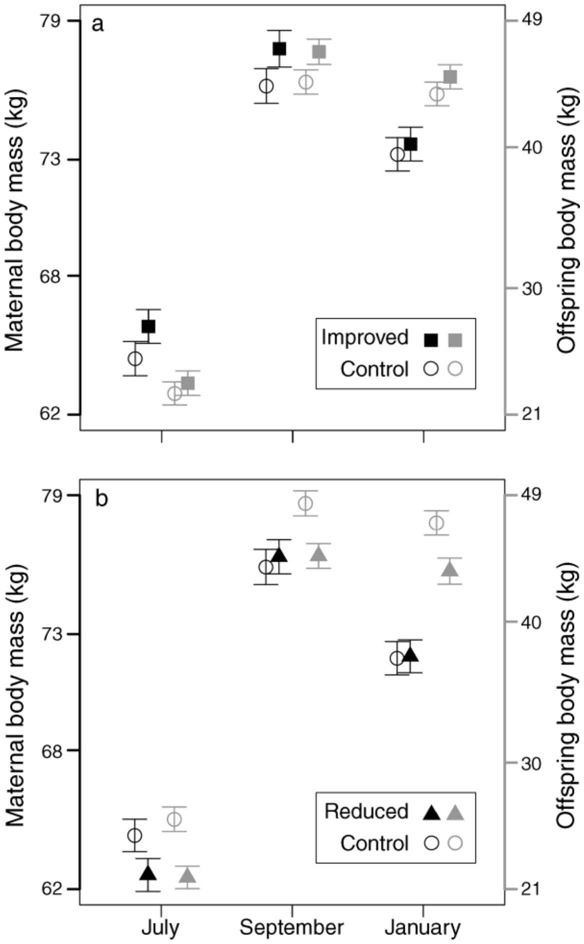

FIG. 2. Estimated maternal (left-hand axis; black solid or black outlined symbols) and offspring (right-hand axis; gray solid or gray outlined symbols) body mass (mean ± SE) for each experimental group for each season (July, September, and January) in 2003 for experimentally (a) improved and (b) reduced winter feeding conditions based on the analyses in Table 3.

When reproduction competes with the amount of resources available for survival during an unpredictable nonbreeding season, then individuals should adopt what we have termed a risk-sensitive reproductive allocation (see also Boyce 1979, Boyce and Daley 1980, Erikstad et al. 1998, Lindström 1999). Long-lived animals, such as reindeer, are expected to be particularly risk sensitive. A risk-averse reproductive allocation implies an asymmetric response to environmental change in the sense that females should be more responsive to reductions than to improvements of the environment. Accordingly, reindeer in the present study readily reduced their reproductive allocation when winter conditions were reduced, whereas they more slowly increased their reproductive allocation when winter conditions were improved. Moreover, according to the risk-averse allocation hypothesis, females should adjust their reproductive allocation according to winter conditions that are below average conditions (Boyce and Daley 1980, Stephens and Krebs 1986). The increased reproductive allocation of female reindeer as a response to additional feeding over several years can be understood in light of this prediction, because long-term feeding implied both an increased average and a reduced variance in winter conditions.

Ecological questions should be assessed with an analytical approach that combines statistical analyses of observational data, experiments, and mathematical models (e.g., Turchin 1995). Research on large wild mammals has typically been based on long-term observational data, with a lack of experimental evidence (e.g., Caughley 1981, Gaillard et al. 1998). Carefully designed experiments based on marked individuals may reveal mechanisms that cannot be reliably understood based on nonexperimental study protocols (sensu, e.g., Festa-Bianchet and Jorgenson 1998, Gaillard et al. 1998). For example, many recent analyses of climatic effect signatures in population time series have been used to infer the likely consequences of future climate change (Stenseth et al. 2002). The predicted consequences commonly invoke more frequent population collapses (e.g., Post 2005). Such inferences are based on an underlying assumption that animals have a nonplastic life history strategy that is not adequately adaptive to new climate regimes. However, animals may indeed be able to respond to changes in the environments by adjusting their reproductive allocation, as we have shown for subarctic reindeer. Thus, reindeer populations may be more resilient than previously thought (cf. Tveraa et al. 2007). For example, climate change is expected to increase the amount of snow and ice on reindeer winter pastures (Iversen 2003), thereby reducing the winter conditions for the herds. Contrary to recent studies (e.g., Post 2005), we expect these changes to result in a more risk-averse life history that will buffer the negative effects of climate (see also Tveraa et al. 2007). Consequently, we propose that future studies should focus more on how long-lived organisms, such as large terrestrial herbivores, adjust their life history to counteract climate changes. In particular, we believe that a valuable new focus in life history studies would be to investigate how environmental stochasticity has shaped the degree of risk-sensitive reproductive strategies.

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APPENDIX

Model selection and the pool of candidate models (*Ecological Archives* E089-046-A1).

SUPPLEMENT

Raw data used in statistical analyses of risk-sensitive reproductive allocation in reindeer (*Rangifer tarandus*) (*Ecological Archives* E089-046-S1).

Ecological Archives E089-046-A1

Bård-Jørgen Bårdsen, Per Fauchald, Torkild Tveraa, Knut Langeland, Nigel Gilles Yoccoz, and Rolf Anker Ims. 2008. Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. *Ecology* 89:829–837.

Appendix A. Model selection and the pool of candidate models.

TABLE A1. The relative evidence for each candidate model (*i*) in Table 1 (Long-term feeding) and Table 3 (Experiment I and II) was assessed by rescaling and ranking models relative to the value of the model with the lowest *Akaike's Information Criterion* value (Δ*i*; the model in bold were selected and used for inference in each analysis as its Δ*i* equals zero). The models were fitted by *maximum likelihood* (ML) as the *restricted maximum likelihood* (REML) fit used in the Table 1 and 3 are not recommended when several models are compared to each other (Pinheiro and Bates 2000). The predictors included in the different models are marked with an "x".

i	**Manipulation**†	**Season**†	**Manip. × seas.**†	Year	Initial body mass (IBM)	Manip. × IBM	Manip. × Year	df	Female body mass, Δ*i*			Calf body mass, Δ*i*		
									Long-term feeding	Experiment I	Experiment II	Long-term feeding	Experiment I	Experiment II
1.	**x**	**x**	**x**	x	x	x	x	12	2.20	3.51	0.73	1.80	2.85	0.89
2.	**x**	**x**	**x**	x	x	x		11	0.37	1.70	***0.00***	***0.00***	1.43	***0.00***
3.	**x**	**x**	**x**	x	x			10	***0.00***	***0.00***	4.02	2.90	***0.00***	0.35
4.	**x**	**x**	**x**	x				7	85.08	53.26	66.85	10.39	12.42	2.14
5.	**x**	**x**	**x**					6	89.12	68.81	67.87	37.10	31.43	26.14

† The three predictors in bold were kept in all models based on our *a priori* expectations of the experimental translocation of animals in the three seasons of interest, i.e., we aimed at estimating the effect of experimental manipulation in the three different seasons.

TABLE A2. The relative evidence for each candidate model (*i*) in Table 2 was assessed by rescaling and ranking models relative to the value of the model with the lowest *Akaike's Information Criterion* value (Δ*i*; the model in bold were selected and used for inference in each analysis as its Δ*i* equals zero). Season was not included as a predictor in these analyses as updated calf presence in the autumn was used as a proxy for production throughout all seasons. The predictors included in the different models are marked with an "x".

i	**Manipulation**†	Year	Initial body mass (IBM)	Manip. × Year	Manip. × IBM	df	Calf production, Δ*i*		
							Long-term feeding‡	Experiment I‡	Experiment II
1.	**x**	(x)	x	(x)	x	6(4)	1.65	2.73	3.13
2.	**x**	(x)	x	(x)		5	—	—	1.15
3.	**x**	(x)	x			4(3)	1.99	1.91	0.43
4.	**x**	(x)				3	—	—	***0.00***
5.	**x**					2	***0.00***	**0.00**	0.23

† The predictor in bold was kept in all models based on our a priori expectations of the experimental translocation of animals, i.e., we aimed at estimating the effect of experimental manipulation.
‡ Data from the year 2004 was removed from two analyses as a dog intruded the calf paddock killing at least two calves in one of the experimental groups. Consequently, the terms including year were not included in these models (the markings not included as well as the degrees of freedom for these analyses are given in parentheses).

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PAPER 2

Experimental evidence of costs of lactation in a low risk environment for a long-lived mammal

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Experimental evidence of costs of lactation in a low risk environment for a long-lived mammal

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In a previous experiment we have documented that organisms adopt a risk-sensitive reproductive allocation when summer reproductive investment competes with survival in the coming winter (Bårdsen et al. 2008). This tradeoff is present through autumn female body mass, which acts as an insurance against unpredictable winter environmental conditions. We tested this hypothesis experimentally on female reindeer experiencing stable and benign winter feeding conditions. Additional supplementary feeding and removal of newborns represented two sets of experimental manipulations. Females in the supplementary feeding group increased more in winter body mass relative to control females. This manipulation, however, did not have any effect on summer body mass development for neither females nor offspring, but we found a positive effect of feeding on offspring birth mass for smaller females. In contrast, offspring removal did have a positive effect on summer body mass development as females in this group were larger in the autumn body mass relative to control females. In essence, we documented two immediate effects as: (1) supplementary feeding did have a positive effect on spring body mass for smaller females; and (2) offspring removal did increase the female summer somatic growth as this had a positive effect on female autumn body mass. Additionally, we tested for lagged effects, but we could not document any biologically significant effects of neither manipulation in the coming spring. The fact that we only found rather weak effects of both manipulations was as expected for risk sensitive individuals experiencing benign environmental conditions over many years.

A central issue in life-history theory is how individuals balance reproductive investments against their own chances to survive and reproduce in the future (Stearns 1992, Daan and Tinbergen 1997, Stearns and Hoekstra 2000). This tradeoff between current reproduction and future survival and reproduction is more commonly referred to as the cost of reproduction (sensu Williams 1966), and this cost can roughly be divided in two: immediate, where individuals pay the costs during nurturing; and delayed, where individuals pay the costs post offspring maturation. Delayed cost of reproduction can for mammalian females be divided in two: (1) post-lactational parental care; and (2) maternal recovery, whereas immediate costs can be divided in three: (1) mating; (2) gestation (including conception and parturition); and (3) lactation (reviewed by Gittleman and Thompson 1988). Biologists have for a long time believed that the cost of lactation is large relative to that of other reproductive stages but most studies have focused on gestation vs lactation (Gittleman and Thompson 1988): e.g. humans *Homo sapiens* and other primates (Anderson 1983, Bronson 1995, Dufour and Sauther 2002, Ellison 2003), large terrestrial herbivores; moose *Alces alces* (Sand 1998), reindeer/caribou *Rangifer tarandus* (Reimers 1983, Cameron et al. 1993, 2002) and red deer *Cervus elaphus* (Clutton-Brock et al. 1989), as well as rodents; Guinea pig *Cavia porcellus* (Kunkele 2000).

Reproductive patterns exhibit large interspecific variation (Stearns 1992, Coulson et al. 2000), but for large mammals a surprisingly large intraspecific variation between populations and even between individuals is apparent (Sand 1996, Sæther et al. 1996). Environmental factors are believed to be of special importance in explaining variation in reproductive performance among populations (Tveraa et al. 2007), and even within the same population over time (Bårdsen et al. 2008). For large herbivores living in the Northern Hemisphere, late winter feeding conditions have profound effects on both survival and reproduction (Coulson et al. 2000, 2001, Patterson and Messier 2000, DelGiudice et al. 2002). Thus, different environments favour different traits, and in temporally variable environments animals traits will change accordingly (Sæther 1997, Festa-Bianchet and Jorgenson 1998, Forchhammer et al. 2001, Gaillard and Yoccoz 2003, Adams 2005, Bårdsen et al. 2008). Such changes can involve phenotypic plasticity, which are of considerable interest in order to predict potential climate-effects (Sæther et al. 2000, Stenseth et al. 2002).

Most large terrestrial herbivores in northern ecosystems are considered capital breeders (Festa-Bianchet et al. 1998), because they rely, at least partly, on accumulated body reserves for reproduction (Jönsson 1997, Stearns 1992). Capital and income breeding strategies represent options at extreme ends of a continuous distribution of choices for energy use defined by foraging decisions, and theory predicts that an organism's breeding strategy will have important consequences for its fitness. Capital breeders should adopt a risk sensitive reproductive allocation strategy when reproduction competes with the amount of resources available for survival during an unpredictable non-breeding season (sensu Bårdsen et al. 2008). For large terrestrial herbivores in northern and mountain environments reproduction generally takes place during the favourable season (summer), whereas survival is particularly constrained in the unfavourable season (winter: Sæther 1997). In these environments individuals should retain sufficient body reserves in the autumn as to ensure survival during especially harsh winters (Erikstad et al. 1998). Individuals, thus, trade the amount of resources to allocate in their own body reserves against the amount of resources to allocate in reproduction during summer, where the latter affect an individual's autumn body reserves negatively (Bårdsen et al. 2008).

Animals should respond more strongly to deterioration than to improvement of environmental conditions (Bårdsen et al. 2008). This can be exemplified as follows: for a given distribution of winter conditions, a risk prone reproductive strategy involves high reproductive allocation that will result in high reproductive reward during benign winters, but high survival cost during harsh winters. A low reproductive allocation will, on the other hand, result in stable winter survival but lower reproductive reward. This represents a risk averse reproductive strategy. Additionally, Bårdsen et al. (2008) argues that when benign winter conditions appear over several years, individuals should increase their reproductive allocation. This is because the amount of autumn body reserves needed as insurance against winter starvation is lowered under benign conditions. This reasoning is supported empirically by the fact that many organisms are able to buffer their reproductive strategies according to environmental factors: mammals; e.g. humans (Bronson 1995, Lycett and Dunbar 1999, Quinlan 2007), *Rangifer* (Adams 2005, Tveraa et al. 2007, Bårdsen et al. 2008), bighorn sheep *Ovis canadensis* (Festa-Bianchet and Jorgenson 1998) and Weddell's seals *Leptonychotes weddellii* (Hadley et al. 2007), and long-lived birds (theoretical approach: Drent and Daan 1980, Erikstad et al. 1998); e.g. Antarctic petrel *Thalassoica antarctica* (Varpe et al. 2004).

In this study, we set up an experiment in sub-arctic Finland designed to test predictions about costs of lactation under benign winter feeding conditions for reindeer. In January 2007, we allocated females between four experimental groups consisting of two treatments (Fig. 1): (1) environmental manipulation with control animals on natural pastures and one group where individuals received supplementary winter feeding (supplementary feeding; SF); and (2) reproductive manipulation with control animals who lactated and one group where offspring was removed 0–2 days after parturition (lactation; LA). Immediate costs of reproduction, i.e. the lactation period, was measured by individual survival and seasonal development in body mass, whereas the relationship between maternal and offspring body mass was used as a measure of maternal allocation. Delayed costs of reproduction, i.e. the post-lactational period, was measured by body mass of females and their newborn offspring in the spring the year following experimental manipulation.

This experiment will give us answers to the following questions: (1) what is the immediate cost of reproduction under different environmental conditions during late gestation for female reindeer in the spring ('immediate effects of manipulated winter conditions') versus in the autumn ('summer somatic allocation')? (2) How does

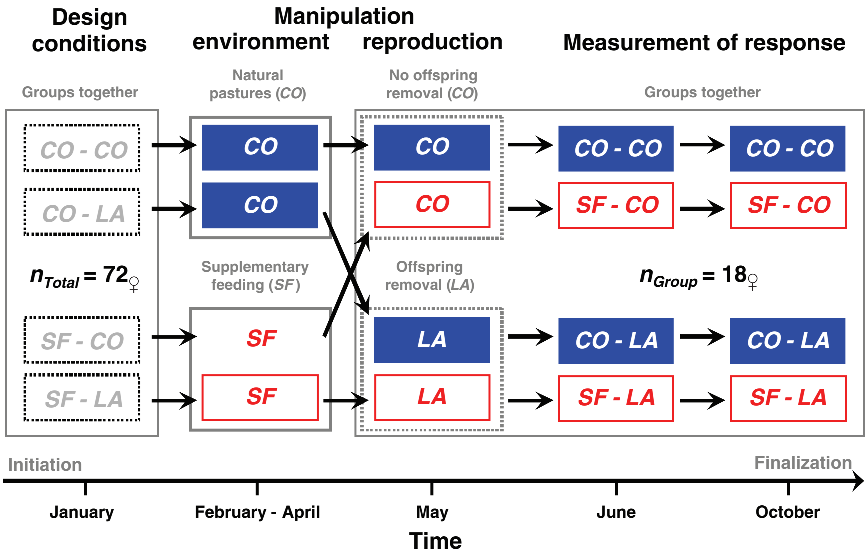

Figure 1. The study was designed with respect to initial body mass, i.e. pre-manipulative body conditions measured at the 8 January, of 72 pregnant females (♀). These were allocated to each experimental groups (n = 18 per group) following a stratified-randomized design algorithm. Manipulation of feeding conditions (CO; 'control' on natural pastures and SF; 'supplementary feeding') was performed in winter whereas manipulation of reproduction (CO; 'control' who kept their offspring and LA; manipulation of lactation by offspring removal 0–2 days after birth) was performed in the spring.

female reproductive status ('barren' vs 'lactating') affect female body condition in the autumn ('summer somatic allocation')? (3) How does environmental conditions during gestation affect female reproductive allocation and offspring body condition in the spring ('immediate effects of winter conditions') versus in the autumn ('summer reproductive allocation')? (4) To what extent does delayed, i.e. lagged, effects of environmental and reproductive manipulation affect female and offspring body condition and birth date in spring of the year following the experiment ('delayed costs of reproduction')?

Methods

Study area and the experimental reindeer herd in Kaamanen, Finland

The study was carried out in Kaamanen Experimental Reindeer Station (69°N, 27°E), where a herd of ~ 80 females with known life histories has been monitored for several decades (Holand et al. 2006, Weladji et al. 2006, Røed et al. 2007). The total study area of 43.8 km^2 is fenced and sub-divided into several smaller enclosures used on a seasonal basis, and within enclosures reindeer are freely grazing on natural pastures except for the calving season (May to early June) in which they are kept within a calf paddock (~ 8 ha in size). From 15 January to 30 April a subset of the herd, the supplementary feeding group, was given 2 kg $individual^{-1}$ day^{-1} in the form of commercial reindeer pellets (Poron-Herkku, Rehuraisio, Finland). Another subset of the herd, the natural pastures group, was given feeding in the form of 200 g $individual^{-1}$ day^{-1}. During a usual winter, reindeer in Kaamanen are given ~ 2 kg hay and concentrate, i.e. ~ 0.5 feeding units, $individual^{-1}$ day^{-1} from January to April. This equals 46% of the daily feeding requirements of reindeer as they require ~ 1.1 feeding units day^{-1} (Nieminen unpubl.). Population density may in interaction with the environment affect the reindeer's perception of the environment (Bårdsen et al. unpubl.), but reindeer density within the areas has been stable over years due to autumn slaughtering (2004–2008: mean $= 2.8$ $individual^{-1}$ km^{-2} (range $=$ 2.6–2.9)).

Experimental protocol

On 8 January 2007 animals were gathered, their gestational status ('pregnant' or 'barren') and body mass were recorded. Gestational status was assessed with an ultrasound scanner (with a 7.5 MHz rectal probe, measures taken by veterinary Heikki Sirkkola, Hämeenlinna, Finland), and only pregnant females were included in the experiment. From this subsample of data individuals were assigned to one of two experimental manipulations (four experimental groups totally; Fig. 1): (1) environmental manipulation; (1a) control females on natural pastures (control) and (1b) manipulation of winter conditions by supplementary feeding. (2) Reproductive manipulation; (2a) control females that were lactating (control) and (2b) manipulation of lactation by offspring removal 0–2 days after parturition. Initial female body mass, i.e. pre-manipulative body conditions, a potentially confounding covariate (Kojola 1993, Clutton-Brock et al. 1996, Festa-Bianchet et al. 1998, Tveraa et al. 2003, Adams 2005, Bårdsen et al. 2008), was equally distributed across the experimental groups by performing a stratified-randomized design (Fauchald et al. 2004). First, 72 females were sorted according to their body masses. Second, 18 strata of approximately similar body masses were formed. Third, individuals within each stratum were randomly allocated to each experimental group (sensu A1). Individual body mass and presence ('present' or 'absent') were in 2007 (when assessing immediate effects) recorded on gatherings on 5 March, 14 April, 5 June and 22 October (Fig. 1), whereas in 2008 (when assessing delayed effects) this information was measured on the 23 April. Individual body mass was recorded to the nearest 0.1 kg using an electronic balance. During the calving season newborns were caught by hand, individually marked and their body mass and sex was recorded. Date of birth ($1 = 1$ May, $2 = 2$ May, $\ldots$, $k = k$ days from 1 May) as well as female reproductive status ('reproducing' or 'barren') was also recorded. The calving area was visited daily.

Statistical analyses

Missing values, survival, reproductive success and initial female body mass

None out of 284 female body masses were missing, but 4 of 66 offspring body masses were missing from June to October 2007. One female in the offspring removal groups had a calf in the autumn and was thus removed from the analyses. The effect of missing values on initial female body mass was, thus, considered to be practically unimportant (sensu Bårdsen et al. 2008). Two females did not give birth (both in the same experimental group; supplementary feeding with no offspring removal) and one female's reproductive status was unknown in 2007. Such a high reproductive success rate (1.0 in three groups and 0.9 in one group; $n_{group} = 18$) makes it impossible to relate reproductive success to experimental manipulation or initial female body mass. All individuals survived until October (two offspring body masses were missing in October), which again means that it was impossible to relate survival to any of the above mentioned variables. In 2008, two females did not give birth and one female's reproductive status was unknown (all in the same experimental group; females with no offspring removal on natural pastures in the preceding winter). Moreover, 12 females were missing in 2008 due to slaughtering of animals in October 2008. Two animals where lacking in each of the natural pasture experimental groups, whereas four animals where lacking in each of the two supplementary feeding experimental groups

We tested the design and found no statistically significant differences between the experimental groups for initial female body mass and age (Appendix A1). Initial female body mass and age were highly correlated for younger females (≤ 4 years; Pearson's product-moment correlation, $r = 0.84$ (0.57, 0.95; $DF = 13$)), but not for older ones (>4 years; $r = 0.09$ (-0.19, 0.34; $DF = 53$)). Moreover, no senescent individuals (maximum age was 13 years; $n_{females < 11\ years} = 5$) and few young individuals ($n_{females > 4\ years} = 12$) were included in the study. Consequently, we did not include age in any further analyses. All statistical analyses were carried out in R

(R Development Core Team 2007 <http://www.R-project.org>).

Immediate effects – responses to experimental manipulations within 2007

Allocation in reproduction vs somatic growth: female and offspring body mass. Linear mixed-effect models (LME) applied using the NLME package (Pinheiro and Bates 2000, Pinheiro et al. 2008) were used to analyze the effect of the predictors on body mass of the females and offspring. For females, experimental manipulation of environment (control and supplementary feeding) and reproduction (control and lactation), initial female body mass (January prior to manipulation) and season (March, April, June and October) were applied as fixed effects (Fig. 1), whereas female identity was included as a random effect (Pinheiro and Bates 2000). All mixed effect-models in the present study were fitted with random intercepts only.

In order to assess the cost of lactation under different winter conditions it was important to make comparisons between maternal and offspring body masses. Our study is based on planned comparisons, and the predictions can then be tested statistically by estimating the following effects: (1) the main effect of environmental manipulation (supplementary feeding); (2) the main effect of reproductive manipulation (lactation); (3) the main effect of season; (4) the two-way interaction between supplementary feeding and lactation; (5) the two-way interaction between supplementary feeding and season; (6) the two-way interaction between lactation and season; and (7) the three-way interaction between supplementary feeding, lactation and season. In sum, it is important to estimate the difference in body mass for the different experimental groups across the four different seasons. Consequently, the above mentioned predictors were kept in all candidate models based on our a priori expectations (for extensive reviews of the theory behind the model selection philosophy adopted in the present study see Anderson et al. 2001, Burnham and Anderson 2002). Thus, we started with a model containing all the above predictors and two-way interactions between the two experimental manipulations and the other predictors. From this model, we formed a pool of candidate models where all covariates (initial body mass and the sex of the offspring born in 2007) and interactions were removed sequentially (Appendix A2: Table A2.1). From this pool of models we selected the model with the lowest Akaike's information criterion (AIC) value (Burnham and Anderson 2002). Following Pinheiro and Bates (2000) maximum likelihood fitted models were used when models were compared to each other (Appendix A2), whereas a restricted maximum likelihood fitted model was used for parameter estimation. For offspring we included manipulation of environment (control and supplementary feeding) and all above mentioned predictors except those including reproductive manipulation (the offspring removal groups did not contain any reproductive data so we removed it). As this study consisted of planned comparisons, with well-defined control groups, we used the treatment contrast comparing treatment to control, and Wald statistics to test the hypothesis that the contrasts were not significantly different from zero (Pinheiro and Bates 2000). All statistical tests in this study were two-tailed, the null-hypothesis was rejected at an α-level of 0.05.

Spring reproductive allocation: birth mass and date. Linear models (LM) were used to analyze the effect of environment manipulation (control and supplementary feeding) and initial female body mass on birth date and birth mass of the offspring. For the residuals in the analyses of birth date to fulfill the normality assumption we square root transformed the response in this analysis including both the results presented in figures and tables. We adopted the same model selection procedure as in the analyses of seasonal body mass development except that season and its interaction with manipulation were not included as predictors in these analyses (Appendix A2: Table A2.2).

Delayed effects – responses to experimental manipulations in 2008

Allocation in reproduction vs. soma: female spring body mass, offspring birth mass and birth date LM were used to analyze the effect of experimental manipulation of environment (control and supplementary feeding), manipulation of reproduction (control and lactation) and initial female body mass on spring female body mass, birth date and birth mass of the offspring in the year following the experimental manipulations. We adopted the same model selection procedure as in the analyses of reproductive allocation above except that the three-way interaction between the already mentioned variables was included as predictors in these analyses (Appendix A2: Table A2.3).

Results

Immediate effects – responses to experimental manipulations within 2007

Allocation in reproduction vs somatic growth: female and offspring body mass

Supplementary feeding had a positive effect on female body mass in March (main effect of supplementary feeding: 3.78 kg, Table 1a). During winter and summer we did not find evidence of any effects of reproductive manipulation in the form of offspring removal (lactation) on female body mass as none of the following estimates were statistically significant in March, April or June (Table 1a, Fig. 2a): (1) the main effect of lactation; (2) the two-way interaction between lactation and supplementary feeding; (3) the two-way interaction between lactation and season; and (4) the three-way interaction between lactation, supplementary feeding and season. Additionally, initially smaller females were smaller relative to larger ones (initial body mass: 0.81 kg).

Reindeer on natural pastures gained on average 3.65 kg in body mass from January to April (main effect of April, Table 1a). Nevertheless, the relative difference between the four experimental groups found in March, i.e. the positive effect of supplementary feeding, was constant throughout winter as none of the following estimates was statistically significant for April (Table 1a): (1) the two-way interaction between supplementary feeding and season; (2) the two-way interaction between lactation and season; and (3) the three-way interaction supplementary feeding, lactation and season. Consequently, the only real effect of manipulation during winter was a general positive effect of supplementary feeding on female body mass, and this effect was additive or equal across the two groups (Table 1a, Fig. 2a). As found previously, improved winter conditions did not have large positive effects on female body mass the following summer (Fauchald et al. 2004, Bårdsen et al. 2008). In fact, females in all experimental groups dropped to approximately similar body mass in June (Table 1a, Fig. 2a).

A general increase in body mass from March to October was evident (main effect of October: 4.18 kg). In this season, however, several interesting statistical significant interactions were present, making it evident that a shift in importance from environmental towards reproductive manipulation occurred. This is clearly evident in the visual representation of the model (Fig. 2a), but it was formally tested by comparing the following effects: First, the significant negative interaction between season (October) and supplementary feeding of −3.87 kg was larger than the main effect of supplementary feeding. This simply means that the positive effect of supplementary feeding present in both March and April had completely disappeared in the autumn (Table 1a). Second, the significant negative interaction between season (October) and lactation of 4.71 kg was large compared to the small and non-significant main effect of lactation, where the latter estimate represents how this predictor affected female body mass in March. Thus, in October the offspring removal group was on average >4 kg heavier compared to the control group consisting of lactating females. Third, the lack of a large estimated three-way interaction between lactation, supplementary feeding and season means that the effect of lactation was additive within supplementary feeding across all seasons. For October, this means that the positive effect of offspring removal was similar across the two environmental manipulation groups (females in the natural pastures and supplementary feeding groups did not respond significantly different to offspring removal).

In the analysis of offspring body mass development we found no positive effect of supplementary feeding on neither summer (main effect of supplementary feeding: Table 1b) nor autumn body mass (interaction between supplementary feeding and season: Table 1b). This in-

Table 1. Estimates from linear mixed effect models (LME) relating female (a) and offspring (b) body mass to experimental manipulation of winter conditions (CO; 'natural pastures', and SF'; 'supplementary feeding') and experimental manipulation of lactation (CO; 'lack of offspring removal' and 'LA'; 'offspring removal'), season (March, April, June and October) and initial female body mass. The intercept shows March mass for control females. To make the Intercept biologically meaningful initial body mass was centered (subtracting the average body mass). Estimated parameters are for a model selected from a pool of candidate models (Appendix 2 and Fig. 2).

Parameter	Allocation in soma vs reproduction		
	Value (95% CI)	DF	p-value
(a) Female body mass (kg)[a]			
Fixed effects			
Intercept	76.83 [74.75,78.91]	197	
Environmental manipulation (SF)	3.78 [0.84,6.72]	65	0.01
Reproductive manipulation (LA)	−0.47 [−3.41,2.48]	65	0.75
Season (April)	3.65 [1.19,6.10]	197	<0.01
Season (June)	−7.41 [−9.87, −4.96]	197	<0.01
Season (October)	4.18 [1.72,6.63]	197	<0.01
Initial body mass[b]	0.81 [0.72,0.90]	65	<0.01
Env. man. (SF) × Reprod. man. (LA)	0.28 [−3.88,4.44]	65	0.89
Env. man. (SF) × Season (April)	−0.20 [−3.63,3.22]	197	0.91
Env. man. (SF) × Season (June)	−2.53 [−5.96,0.89]	197	0.15
Env. man. (SF) × Season (Oct.)	−3.87 [−7.32, −0.42]	197	0.03
Reprod. man. (LA) × Season (April)	0.19 [−3.24,3.61]	197	0.91
Reprod. man. (LA) × Season (June)	1.13 [−2.29,4.56]	197	0.51
Reprod. man. (LA) × Season (Oct.)	4.71 [1.29,8.14]	197	0.01
Env. man. (SF) × Reprod. man. (LA) × Season (April)	1.19 [−3.65,6.04]	197	0.63
Env. man. (SF) × Reprod. man. (LA) × Season (June)	−0.90 [−5.74,3.95]	197	0.72
Env. man. (SF) × Reprod. man. (LA) × Season (Oct.)	2.63 [−2.24,7.49]	197	0.29
Random effects: female[c]			
Among females standard deviation	2.40 [1.82,3.17]	$n_{Obs.}=279$	
Within females standard deviation (residuals)[c]	3.63 [3.29,4.01]	$n_{Ind.}=70$	
(b) Calf body mass (kg)			
Fixed effects			
Intercept	11.72 [8.95,14.49]	28	
Environmental manipulation (SF)	−0.30 [−3.48,2.88]	27	0.85
Season (October)	36.57 [33.8,39.35]	28	<0.01
Offspring sex (male)	3.33 [0.65,6.02]	27	0.02
Initial body mass[b]	0.26 [<0.01,0.51]	27	0.05
Env. man. (SF) × Season (October)	−2.65 [−6.66,1.35]	28	0.18
Env. man. (SF) × Initial body mass[b]	0.03 [−0.31,0.36]	27	0.87
Random effects: female[c]			
Among females standard deviation	1.90 [0.73,4.96]	$n_{Obs.}=62$	
Within females standard deviation (residuals)	3.83 [2.96,4.95]	$n_{Ind.}=32$	

[a] One outlying observation (standardized residual = −6.25) was excluded from the analysis. This exclusion did not affect the results notably.

[b] Maternal body mass in January (i.e. before onset of manipulation).

[c] Female random terms involved only the constant term (i.e. random intercepts fitted per female).

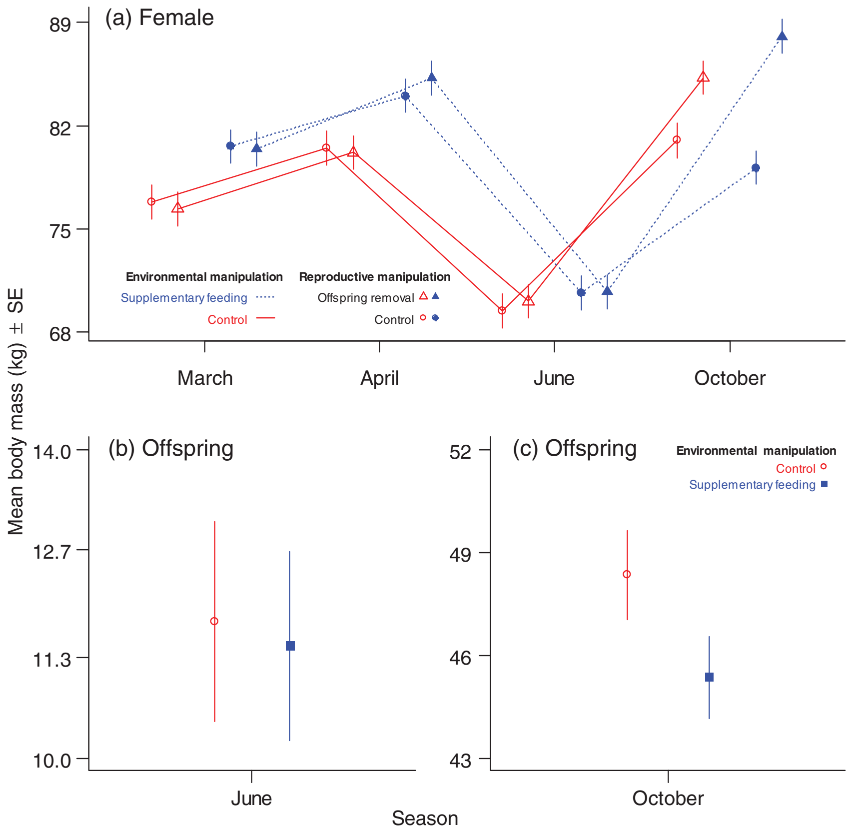

Figure 2. Estimated mean maternal (a) and offspring (b–c) body mass for each experimental group in each season presented with ±1 SE (bars) based on the analyses presented in Table 1.

dicates a lack of increased reproductive allocation for the females experiencing improved winter feeding conditions (Fig. 2b). Initially smaller females produced smaller offspring relative to initially larger females, and this effect was present in both summer and autumn (main effect of initial body mass: 0.29 kg, Table 1b). Moreover, male offspring was larger than female offspring in both seasons (Table 1b). To summarize, females experiencing improved winter conditions invested more in somatic growth during late winter, but they did not seem to translate this to increased reproductive allocation during summer. On the other hand, manipulation of lactation did have a large effect on female somatic growth during summer.

Spring reproductive allocation: birth mass and date

Average birth mass was not higher in the supplementary feeding group (main effect of supplementary feeding, Table 2a). Smaller females (≤72 kg) in the control group on natural pastures produced significantly smaller offspring relative to larger females (main effect of initial body mass: 0.09 kg, Table 2a, Fig. 3a). This effect was, however, not present in the supplementary feeding group where a significantly weaker effect of initial female body mass was present (interaction between supplementary feeding and initial body mass: −0.07 kg, Table 2a, Fig. 3a). This means that the positive relationship between initial female body mass and birth mass found for the control group on natural pastures was not present for females in the supplementary feeding group. Average (squared root) birth date was not related to manipulation (main effect of supplementary feeding: Table 2b). Smaller females in both groups gave birth later relative to larger females (main effect of initial body mass: −0.04 kg, Table 2b, Fig. 3b). To summarize, smaller females experiencing improved winter conditions seemed to increase their reproductive allocation during gestation, measured as increased birth mass, compared to smaller females on natural pastures (Fig. 3a).

Delayed effects – responses to experimental manipulations in 2008

Allocation in reproduction vs soma: female spring body mass, offspring birth mass and birth date

We found no particularly strong effects of manipulation in the year following the experiment: First, average female spring body mass was not statistically different for either environmental or reproductive manipulation (main effect of lactation and supplementary feeding: Table 3a). Initially smaller females were still smaller the year after manipulation relative to larger females (main effect of initial body mass: 0.97 kg, Table 3a, Fig. 4a–b). This relationship was not statistical significantly different between the two reproductive manipulation groups (interaction between lactation and initial body mass: Table 3a), but this relationship was weaker for females in the supplementary feeding group compared to the control group on natural pastures (interaction between supplementary feeding and initial body mass: – 0.30 kg, (Table 3a, Fig. 4a–b). Smaller females that received supplementary feeding the preceding

Table 2. Estimates from linear models (LM) relating offspring birth mass (a) and birth date (b) to experimental manipulation of winter conditions (CO; 'natural pastures', and SF'; 'supplementary feeding') and initial female body mass. The intercept shows mass for control females. To make the Intercept biologically meaningful initial body mass was centered (subtracting the average body mass). Estimated parameters are for a model selected from a pool of candidate models (details in Appendix 2 and Fig. 3).

Parameter	Reproductive allocation	
	Value (95% CI)	p-value
(a) Offspring birth mass (kg)[a]		
Intercept	6.25 [5.96,6.55]	
Environmental manipulation (SF)	0.15 [−0.28,0.57]	0.50
Initial body mass[b]	0.09 [0.05,0.13]	<0.01
Env. man. (SF) × Initial body mass[b]	−0.07 [−0.12, −0.01]	0.02
(adjusted $R^2 = 0.25$, $F = 8.34$, $DF = 3,63$, $p < 0.01$)		
(b) Offspring birth date (days)[c]		
Intercept	3.47 [3.14,3.80]	
Environmental manipulation (SF)	0.14 [−0.32,0.61]	0.54
Initial body mass[b]	−0.04 [−0.07, −0.01]	0.01
(adjusted $R^2 = 0.08$, $F = 3.72$, $DF = 3,64$, $p = 0.03$)		

[a] One potential outlying observation, i.e. the birth mass of 9.2 kg, was detected, but as its removal did not affect the conclusion drawn from this analysis we kept it in the analysis.

[b] Maternal body mass in January (i.e. before onset of manipulation).

[c] Birth date, i.e. the number of days from 1 May, was square root transformed in order to approximate normally distributed residuals. Consequently, the reported estimates in this table are on square root scale.

winter (12–14 months before) was, thus, larger compared to smaller females on natural pastures. Second, average offspring birth masses were not statistical significantly different across both types of manipulation (main effect of supplementary feeding and lactation: Table 3b, Fig. 4c–d). Again we documented that larger females gave birth to larger offspring the year following manipulation (main effect of initial body mass: Table 3b, Fig. 4c–d). This shows that female body mass in January 2007 was still a predictor of birth body mass 14–15 months ahead. Third, in the analysis of offspring birth date we found no delayed effects at all as neither manipulations or initial female body mass was present (Table 3c, Fig. 4e–f). To summarize, except for a lagged positive effect of initial female body mass and a

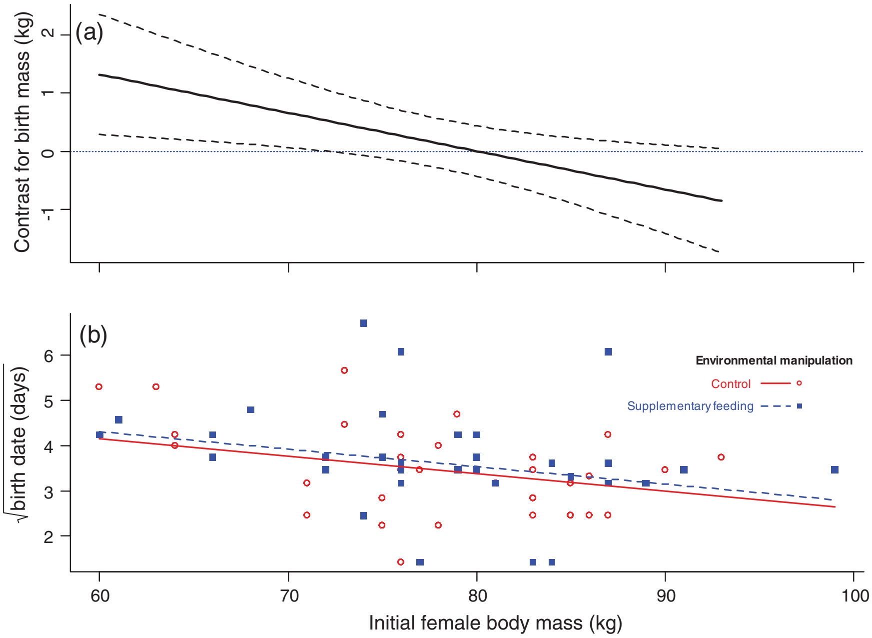

Figure 3. Birth mass contrast between SF and control females (a), and birth date (b), square root transformed, in 2007 as a function of initial female body mass (8 January) and experimental group (birth mass; mean = 6.32 kg ± 1 SD, n = 67 and birth date; mean = 13.48 days ± 7.37 SD, n = 67). This is a visualization of data and models with non-centered initial body mass presented in Table 2. Due to the interaction shown in Table 2a we show the contrast, i.e. the difference, and 95% CI for the difference between the control and the supplementary feeding groups (a). The plot showing the estimated difference between fed and control animals was produced using the 'estimable' function in the 'gregmisc' library for R (Warnes 2008).

Table 3. Estimates from linear models (LM) relating offspring birth mass (a) and birth date (b) to experimental manipulation of winter conditions (CO; 'natural pastures', and SF'; 'supplementary feeding'), reproductive manipulation (CO; 'lack of offspring removal' and 'LA'; 'offspring removal') and initial female body mass. The intercept shows mass for control females. To make the Intercept biologically meaningful initial body mass was centered (subtracting the average body mass). Estimated parameters are for a model selected from a pool of candidate models (details in Appendix 2 and Fig. 4).

Parameter	Lagged effects	
	Value (95% CI)	p-value
(a) Female spring mass (kg)		
Intercept	84.13 [82.27,85.99]	
Environmental manipulation (SF)	1.84 [−0.83,4.52]	0.17
Reproductive manipulation (LA)	1.46 [−1.13,4.05]	0.26
Initial body mass[a]	0.97 [0.77,1.17]	<0.01
Env. man. (SF) × Reprod. man (LA)	−1.70 [−5.50,2.10]	0.37
Env. man. (SF) × Initial body mass[a]	−0.30 [−0.53, −0.07]	0.01
Reprod. man (LA) × Initial body mass[a]	−0.06 [−0.29,0.17]	0.60
(adjusted $R^2 = 0.78$, $F = 34.39$, $DF = 6,51$, $p < 0.01$)		
(b) Offspring birth mass (kg)[b]		
Intercept	6.22 [5.86,6.59]	
Environmental manipulation (SF)	−0.20 [−0.70,0.30]	0.43
Reproductive manipulation (LA)	0.02 [−0.46,0.51]	0.92
Initial body mass[a]	0.03 [0.01,0.05]	0.01
Env. man. (SF) × Reprod. man (LA)	0.45 [−0.24,1.14]	0.20
(adjusted $R^2 = 0.12$, $F = 2.76$, $DF = 4,50$, $p = 0.04$)		
(c) Offspring birth date (days)[c]		
Intercept	4.06 [3.63,4.48]	
Environmental manipulation (SF)	−0.18 [−0.75,0.40]	0.54
Reproductive manipulation (LA)	−0.09 [−0.65,0.47]	0.76
Env. man. (SF) × Reprod. man (LA)	0.38 [−0.41,1.18]	0.34
(adjusted $R^2 = -0.03$, $F = 0.40$, $DF = 3,51$, $p = 0.75$)		

[a] Maternal body mass in January 2007 (i.e. before onset of manipulation).

[b] One potential outlying observation, i.e. the birth mass of 9.1 kg, was detected, but as its removal did not affect the conclusion drawn from this analysis we kept it in the analysis.

[c] Birth date, i.e. the number of days from 1 May, was square root transformed in order to approximate normally distributed residuals. Consequently, the reported estimates in this table are on square root scale.

positive effect of supplementary feeding for smaller females we found no biologically significant lagged effects.

Discussion

In the present study we demonstrated an immediate, but no delayed, cost of reproduction for female reindeer as manipulation of lactation resulted in a higher autumn body mass, and this cost were not related to environmental conditions during late gestation. We also found an immediate positive effect of winter feeding conditions on female body mass during late gestation, but this effect was not present in the following seasons within the same year and in spring the following year. We found conflicting evidence of increased summer reproductive allocation due to experimentally improved winter feeding conditions. First, we found no effect of supplementary feeding on June or October offspring body mass. This indicates that improved winter conditions did not increase female reproductive allocation during spring (from birth to June) or summer (from June to October) in 2007. Second, we found that smaller females in the supplementary feeding group gave birth to larger offspring compared to control females on natural pastures. This indicates that improved winter conditions lead to increased reproductive allocation for smaller females. Third, we found a small delayed, or lagged, effect of supplementary feeding on female body mass for initially smaller females in the spring of 2008. In sum, even though the duration of the present study was only two years we documented a cost of lactation in the autumn and an effect of supplementary winter feeding on female winter and spring body mass and offspring birth mass within the same year as treatments were applied.

For ecological experiments it is always a critical issue if the applied manipulations are relevant for addressing the focal question, and if the level of treatment is realistic with respect to that found in a natural setting. Raising these issues is redundant for manipulation of lactation as loosing offspring, especially in the early phase of lactation, is quite common for many large terrestrial herbivores including *Rangifer* (Adams et al. 1995). Raising these issues for environmental manipulation is more relevant as the experiment were conducted within an experimental research herd (Holand et al. 2006) that has received supplementary feeding for years.

Supplementary winter feeding, using similar pellets as the current study, has been applied in previous experiments (Fauchald et al. 2004, Bårdsen et al. 2008), but the level of treatment in the present study was ∼4-fold of that in these previous experiments. We did prove that the level of supplementary feeding applied had a positive effect on female body mass during late gestation and on offspring birth masses for smaller females. Female body mass did,

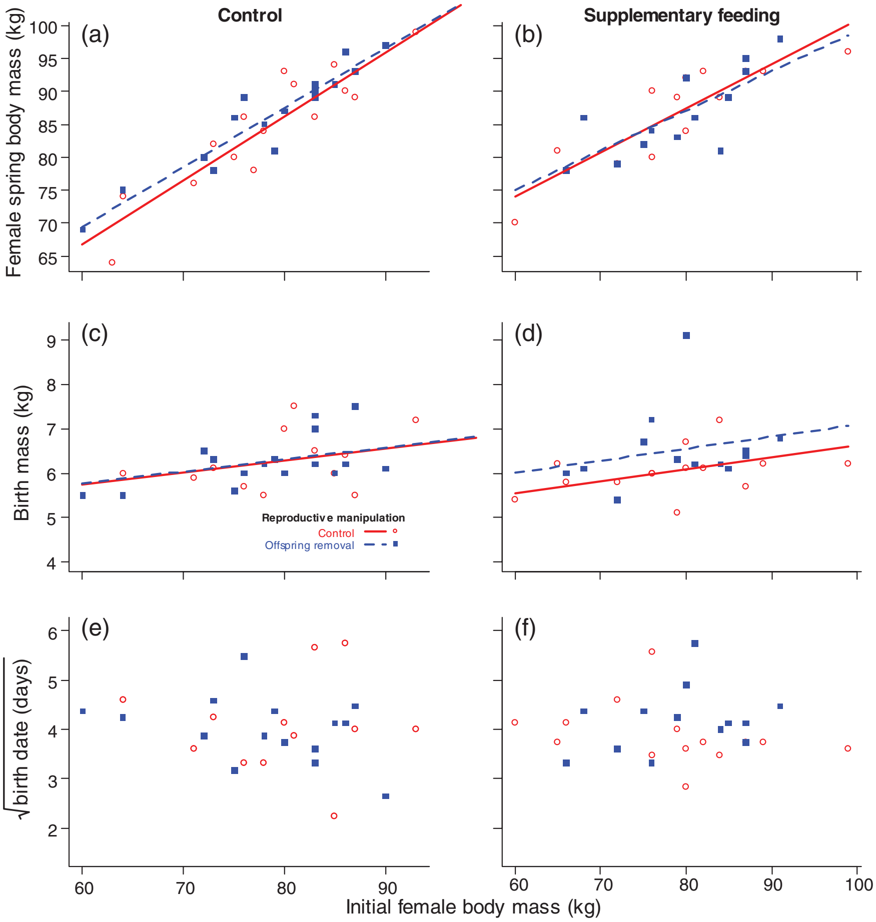

Figure 4. Female spring body mass (a–b), birth mass (c–d) and birth date (e–f), which is square root transformed, in 2008 as a function of initial female body mass (8 January 2007) and experimental group (birth mass; mean = 6.27 kg ± 0.67 SD, n = 55 and birth date; mean = 16.64 days ± 6.08 SD, n = 55). This is a visualization of data and models with non-centered initial body mass presented in Table 3. The panels divide environmental manipulation: left panel (a, c and e) represents controls whereas right panel (b, d and f) represents the supplementary feeding group (details in Table 3).

however, increase from early to late winter in the natural pastures group as well, and this increase in body mass during winter makes this study herd quite different from the other experiments (Fig. 5b in Fauchald et al. 2004). Moreover, winter and spring body masses in this herd is substantially larger compared to most other Fennoscandian herds (Lenvik and Aune 1988, Rødven 2003, Tveraa et al. 2003, Fauchald et al. 2004, Bårdsen et al. 2008, Bårdsen et al. unpubl.). Consequently, the issue of whether this treatment was realistic with respect to a ‘natural’ Fennoscandian setting is hard to argue for. Nevertheless, the forage situation that reindeer in Kaamanen experiences represent an interesting situation when studying risk sensitive life histories as the winter situation for this herd is associated with low levels of risk: winter feeding conditions are overabundant and highly predictable across years. Females in all the experimental groups, thus, seem to invest a large amount of resources into both reproduction and somatic growth. This makes this study quite different from our previous experiments where later winter feeding conditions have been highly unpredictable (Tveraa et al. 2003, Fauchald et al. 2004, Bårdsen et al. 2008). In essence, the present study represents a nice complement to our previous studies as it improves our knowledge about the cost of reproduction and reproductive allocation in a low risk environment.

Cost of reproduction

Lactation was clearly immediately costly for reindeer as barren females were larger compared to lactating females in the autumn, whereas all experimental groups were of equal size in the summer. The latter result supports earlier findings that female reindeer regulate their body mass down to some minimum spring threshold in order to take care of their newborns at a time when the chance of starvation is low (Fauchald et al. 2004, Bårdsen et al. 2008). Barren females invested more in somatic growth during summer compared to lactating ones as they gained more in body mass compared to lactating females. We found no delayed costs of reproduction as no lagged effects of reproductive manipulation was present in the spring of 2008.

The cost of reproduction for large herbivores living in northern hemisphere is generally, not related to reduced survival but rather to reduced future reproduction (Festa-Bianchet et al. 1998, Festa-Bianchet and Jorgenson 1998), and adult survival is high and constant relative to juvenile survival for these organisms (Gaillard et al. 1998, 2000). Nevertheless, reproductive allocation has a negative effect on maternal body mass for reindeer (Bårdsen et al. 2008, this study). Such a cost of reproduction with respect to maternal autumn body mass can have important effects on other life history traits as well (through correlations with body mass), e.g.: (1) reproductive success (Cameron et al. 1993, Kojola 1993, Fauchald et al. 2004); (2) female age (Reimers et al. 1983, Kojola et al. 1998, Rødven 2003); (3) survival of both juveniles and adults (Tveraa et al. 2003); and (4) social rank (Kojola 1989, Holand et al. 2004, Fauchald et al. 2007). A combination of an extreme winter and low body mass will be fatal even for adult reindeer (Tveraa et al. 2003).

Risk sensitive in the context of the present study combines the probability of encountering an extreme winter and the consequences such winters have on survival and reproductive success. The animals cannot manipulate the probability of encountering such a winter, but they can buffer the adverse consequences of such winters by reducing their reproductive allocation (Adams 2005, Bårdsen et al. 2008, this study). Thus, it is important to keep in mind that female reindeer do not prepare for an average winter, but for extreme events that might happen from time to time. In sum, the immediate cost of lactation found in the present study are in accordance with numerous observational studies on mammals (Clutton-Brock et al. 1989, Dufour and Sauther 2002) and with the general finding that reproduction is costly: mammals in general (Sand 1996, Festa-Bianchet et al. 1998, Lambin and Yoccoz 2001, Lummaa and Clutton-Brock 2002, Tveraa et al. 2003, Tavecchia et al. 2005), birds (Lindén and Møller 1989, Moreno 1989, Monaghan and Nager 1997) and plants (Obeso 2002).

Reproductive allocation

We found no evidence of a positive immediate effect of improved winter conditions on reproductive allocation during summer, which was measured as an increase in offspring body mass from early summer to autumn in 2007. Actually, this was not surprising as this is the third experiment on reindeer where no positive effects of winter feeding on reproductive output has been documented (Fauchald et al. 2004, Bårdsen et al. 2008). Nevertheless, we were able to find evidence of a positive effect of improved winter on offspring birth mass for smaller females. This finding may indicate that there is an upper body mass threshold, i.e. a regulatory mechanism controlling the amount of resources a mother can give to a fetus, affecting reproductive output in the spring as both smaller and larger females produced offspring of similar size in the supplementary feeding group. Existence of body mass thresholds affecting reproduction has been found previously (reviewed by Gaillard et al. 2000): lower body mass thresholds above which most females reproduce and below which they do not has been found in e.g. red deer (Albon et al. 1983), moose (Sæther and Haagenrud 1983, Sæther et al. 1996), bighorn sheep (Jorgenson et al. 1993) and reindeer (Reimers 1983, Skogland 1985), whereas an upper threshold where increasing mass do not lead to increased reproductive output as has been found previously for reindeer (Lenvik et al. 1988). Moreover, except for the finding that initially small females that received supplementary winter feeding the previous year were larger compared to control females we did not find any lagged effects of manipulation in the spring of 2008. In essence, improved winter feeding conditions lead to increased reproductive allocation in the fetus during gestation but not during the lactation period.

Risk sensitive life histories

In a previous experimental study we concluded that when reproduction competes with the amount of resources available for survival during an unpredictable non-breeding season, individuals adopted a risk sensitive regulation of their reproductive allocation (sensu Bårdsen et al. 2008). Moreover, Bårdsen et al. (2008) argued that for a given distribution of winter conditions, a risk prone reproductive strategy involves high reproductive allocation that will result in high reproductive reward during benign winters but high survival cost during harsh winter. A low reproductive allocation will, on the other hand, result in stable winter survival but lower potential reproductive reward, and this represents a risk averse reproductive strategy. These contrasting reproductive strategies can only be understood in relation to the expected environmental conditions, i.e. the distribution of past environmental conditions experienced by the females. Based on that, Bårdsen et al. (2008) argued that when benign winter conditions appear over several years, individuals should increase their reproductive allocation. This increase in reproductive allocation should happen even though individuals have to trade allocation in reproduction over their own chance to survive (if a harsh winter do occur) as the amount of autumn body reserves needed as insurance against winter starvation is lowered under benign conditions. Similarly, this means that the cost of reproduction is lowered when winter conditions are improved as survival probabilities for both females and offspring are improved under benign conditions. The winter feeding conditions in Kaamanen are superior compared to most other Fennoscandian herds so our finding of no large delayed, but some immediate, costs of reproduction and reproductive investments due to improved conditions, thus, fits well with theory.

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Appendix 1. Test of experimental design

We tested the design and found no statistical significant differences between the experimental groups for initial female body mass and age (Fig. A1.1). We used a two-way analysis of variance (using the treatment contrast: Venables and Ripley 2002) including both manipulations and the interaction between them (Table A1.1).

Reference

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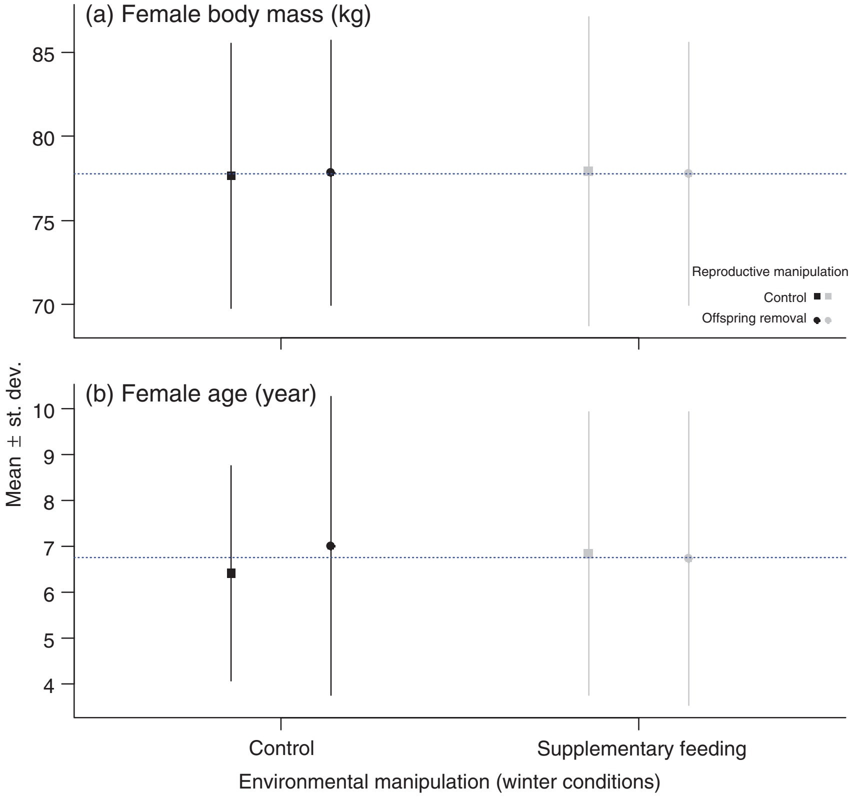

Figure A1.1. Estimated mean initial female body mass (8 January) and age for the different experimental groups presented with ±1 SD (bars).

Table A1.1. Estimates from linear models (LM) relating initial female body mass (a) and age (b) to experimental manipulation of winter conditions (CO; 'natural pastures', and SF'; 'supplementary feeding') and experimental manipulation of lactation (CO; 'lack of offspring removal' and 'LA'; 'offspring removal'). The intercept shows estimated values for control females for both manipulations.

Parameter	Reproductive investment	
	Value (95% CI)	p-value
(a) Initial body mass (kg)		
Intercept	77.65 [73.63,81.66]	
Environmental manipulation (SF)	0.30 [−5.30,5.89]	0.92
Reproductive manipulation (LA)	0.19 [−5.41,5.78]	0.95
Env. man. (SF) × Reprod. man. (LA)	−0.13 [−8.04,7.78]	0.97
(adjusted $R^2 = -0.05$, $F = 0.01$, $DF = 3,66$, $p > 0.99$)		
(b) Initial female age (years)		
Intercept	6.41 [4.95,7.88]	
Environmental manipulation (SF)	0.42 [−1.62,2.46]	0.68
Reproductive manipulation (LA)	0.59 [−1.45,2.63]	0.57
Env. man. (SF) × Reprod. man. (LA)	−0.66 [−3.51,2.23]	0.65
(adjusted $R^2 = -0.04$, $F = 0.12$, $DF = 3,66$, $p = 0.95$)		

Appendix 2. Model selection and the set of candidate models

Selecting the models used for inference in the three analyses presented was performed within a model selection framework (Buckland et al. 1997, Anderson et al. 2000, Burnham and Anderson 2002): First, a set 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 included some predictors in the analyses based on our a priori expectations (see main text for details; Table A2.1–3). Second, in each analysis, rescaling and ranking models relative to the value of the model with the lowest Akaike’s information criterion (AIC) value was performed (Burnham and Anderson 2002: Δ_i denotes this difference for model i). We, then, selected the simplest model (i.e. the model with the fewest degrees of freedom) with a $\Delta_i \leq 1.5$.

References

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Table A2.1. The relative evidence for each candidate LME model in Table 1 (i) was assessed by rescaling and ranking models relative to the value of the model with the lowest Akaike’s information criterion value (Δ_i; the model **underlined in bold** were selected and used for inference in each analysis as its Δ_i equals zero). The models were fitted by maximum likelihood (ML) as the restricted maximum likelihood (REML) fit used in the Table 1 and 3 are not recommended when several models are compared to each other (Pinheiro and Bates 2000). Each predictor included in a model is marked with an ‘x’, whereas those marked with a ‘-‘ is not available for that specific analysis.

i	Environmental manipulation[a]	Reproductive manipulation[a]	Season[a]	Env. manip. × Reprod. manip.[a]	Env. manip. × seas.[a]	Reprod. manip. × seas.[a]	Env. manip. × Reprod. manip. × seas.[a]	Initial body mass (IBM)	Reprod. manip. × IBM	Env. manip. × IBM)	Offspring sex (OFS	Env. manip. × OFS	Reprod. manip. × OFS	DF	Investment in soma vs reproduction Δ_i
(a) Female body mass (kg)															
1.	**x**	**x**	**x**	**x**	**x**	**x**	**x**	x	x	x	x	x	x	24	3.66
2.	**x**	**x**	**x**	**x**	**x**	**x**	**x**	x	x	x	x	x		23	1.93
3.	**x**	**x**	**x**	**x**	**x**	**x**	**x**	x	x	x	x			22	2.24
4.	**x**	**x**	**x**	**x**	**x**	**x**	**x**	x	x	x				21	1.96
5.	**x**	**x**	**x**	**x**	**x**	**x**	**x**	x	x					20	0.00
6.	**x**	**x**	**x**	**x**	**x**	**x**	**x**	x						19	**1.04**[b]
7.	**x**	**x**	**x**	**x**	**x**	**x**	**x**							18	119.42
(b) Offspring body mass (kg)[c]															
1.	**x**	–	**x**	–	**x**	–	**x**	x	x	–	x	x	–	10	1.27
2.	**x**	–	**x**	–	**x**	–	**x**	x	x	–	x			9	**0.00**
3.	**x**	–	**x**	–	**x**	–	**x**	x	x					8	4.87
4.	**x**	–	**x**	–	**x**	–	**x**	x						7	3.56
5.	**x**	–	**x**	–	**x**	–	**x**							5	13.20

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

[b] We lack information on the sex of the offspring for a few females: (i) we do not know if one female gave birth and (ii) one female did not give birth. Since offspring sex was not important we fitted the selected model to data where we also included these three individuals.

[c] Data from March to May was not included in these analyses as the first gathering with all offspring included was in June.

Table A2.2. The relative evidence for each candidate LM model in Table 2 (i) was assessed by rescaling and ranking models relative to the value of the model with the lowest Akaike's information criterion value (Δ_i; the model in **underlined in bold** were selected and used for inference in each analysis as its Δ_i equals zero). Each predictor included in a model is marked with an 'x'

i	Environmental manipulation[a]	Initial body mass (IBM)	Env. manip. × IBM	Offspring sex (OFS)	Env. manip. × OFS	DF	Reproductive investment
							Δ_i
(a) Offspring birth mass (kg)							
1.	**x**	x	x	x	x	7	2.06
2.	**x**	x	x	x		6	0.43
3.	**x**	x	x			5	**0.00**[b]
4.	**x**	x				4	4.35
5.	**x**					3	17.91
(b) Offspring birth date (days)[c]							
1.	**x**	x	x	x	x	7	3.71
2.	**x**	x	x	x		6	1.71
3.	**x**	x	x			5	1.53
4.	**x**	x				4	**0.00**[b]
5.	**x**					3	5.10

[a] The predictor in bold was kept in all models based on our a priori expectations.

[b] We lack information on the sex of the offspring for a few females (Table A2.1). Since offspring sex was not important we fitted the selected model to data where we also included these individuals.

[c] Birth date, i.e. the number of days from 1 May, was square root transformed in order to approximate a normal distribution for the residuals.

Table A2. 3. The relative evidence for each candidate LM model in Table 3 (i) was assessed by rescaling and ranking models relative to the value of the model with the lowest Akaike's information criterion value (Δ_i; the model in **underlined in bold** were selected and used for inference in each analysis as its Δ_i equals zero). Each predictor included in a model is marked with an 'x'

i	Environmental manipulation[a]	Reproductive manipulation[a]	Env. manip × Reprod. manip[a]	Initial body mass (IBM)	Reprod. manip. × IBM	Env. manip. × IBM	Env. manip × Reprod. manip × IBM	Offspring sex (OFS)	Reprod. manip. × OFS	Env. manip. × OFS	DF	Lagged effects
												Δ_i
(a) Female spring mass (kg)												
1.	**x**	**x**	**x**	x	x	x	x	x	x	x	12	5.30
2.	**x**	**x**	**x**	x	x	x	x	x	x		11	4.18
3.	**x**	**x**	**x**	x	x	x	x	x			10	3.39
4.	**x**	**x**	**x**	x	x	x	x				9	1.94
5.	**x**	**x**	**x**	x	x	x					8	**0.00**[b]
6.	**x**	**x**	**x**	x	x						7	4.51
7.	**x**	**x**	**x**	x							6	2.60
8.	**x**	**x**	**x**								5	84.29
(b) Offspring birth mass (kg)												
1.	**x**	**x**	**x**	x	x	x	x	x	x	x	12	9.85
2.	**x**	**x**	**x**	x	x	x	x	x	x		11	9.08
3.	**x**	**x**	**x**	x	x	x	x	x			10	7.31
4.	**x**	**x**	**x**	x	x	x	x				9	5.42
5.	**x**	**x**	**x**	x	x	x					8	3.47
6.	**x**	**x**	**x**	x	x						7	1.82
7.	**x**	**x**	**x**	x							6	**0.00**[b]
8.	**x**	**x**	**x**								5	5.42
(c) Offspring birth date (days)[c]												
1.	**x**	**x**	**x**	x	x	x	x	x	x	x	12	7.61
2.	**x**	**x**	**x**	x	x	x	x	x	x		11	5.80
3.	**x**	**x**	**x**	x	x	x	x	x			10	3.89
4.	**x**	**x**	**x**	x	x	x	x				9	4.04
5.	**x**	**x**	**x**	x	x	x					8	4.98
6.	**x**	**x**	**x**	x	x						7	3.21
7.	**x**	**x**	**x**	x							6	1.27
8.	**x**	**x**	**x**								5	**0.00**[b]

[a] The predictor in bold was kept in all models based on our a priori expectations.

[b] We lack information on the sex of the offspring for a few females (Table A2.1). Since offspring sex was not important we fitted the selected model to data where we also included these individuals.

[c] Birth date, i.e. the number of days from 1 May, was square root transformed in order to approximate a normal distribution for the residuals.

ERRATA: author suggested corrections for the proof

P1, title. '(…) costs of lactation (…)' *should read* '(…) cost of lactation (…)' as we only documented one cost of lactation: the effect of 'LA' on female bm in the autumn of 2007.

P1, addresses. Mauri Nieminen is not employed at NINA. His affiliation is solely at 'Finnish Game and Fisheries Research Inst., Reindeer Research Station, FI-99910 Kaamanen, Finland'.

P1, Abstract. 'In contrast, offspring removal did have a positive effect on summer body mass development as females in this group were larger in the autumn body mass relative to control females' should read 'In contrast, offspring removal did have a positive effect on summer body mass development as females in this group were larger in the autumn relative to control females'.

P1, 1st paragraph (left column), line 7 from below. '(…) reproductive stages but most studies have (…)' *should read* '(…) reproductive stages, but most studies have (…)'.

P2, Figure 1. The frame around one of the boxes is missing: The first 'SF' box should have a similar frame as the other 'SF' box.

P3, 2nd paragraph (right column), line 27 from above. 'One female in the offspring removal groups had (…)' *should read* 'One female in the offspring removal group had (…)'.

P3, 2nd paragraph (right column), line 15 from below. '(…) in October 2008 (…)' *should read* '(…) in October 2007 (…)'.

P3, 1st paragraph (right column), line 19-20 from above. '(…) (1 = 1 May, 2 = 2 May, …, k = k days from 1 May) (…)' *should read* '(…) (1 = 1 May) (…)'.

P4, 2nd paragraph (left column), line 10-14 from above. 'For females, experimental manipulation of environment (control and supplementary feeding) and reproduction (control and lactation), initial female body mass (January prior to manipulation) and season (March, April, June and October) were applied as fixed effects (Fig. 1), (…)' *should read* "For females, experimental manipulation of environment (control and supplementary feeding) and reproduction (control and lactation), initial female body mass (January prior to manipulation), season (March, April, June and October) and offspring sex (female and male) were applied as fixed effects (Fig. 1), (…)'.

P4, 3rd paragraph (left column), line 16-15 from below. 'From this pool of models we selected the model with the lowest Akaike's information criterion (AIC) value, (…)' *should read* 'From this pool of models we selected the most parsimonious model as assessed by the Akaike's information criterion (AIC) (…)'.

P9, 1st paragraph (left column), line 9 from below. '(…) low levels of risk: winter feeding conditions are overabundant (…)' *should read* '(…) low levels of risk: winter forage is overabundant (…)'.

P10, 2nd paragraph (right column), line 1 from below. '(…) Bustnes, Svein A. Hanssen (…)' *should read* '(…) Bustnes, Sveinn A. Hanssen (…)'.

P13, 1st paragraph (left column), line 1 from above. '(…) no statistical significant (…)' *should read* '(…) no statistical significantly (…)'.

P13, Table A1.1, heading. 'Reproductive investment' *should read* 'Design conditions'.

P14-16, Table A2.1-3, table text. '(…) Δ_i equals zero' *should read* '(…) $\Delta_i \geq 1.5$'.

P14-15, Table A2.1-2, label for last column to the right. 'investment' *should read* 'allocation'.

P1-16, 'search and replace': non-consistency in the text.
1. We have used 'vs', 'vs.' and 'versus' non-consistently throughout the manuscript.
2. In the proof 'a priori [in normal text]' have been used whereas '*a priori* [in *italics*]' is used consistently in the literature.
3. The appendices are in the main text referred to as both 'Appendix A1' and 'Appendix A2' or as 'Appendix 1' and 'Appendix 2'. We do not have any preferences, but we think that this should be consistent. Please do note that we started the labelling of all figures/tables in the appendixes with 'A'. Figure 1 in Appendix 1 is for example labelled as 'Figure A1.1'.

PAPER 3

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

Bårdsen, B.-J., T. Tveraa, P. Fauchald & K. Langeland

Manuscript

Running head: Risk sensitive reproductive allocation

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.

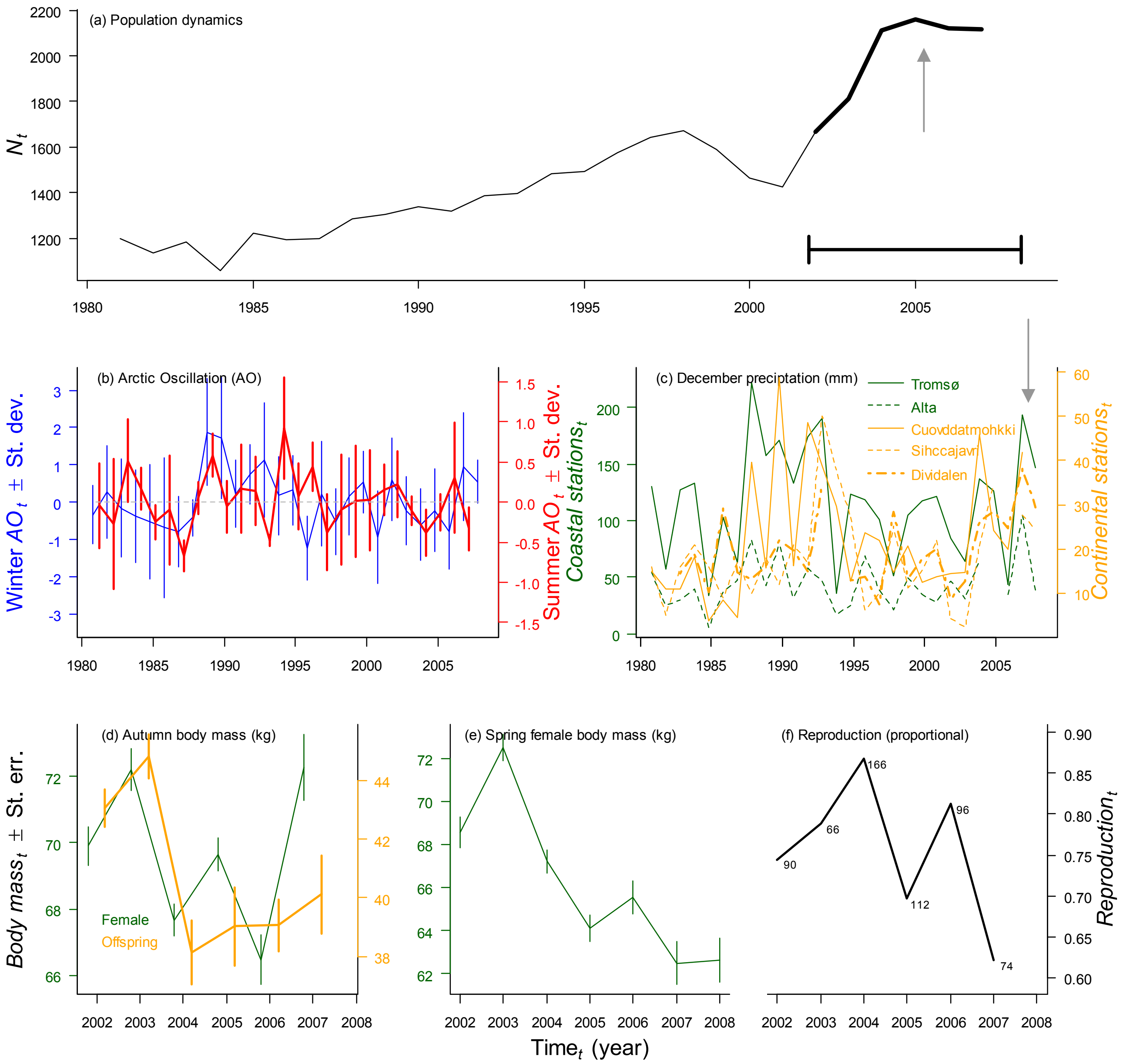
(a) Population dynamics
N_t
2200
2000
1800
1600
1400
1200
1980
1985
1990
1995
2000
2005
(b) Arctic Oscillation (AO)
Winter AO $_t$ ± St. dev.
Summer AO $_t$ ± St. dev.
3
2
1
0
-1
-2
-3
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
(c) December precipitation (mm)
Coastal stations$_t$
Continental stations$_t$
Tromsø
Alta
Cuovddatmohkki
Sihccajavri
Dividalen
200
150
100
50
0
60
50
40
30
20
10
(d) Autumn body mass (kg)
Body mass$_t$ ± St. err.
Female
Offspring
72
70
68
66
44
42
40
38
(e) Spring female body mass (kg)
72
70
68
66
64
62
(f) Reproduction (proportional)
Reproduction$_t$
90
66
166
112
96
74
0.90
0.85
0.80
0.75
0.70
0.65
0.60
2002
2003
2004
2005
2006
2007
2008
Time$_t$ (year)

Fig. 1.

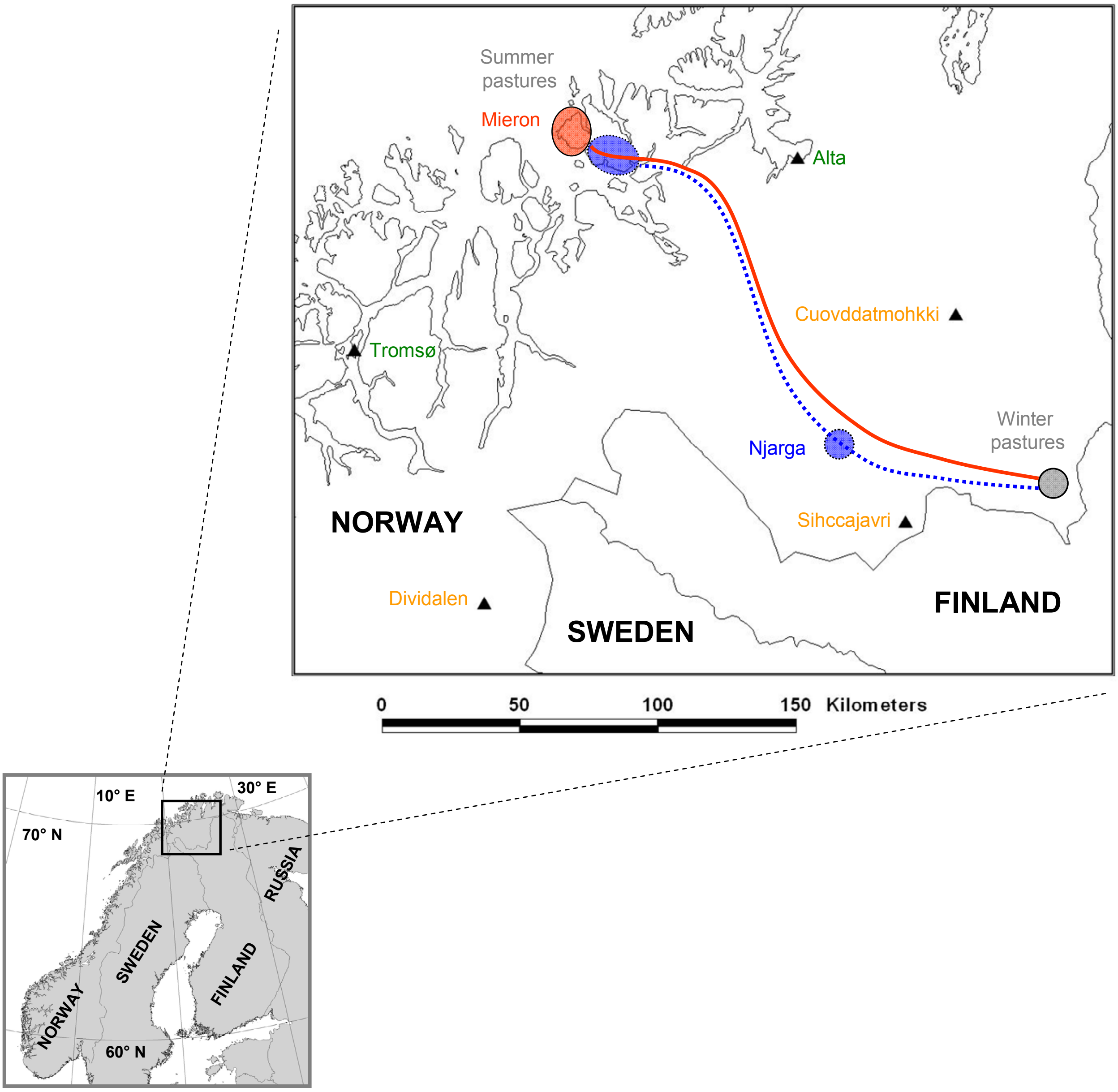
Summer pastures
Mieron
Alta
Cuovddatmohkki
Tromsø
Njarga
Winter pastures
NORWAY
Sihccajavri
Dividalen
SWEDEN
FINLAND
0
50
100
150
Kilometers
10° E
30° E
70° N
RUSSIA
SWEDEN
FINLAND
NORWAY
60° N

Fig. 2.

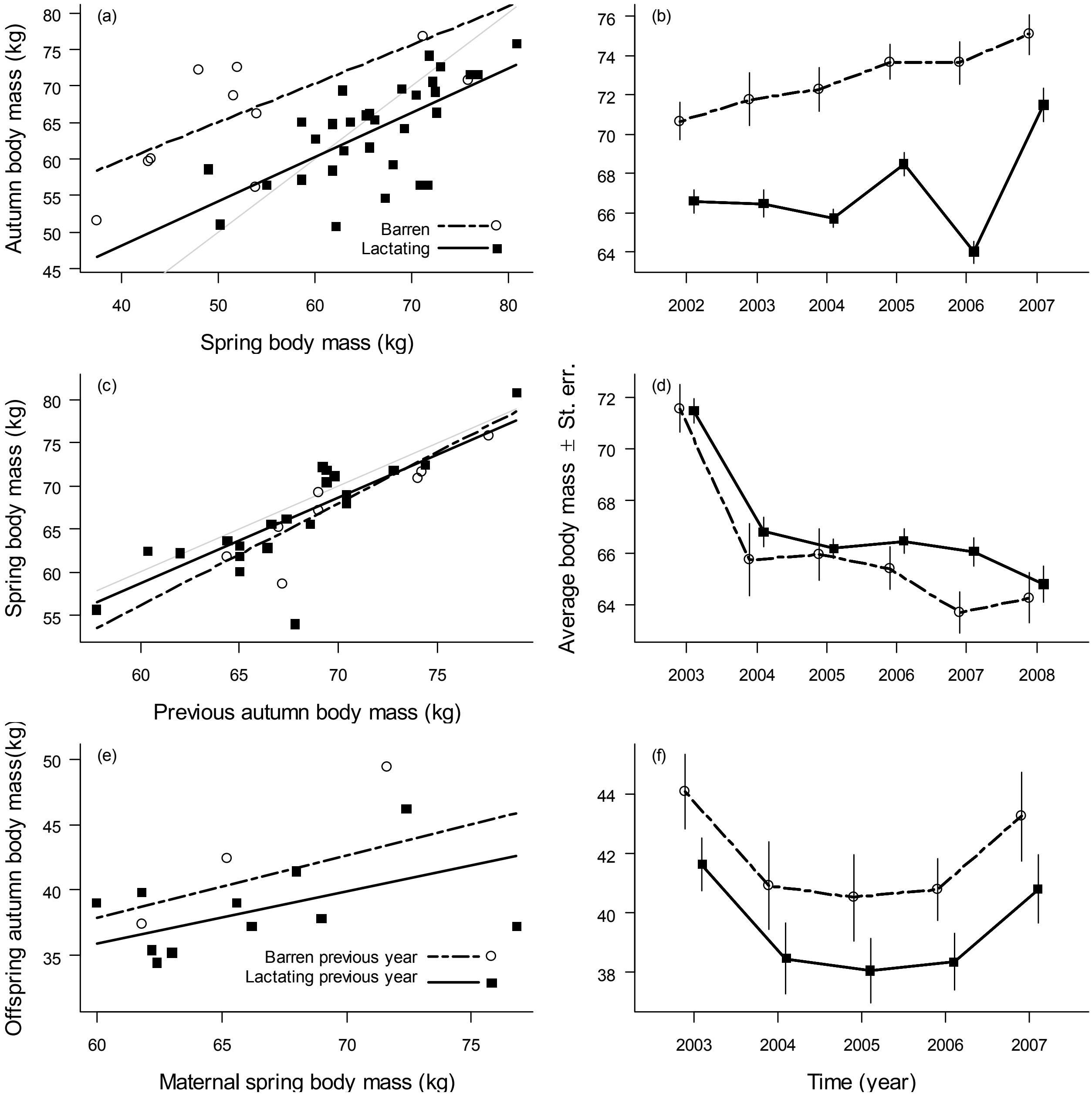
(a)
Autumn body mass (kg)
80
75
70
65
60
55
50
45
40
50
60
70
80
Spring body mass (kg)
Barren
Lactating
(b)
76
74
72
70
68
66
64
2002
2003
2004
2005
2006
2007
(c)
Spring body mass (kg)
80
75
70
65
60
55
60
65
70
75
Previous autumn body mass (kg)
(d)
Average body mass ± St. err.
72
70
68
66
64
2003
2004
2005
2006
2007
2008
(e)
Offspring autumn body mass(kg)
50
45
40
35
60
65
70
75
Barren previous year
Lactating previous year
Maternal spring body mass (kg)
(f)
44
42
40
38
2003
2004
2005
2006
2007
Time (year)

Fig. 3.

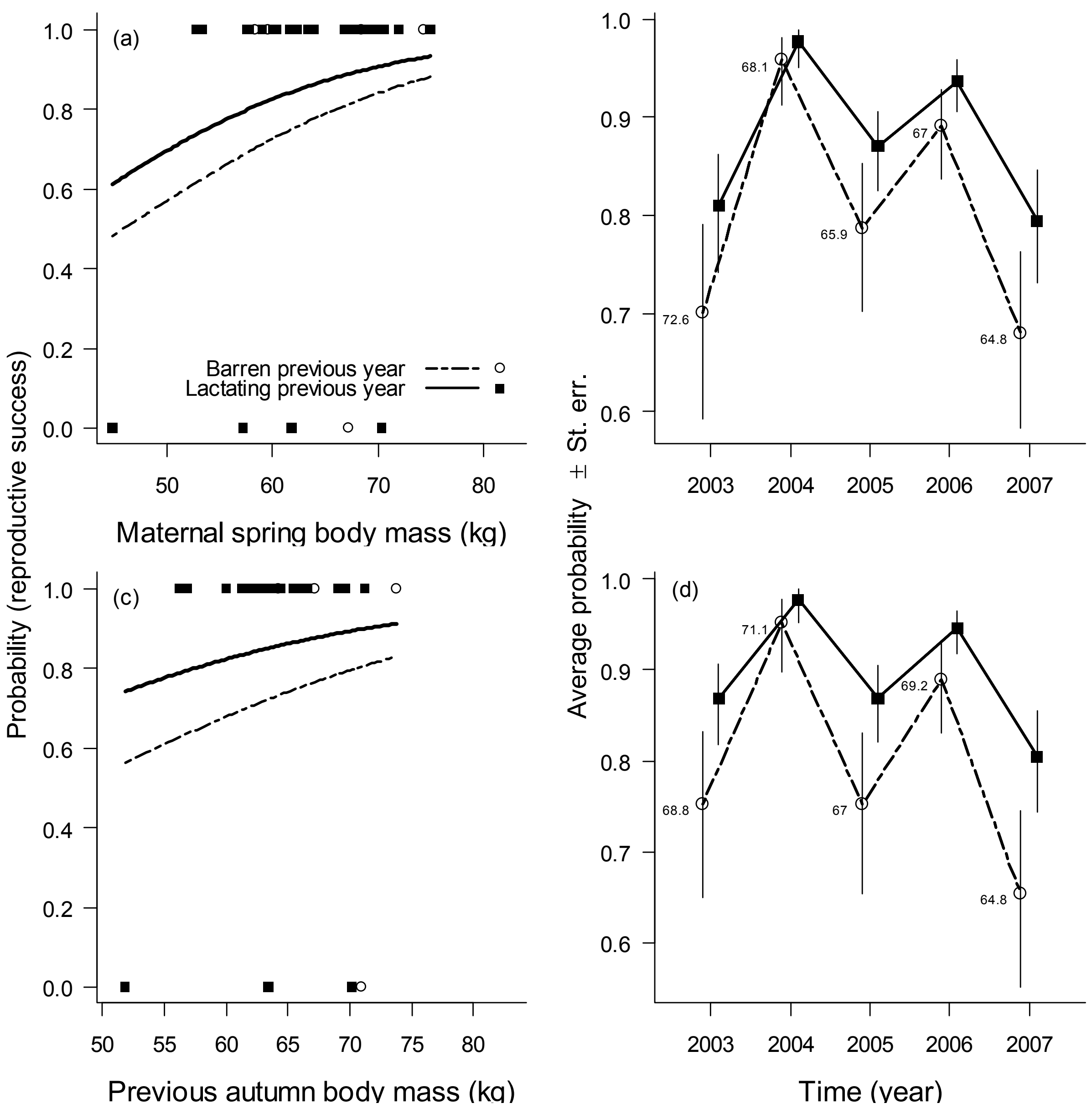
(a)
1.0
0.8
0.6
0.4
0.2
0.0
Barren previous year
Lactating previous year
50
60
70
80
Maternal spring body mass (kg)
Probability (reproductive success)
(c)
50
55
60
65
70
75
80
Previous autumn body mass (kg)
Average probability ± St. err.
1.0
0.9
0.8
0.7
0.6
68.1
67
65.9
72.6
64.8
2003
2004
2005
2006
2007
(d)
71.1
69.2
68.8
67
64.8
Time (year)

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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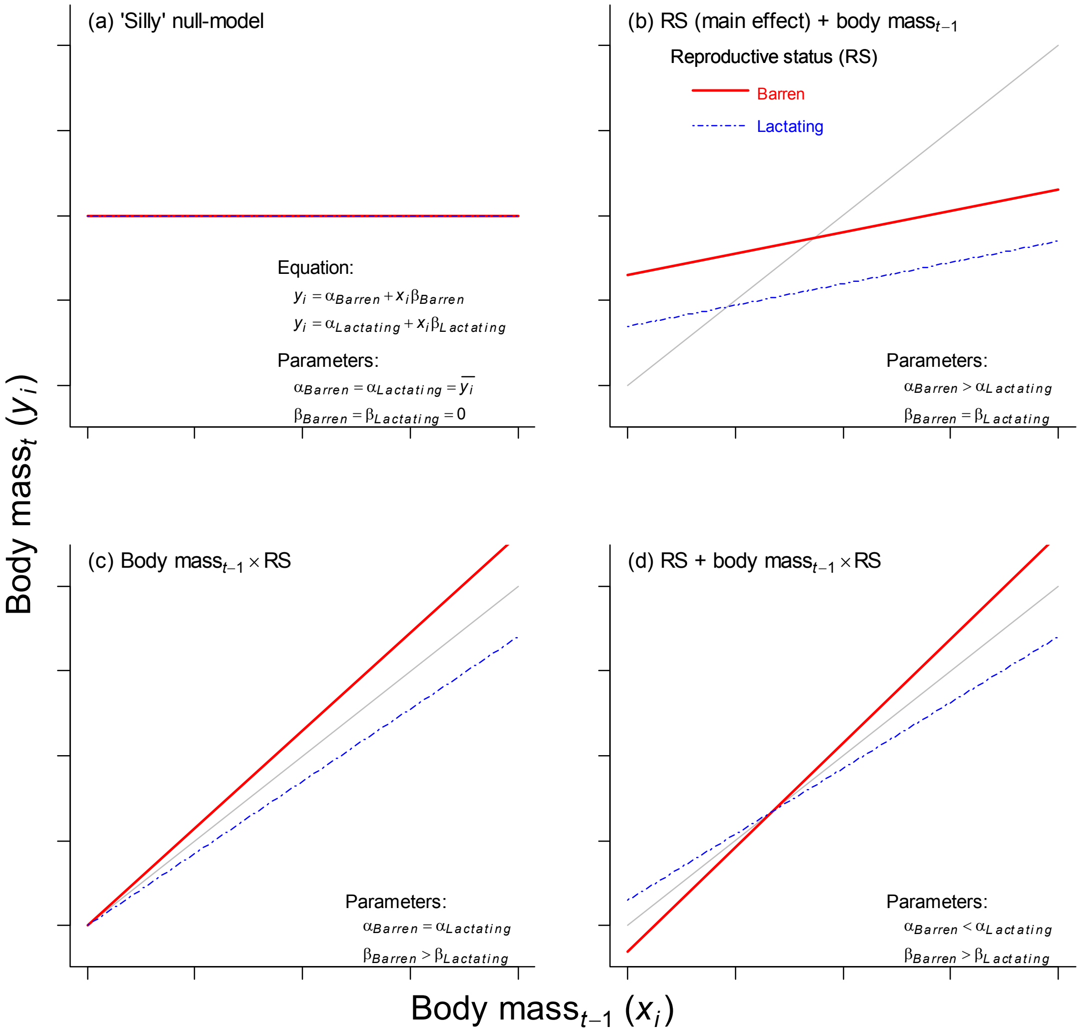

Fig. S1.1. A graphical representation of possible predictions in the analyses of body mass. Body mass in any point in time (t) can be a function of body mass earlier ($t-1$; hereafter termed initial body mass) and reproductive status (hereafter RS; 'barren' versus 'lactating'). The two equations (a) 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 α = 0 and β = 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*).

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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 (Δi). 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	**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
10.	***x***	***x***	***x***	*x*	*x*				*x*							*16*	*0.00*
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 *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	**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 *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	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 (Δ*i*; 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 *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 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
11.	***x***	***x***	***x***	*x*	*x*											*9*	*0.00*
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.

PAPER 4

Plastic reproductive allocation as a buffer against environmental unpredictability – linking life history and population dynamics to climate

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Manuscript

Running head: Plastic reproductive allocation and environmental unpredictability

Title: Plastic reproductive allocation as a buffer against environmental unpredictability – linking life history and population dynamics to climate

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Abstract: Organisms adopt a risk sensitive reproductive allocation when summer reproductive allocation competes with survival in the coming winter. Autumn female body mass, which represents an insurance against unpredictable winter conditions, is traded against reproductive allocation during summer. In our model, climate had large effects on individual optimization as: (1) Dynamic strategies were needed to buffer climate effects. (2) Females were risk averse, as strategies involving a low reproductive allocation per unit female spring body, had the highest fitness under unpredictable and poor environmental conditions. These strategies resulted in high expected female age and adult body size in harsh environments. (3) Negative density dependence had a strong negative effect on offspring body mass and survival. This effect was larger than negative effects of climate so we did not find clear negative effects of environmental conditions on reproduction. (4) Moreover, the optimal reproductive strategies together with environmental conditions had significant impact on population dynamics. First, populations inhabiting benign environments were most sensitive to climatic perturbations due to their characteristically high density, which limited the possibility for individuals to buffer adverse climatic effects. Second, populations inhabiting harsh environments were least sensitive to climatic perturbations. Winter conditions 'harvested' these populations, especially younger individuals, with the consequence of releasing these populations from negative density dependence resulting in a high reward for a given allocation.

Key words: evolution; environmental stochasticity; individual based modeling (IBM); phenotypic plasticity; prudent parent; *Rangifer tarandus*; risk sensitive life histories; time-series.

INTRODUCTION

A central issue in life-history theory is how individuals allocate resources between current reproduction and future survival, a trade-off known as the cost of reproduction (e.g. Roff 1992, Stearns 1992). Recent studies suggest that severe climatic conditions may have a strong impact on the cost of reproduction in large mammals (Clutton-Brock and Pemberton 2004). The effect of environmental stochasticity on the cost of reproduction and life-history evolution is generally poorly understood except that long-lived organisms are known for favoring own survival over reproduction (Gaillard et al. 1998, Gaillard et al. 2000, Gaillard and Yoccoz 2003).

Many organisms inhabit highly unpredictable environments caused by temporal variation in abiotic weather conditions and/or biotic factors such as population density (e.g. McNamara et al. 1995, Clutton-Brock et al. 1996, Coulson et al. 2001, Tveraa et al. 2007). Environmental variability usually consists of both predictable seasonal trends and unpredictable stochastic variation around this trend. Consequently, organisms have to make behavioural decisions in one season without full knowledge about future environmental conditions (e.g. McNamara et al. 1995, Bårdsen et al. 2008). If, for example, the winter season represents a bottleneck for survival and winter weather conditions are highly variable, individuals ensure that they retain sufficient reserves during summer in order to survive the coming winter (see Erikstad et al. 1998, Bårdsen et al. 2008). If reproduction also takes place during summer they have to balance reproductive allocation during summer, when, in fact, they pay a delayed cost of reproduction in the coming winter. Formally, this means that behavioural decisions has to be taken before the future state of the environment is known.

When reproduction competes with the amount of resources available for survival during an unpredictable non-breeding season, individuals should adopt a risk sensitive regulation of their reproductive allocation (see Stephens and Krebs 1986, Kacelnik and Bateson 1996 and references therein for a discussion of the concept of risk sensitivity, Bårdsen et al. 2008, provide details on risk sensitive reproductive allocation) For a given distribution of winter conditions, a *risk prone reproductive strategy* involves high reproductive allocation that will result in high reproductive rewards during benign winters but a high survival cost during harsh winters. A low reproductive allocation will, on the other hand, result in consistently high winter survival and represents a *risk averse reproductive strategy*. Organisms that experience stable and benign winter conditions can, thus, afford high reproductive allocation during summer and low autumn body reserves, whereas organisms experiencing harsh and variable winter conditions lower their reproductive allocation to retain higher autumn body reserves. Adopting a risk averse life history is typical for e.g. temperate large-herbivores where reproductive allocation competes with acquisition and maintenance of body reserves during summer. For these organisms autumn body mass functions as an insurance against stochastic winter climatic severity (Reimers 1972, Skogland 1985, Clutton-Brock et al. 1996, Fauchald et al. 2004, Bårdsen et al. 2008).

The quantity and quality of studies using climate modeling, especially models with a high spatial resolution, have increased over recent years (Tebaldi et al. 2006). By providing future climate scenarios, this branch of science plays an important role in the current debate on potential consequences of future climate change. Scenarios for future climate change generally predict an increase in the average, the variance and even a changed distribution of important climatic variables like precipitation and temperature (e.g. Rowell 2005, Sun et al. 2007). Nevertheless, these changes are predicted to vary both temporally (e.g. Rowell 2005, Tebaldi et al. 2006) and spatially (e.g. Hanssen-Bauer et al. 2005, Rowell 2005, Tebaldi et al. 2006, Sun et al. 2007). How living organisms will respond to these predicted climate changes is unclear as current empirical results are based on climatic effects given the current distribution of important climate variables, but some predictions has been made. For example, on a population-level, predicted consequences of future climate change commonly invoke more frequent population collapses (e.g. Post 2005). Such predictions are problematic as they generally assume a non-plastic life history in the sense that organisms cannot adapt to new climatic regimes (e.g. Bårdsen et al. 2008). We suggest that on the risk prone-risk averse continuum, more risk averse strategies should have a stabilizing effect on population dynamics leading to reduced temporal variation in population density as individuals adjust their reproductive allocation to buffer adverse climatic effects (Tveraa et al. 2007, Bårdsen et al. 2008). Within the concept of risk sensitivity it is the variance, i.e. the predictability, in climatic variables that important. In fact, most studies on this subject have been performed on two or several experimental groups being subject to the same average reward where manipulation have consisted of rewards associated with different levels of variability ('the standard design of risk sensitive experiments': reviewed by e.g. Stephens and Krebs 1986, Kacelnik and Bateson 1996).

The objective of this study is to investigate the effects of different types of environment on reproductive strategies in long-lived mammals and to investigate how the interaction between the optimal strategy and the environment shape population dynamics. We have previously tested some of these concepts empirically on reindeer (or caribou; *Rangifer tarandus*; see below). Reindeer represents a suitable model organism for these questions as: (i) female reindeer give birth to only one offspring per year; (ii) reindeer occupy a wide range of different environments covering several continents; and (iii) reindeer are a long-lived organisms where both survival and reproduction are positively related to body size (Kojola 1993, 1997, Tveraa et al. 2003, Fauchald et al. 2004, Bårdsen et al. 2008). Moreover, female reindeer gain body mass during summer in order to buffer harsh winter conditions (Bårdsen et al. 2008): reindeer who start harsh winters on low body reserves can experience a drastic reduction in subsequent survival (Tveraa et al. 2003). The present study, which is a follow-up to previous empirical studies (Tveraa et al. 2003, Fauchald et al. 2004, Tveraa et al. 2007, Bårdsen et al. 2008), use a state-dependent individual-based model (IBM) to investigate how females should optimize their reproductive allocation in a stochastic environment that contains density dependent processes. This study will give us answers to the following research questions: (1) How does the average and variance in environmental conditions affect the optimal reproductive allocation and (2) how do different reproductive allocation strategies affect vital rates and population dynamics for a given environment?

THE INDIVIDUAL-BASED MODEL (IBM)

Model overview

The IBM developed in the present study is a stochastic density-dependent model where we test if different types of stochastic winter environments have an effect on the optimal reproductive strategy and to what extent it is an interaction between the chosen optimal strategy and environmental conditions in shaping population dynamics. The model excludes males (with an assumed sex ratio of 0.5 at birth) because the focus here is on female life-history traits and because important parameters are widely available for females but not for males. We are, thus, dealing with the female segment of a population over several years; time (t) is discrete (one step equals one year), each step is divided in two distinct seasons: (i) summer where density dependent competition among individuals over a shared food resource occur; and (ii) winter where stochastic environmental conditions affects survival and mass losses. The model will be run for T time steps (from $t = t_0$ to $t = t_0 + T$). Individual state variables include age (j; year) and body mass (kg). Population-level state variables include summer density (D; individuals km^{-2}) and winter environmental conditions (E; relative scale where 'less is better' in the sense that the large positive values represents harsh conditions, which is similar to climatic indexes like AO and NAO). A key point in this model is that individuals do not know the state of the coming winter conditions (E) at the time when reproductive allocation takes place. Consequently, even though processes that affect individuals in one season will have effects in the coming season it is crucial that these processes are treated independently in the model. A detailed description, which follows the 'overview, design concepts and details' (ODD) protocol developed by Grimm et al. (2006) and Grimm & Railsback (2005) is found in A1. Formalities, like model equations, rules and tables presenting the model parameters, are presented in the ODD protocol (A1). All simulations, statistical tests and plotting were performed in the software *R* (R Development Core Team 2007). Since seasonality is the key to understand reproductive allocation strategies in reindeer (Bårdsen et al. 2008) we will give a short overview of the model separated by season (see Figure 1 for schematic overview of processes and scheduling).

Summer (1 May to 31 October: 184 days)

An allocation strategy will at any point in time be a scalar representing an individual's allocation of resources, i.e. spring body mass, to reproduction vs. somatic growth, which is a proxy for survival, during summer. An individual can only invest in reproduction (R) and survival (S); i.e. $R + S = 1$. The reward for a fixed allocation will be limited by the population's summer density (D). That is, an individual with a fixed reproductive allocation strategy will collect a higher average reproductive reward in low- vs. high-density environments. Consequently, the reward of investing in R and S will be implemented in two functions (see A1: Autumn body mass and Gain function sections): (1) one gain function for females where S and D are predictors and (2) one function for offspring where R and D are predictors. In sum, individual autumn body mass, i.e. summer mass development, depends on (Figure 1): (1) spring body mass (in the first year of life this will be an individual's birth mass), (2) the gain function that represents the increase in body mass per kg spring mass, and (3) a basal summer metabolic rate (β_S). Generally, for individual i of age j at time t this relationship can be represented by the following equation (modified from Proaktor et al. 2007):

$$Autumn_{bm_{i,1,t}} = Spring_{bm_{i,j,t}} + \left(Gain_{i,j,t} \times Spring_{bm_{i,j,t}}\right) - \beta_{S_{i,j,t}} . \qquad \text{eqn. 1}$$

Winter (1 November to 31 April: 181 days)

Autumn body mass ($Autumn_{bm}$) is a predictor of the three processes that happens in the autumn and during winter: (1) If $Autumn_{bm}$ is below a threshold (τ_{autumn}) the individual is assumed dead during summer and is removed from further analyses. (2) If $Autumn_{bm} > \tau_{autumn}$, $Autumn_{bm}$ and winter conditions (E) is a predictor of individual winter survival probability [$P(Survival \mid female)$]. (3) If an individual survives the winter, its body mass next spring ($Spring_{bm_{t+1}}$) will depend on $Autumn_{bm_t}$ as well as a winter loss of body mass (β_W). After these processes have been run, time will go one step forward (from t to $t+1$) and the following parameters will be updated (Figure 1); (1) mortality [$P(Survival \mid female)$], (2) spring body mass ($Spring_{bm}$), (3) age (j) and (4) population density (D).

Reproductive investment strategies

The heart of this IBM is how reproductive allocation strategies, which define the relationship between survival vs. reproduction, are defined (Figure 2). When modeling life history strategies one must define what actions are available to an organism, and how the consequence of an action depends on the action itself, the organism's state and the environment (McNamara 1997). In this model, individuals have a built-in reproductive strategy, which defines a behavioural algorithm or rule, which an individual has to follow. An individual (i) of age (j) will at a given time (t) allocation a proportion of its available resources in reproduction ($R_{i,j,t}$). Juveniles ($j \leq 1$) do not invest in reproduction. This ensures that juveniles invest everything in somatic growth. Note that reproductive allocation is defined on a continuous scale as $R_{i,j,t}$ is a scalar defined within the closed interval: $R_{i,j,t} = [0,1]$. Investment in somatic growth, a proxy for survival, is then:

$$R_{i,j\leq 1,t} = 0 \quad \text{if } j \leq 1 . \qquad \text{eqn. 2}$$

$$S_{i,j,t} = 1 - R_{i,j,t} . \qquad \text{eqn. 3}$$

As total energy allocation sums to one, individuals either invest in reproduction or survival and nothing else. The model contain no true senescence (as e.g. the IBM by Proaktor et al. 2007), but age is an important individual-level state variable as it ensures that juveniles do not reproduce and that females do not become unrealistic old. The cost and benefit, assuming a constant female body mass, for different $R_{i,j}$ as a function of density and winter weather condition is shown in Figure 2. Two types of strategies were tested against each other in the simulations.

Fixed reproductive strategies (FS)

A *fixed strategy* (FS) is defined as a scalar between 0 and 1 that represents an allocation rule that an individual will follow throughout its adult life. This type of strategy can simply be defined by a vector such as e.g. $R_i = [0.0, 0.4, 0.4, 0.4, ...]$, which means that this individual will invest zero in reproduction its first year of life, and then 0.4 for the rest of its life.

Dynamic state dependent reproductive strategies (DSDS)

As body mass is a very important predictor for both survival and reproductive output for female *Rangifer* (Kojola 1993, 1997, Tveraa et al. 2003, Fauchald et al. 2004, Bårdsen et al. 2008) it is natural that spring body mass acts as a state variable in the model. Thus, in a *dynamic state dependent reproductive strategy* (DSDS) $R_{i,j,t}$ will be determined and updated each year according to the following equations (see A1):

$$R_{i,j,t} = \frac{1}{1 + e^{-\left[a_R + \left(b_R \times Spring_{bm_{i,j>1,t}}\right)\right]}} \qquad \text{if } j > 1 \text{ \& if } Spring_{bm_{i,j<1,t}} > \tau_{spring} \qquad \text{eqn. 4}$$

$$R_{i,j,t} = 0 . \qquad \text{if } j \leq 1 \text{ or if } Spring_{bm_{i,j<1,t}} \leq \tau_{spring} \qquad \text{eqn. 5}$$

In order to invest in reproduction, females must be older than the juvenile stage ($j > 1$) and they must have a spring body mass ($Spring_{bm_{i,j,t}}$) above a lower threshold value (τ_{spring}). The intercept (a_R) in the equation is constant (Table A1.1) among strategies so that a DSDS can in a simplified way be defined as by the parameter b_R (A1). The inclusion of a lower body mass thresholds above, which females invest in reproduction, and below, which they do not, has been found in several long-lived mammals such as red deer *Cervus elaphus* (Albon et al. 1983), moose *Alces alces* (Sæther and Haagenrud 1983, Sæther et al. 1996), bighorn *Ovis canadensis* (Jorgenson et al. 1993) and reindeer (Reimers 1983, Skogland 1985, Tveraa et al. 2003). Depending on how an individual's spring body mass develops over time, reproductive allocation following a DSDS may end up looking like e.g. $R_i = [0.0, 0.4, 0.7, 0.0, 0.4]$ over 5 time steps. Both the FS and the DSDS strategies are in one sense pure as reproductive allocation is totally given by age (FS & DSDS) and spring body mass (DSDS), but they may also be considered mixed as both adult and offspring survival is probabilistic (Houston and McNamara 1999).

Design

We will answer our research questions by running the model under normally distributed environmental conditions [$E \approx N(x, y)$] characterized by different theoretical averages (x; low values represent environments that can be characterized as *good* whereas high values represent *poor* ones) and theoretical standard deviations (y; synonymous to *unpredictability*) (Figure A1.2). We applied three different theoretical averages ($x = 0.00, -0.15, 0.15$) termed 'control', 'improved' & 'reduced', and 41 different theoretical standard deviations ($y = 0.00, 0.05, 0.10, ..., 2.00$). This gives a total of 123 possible simulations ($x \times y$). Populations went extinct before convergence when $y > 1.55$ so we ended up with a total of 90 simulations. E was generated using the `rnorm` function in *R* (R Development Core Team 2007).

A simulation is said to converge when one winning strategy is left alone. After this happened, we ran the simulation for 20 more years as to 'harmonize' the dynamic between the individuals, which follows the same strategy, in the population and environmental conditions: after this the simulation was run for another 60 years when terminal time (T) was reached and the simulation was terminated. We collected 'pseudo-empirical' data on important output during the last 60 years of each simulation (see A2 for an example simulation). T for each simulation was dependent on both x and y (A3). This, however, was not the case for the estimated values of $\overline{x}$ (hereafter termed environmental average or simply $\overline{E}$) and (ii) $\overline{y}$ [hereafter termed environmental stochasticity or simply $\text{st. dev.}(E)$] who simply were related to their respective theoretic input values (x & y; A3).

Pseudo-empirical statistical analyses

Investment in reproduction and survival

Each simulation output consisted of 60-years of data on environmental conditions, female reproductive success (number of offspring per female) and population spring density, spring and autumn body mass of both offspring and females as well as female reproductive and somatic allocation ($\overline{R}$ & $\overline{S}$). We analysed these generated datasets by standard statistical approaches. First, within simulations we fitted a linear model where each yearly average (value_t) was predicted based on the centred value (subtracting the average) for environmental conditions for the last winter (E_t)^6. Second, we fitted generalized additive models (GAM), using the `mgcv` library (Wood 2008), using the intercepts (intersept) from the 'within simulations analyses' above as responses in an 'across simulation analyses'. We then used the smoothened interaction between both environmental characteristics [i.e. $\text{st. dev.}(E)$ & $\overline{E}$] and smoothened $\overline{D}$ was used as predictors (Wood 2006)^7. Both smooth terms in the GAM were estimated using thin plate regression splines, which means that the degree of complexity within the limits set by 'k' was selected objectively (Wood 2006: 152-160, 226).

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[6] *Within simulation analyses*.-- In *R* each yearly value (*t*) was modelled as follows: '`lm(` value_t `~ I` $\left(E_t - \overline{E}\right)$ `)`'. Centring of environmental conditions means that the intercept in such an analysis represents the estimated, or predicted, values for the average environment for that simulation.

[7] *Across simulation analyses*.-- In *R* the intercept from each analysis above was predicted as follows: '`gam(` intersept `~ s(` $\text{st. dev.}(E)$ `,` $\overline{E}$ `, bs="tp", k=k*3) + s(` $\overline{R}$ `, bs="tp", k=k) )`' where '`k`' equals 4.

Population dynamics and time series analyses

In all time series analyses we adopted the same analytical approach as Tveraa et al. (2007). Consequently, we estimated the density dependent and density independent structure in each population time series by fitting second-order autoregressive models [AR(2)] (as described in e.g. Shumway and Stoffer 2006, Cryer and Chan 2008). We focus on modelling population growth rate, i.e. $\lambda_t = \log_e(X_{t+1}/X_t)$, to avoid problems associated with temporal trends, i.e. non-stationary, in the time series (Cryer and Chan 2008). The linear predictor of the models included the effects of direct density-dependence, delayed density dependence with a lag of one time step $(t-1)$ and the direct effect of E_t on λ_t [formally we have used an ARIMA(p = 2, d = 0, q = 0) model; the `arima` function in *R* (e.g. Ripley 2002, Shumway and Stoffer 2006, Cryer and Chan 2008); E as a covariate was included via the `xreg` argument]. We, thus, estimated the first-order AR coefficient (β_1), the second-order AR coefficient (β_2) and the direct effect of winter climate conditions (ω_1). This model was similar to Tveraa et al.'s (2007) 'baseline model' fitted to 58 populations of semi-domestic reindeer covering a large climatic gradient with large contrasts in management regimes and vegetation characteristics.

Plotting and interpretation of results

Plotting of results (Figure 4-8) with respect to the interaction between $\text{st.dev.}(E)$ and $\overline{E}$ were performed using the `vis.gam` function [plot i shows both environmental predictors for average density ($\overline{D}$)], whereas plotting of $\overline{D}$ (plot ii shows the effect of $\overline{D}$ for the average values for both environmental predictors) (see Wood 2008 for details).

RESULTS

Reproductive strategies

Dynamic stated dependent reproductive strategies (DSDS) were superior to *fixed strategies* (FS) for all environmental conditions, but the selected DSDS varied among different environments. Higher degree of environmental stochasticity (using the theoretic input value, y) resulted in more *risk averse reproductive strategies* for all environmental averages (x; Figure 3a). This relationship was, however, weakest for improved environmental conditions so we conclude that reindeer experiencing generally good environments were less risk sensitive compared to individuals experiencing control and poor conditions. In addition, reindeer experiencing good environments adopted a risk averse strategy relative to the other environmental averages even for low environmental stochasticity. A similar conclusion was reached when estimated average female reproductive allocation ($\overline{R}$) was predicted as a function of environmental stochasticity [$\text{st.dev.}(E)$] and environmental average ($\overline{E}$): (i) improved $\overline{E}$ and increased $\text{st.dev.}(E)$ both had negative effects on $\overline{R}$ (Figure 4,i); and (ii) increased population density ($\overline{D}$) had a negative effect on $\overline{R}$ (Figure 4,ii). Given the optimal reproductive strategy winning in each simulation, we investigated how measures of population averages were related to winter weather conditions [both $\text{st.dev.}(E)$ and $\overline{E}$], and population spring density ($\overline{D}$). Figure 5 shows that $\overline{D}$ was negatively related to both $\text{st.dev.}(E)$ and $\overline{E}$.

Reproductive investment

Frequently used empirical measures of reproduction include; (i) the number of offspring per female (on $\log_e$ scale; hereafter termed reproductive success), (ii) autumn and (iii) spring offspring body mass (used in our previous studies: Bårdsen et al. in press; Bårdsen et al. 2008; Fauchald et al. 2004; Tveraa et al. 2003; **Paper 3**). First, reproductive success was practically unaffected by environmental stochasticity until a certain threshold was reached; then reproductive success decreased as $\text{st.dev.}(E)$ increased. This threshold was reached earlier in good vs. poor environments (Figure 6a,i). For large $\overline{E}$, the effect of $\text{st.dev.}(E)$ was practically unimportant. Second, the relative strength of $\overline{E}$ and $\text{st.dev.}(E)$ was generally similar with respect to both offspring autumn and spring body mass, even though the negative effect of $\text{st.dev.}(E)$ was stronger in the analysis of spring body mass (Figure 6i,b-c). Third, the negative effect of $\overline{E}$ was stronger compared to the negative effect of environmental stochasticity in all three analysis.

The above relationships must be understood in relation to population density ($\overline{D}$) as $\overline{D}$ was clearly negatively related to environmental stochasticity (Figure 5). Larger $\overline{D}$ lead to lowered reproductive success and offspring autumn and spring body mass (Figure 6ii,a-c). This happened even though higher environmental stochasticity clearly resulted in more *risk averse reproductive strategies* (Figure 3a). Moreover, increased values of $\overline{D}$, $\overline{E}$ and $\text{st.dev.}(E)$ resulted in lowered $\overline{R}$ (Figure 4). The moderate effects of environmental conditions relative to $\overline{D}$ may come as a surprise, but it is due to the fact that $\overline{D}$ has a clear negative effect on offspring autumn body mass (eqn. A12), which again will affect both survival and spring body mass (eqns. A16-7). In sum, when it comes to reproductive allocation both the model and previous empirical findings must be understood in relation to density more than perhaps environmental conditions as lowered density dependent (food limitation) may compensate for harsh winter conditions.

Somatic investment

Frequently used empirical measures of parental allocation include (i) expected female age (a proxy for survival as high age is a consequence of high allocation in survival), (ii) autumn and (iii) spring female body mass (used in our previous studies: Tveraa et al. 2003, Fauchald et al. 2004, Bårdsen et al. 2008, Bårdsen et al. in press, **Paper 3**). First, female age was positively related to environmental stochasticity and negatively related to environmental average; the highest expected female age was found in generally poor (high $\overline{E}$ values) and predictable environments [low $\text{st.dev.}(E)$ values] (Figure 7a,i). Intermediate levels of $\text{st.dev.}(E)$ had the most profound negative effect on expected female age, at least in good environments. Second, higher degree of environmental stochasticity resulted in a higher allocation in own growth during summer (Figure 7b,i). Female autumn body mass was not strongly affected by environmental stochasticity until a certain threshold was reached; after which body mass increase rapidly as $\text{st.dev.}(E)$ increased. This threshold value was affected by environmental average as the positive relationships between autumn body mass and $\text{st.dev.}(E)$ seemed to be linear for high $\overline{E}$. Additionally, female autumn body mass positively related to environmental average (Figure 7b,i). Third, for female spring body mass we also found a positive effect of environmental stochasticity, which also seemed to be stronger after reaching a threshold value (Figure 7c,i). We did find a rather strong negative effect for $\overline{E}$, which was the opposite as that found for autumn body mass as generally good conditions (negative $\overline{E}$) gave the highest spring body mass for a given $\text{st.dev.}(E)$.

The relationships involving female body mass may, as in the analysis of reproductive allocation, was more or less confounded with populating density ($\overline{D}$). Large $\overline{D}$, however, resulted in increased expected age (Figure 7a,ii), which means that increased food competition leads to increased allocation in own survival (see also Figure 4a,ii). Larger $\overline{D}$ also had a statistical significantly negative effect on female autumn body mass (Figure 7b,ii), but not on spring body mass (Figure 7c,ii). In sum, we conclude that a worsening of the environment, i.e. increased $\overline{D}$ and/or worsened climate, leads to reduced reproductive allocation at the expense of higher allocation survival.

Population dynamics

The above analyses prove that worsened environmental conditions have negative effects on the amount of resources a female invest in reproduction. Such a change in the life history has important effects on the observed population dynamics. First, we found the strongest direct negative density dependence (β_1) in good and predictable environments; i.e. at low $\overline{E}$ and $\text{st.dev.}(E)$ (Figure 8a,i). Not surprisingly, $\overline{D}$ did have a negative effect on β_1 suggesting that higher density resulted in a stronger direct regulation of populations (Figure 8a,ii). Second, in the analysis of delayed density dependence (β_2) we found that the effect of $\text{st.dev.}(E)$ and $\overline{E}$ was purely additive: increased $\overline{E}$, decreased $\text{st.dev.}(E)$ and increased $\overline{D}$ resulted in increased delayed regulation, but neither effects were statistically significant (Figure 8b). Third, in the analysis of direct effect of environmental conditions (ω_1), the largest negative effect of environmental conditions was present in good environments (Figure 8c,i). This negative environmental effect decreased until a threshold was achieved, after this threshold the relationship flattened (Figure 8c,i). Moreover, increased $\overline{D}$ resulted in a higher impact of ω_1 on population growth rates (Figure 8c,ii). In sum, we conclude that for direct density dependence and the effect of climate were important limitation in generally poor environments and for high density, but that neither was important in poor environments.

DISCUSSION

This study shows that climate has large effects on the amount of resources that virtual reindeer should invest in reproduction vs. survival, which has significant effects on population vital rates and dynamics. First, DSDS were superior compared to FS in all simulations; FS strategies always went extinct, which shows that plastic strategies are needed in order to buffer adverse climate. Second, female reindeer was risk sensitive because more *risk averse reproductive strategies* did win in the evolutionary game in harsh, i.e. unpredictable and poor, winter environments compared to benign, i.e. good and predictable, environments. Third, populations inhabiting benign winter conditions were the most sensitive to climatic perturbations. This was a result of population density, which was highest in benign conditions, rather than environmental conditions. Negative density dependence had a clear negative effect on reproduction relative to the minor impacts of winter climate. Fourth, populations inhabiting harsh environments were least sensitive to climatic perturbations. In these environments we found the largest individuals, which were due to the combined effect low reproductive allocation and low density. Low density lead to a higher reward for a fixed allocation compared to high density; too high density will, thus, limit the possibility for individual's to buffer climate through increased body condition. Harsh winters, thus, act as a substitute for harvest and predation, due to its lowering of survival, leading to low density. Fifth, increased density caused increased negative impacts of occasional harsh winters and increased the strength of direct regulation of populations.

Modelling philosophy and assumptions

All studies using simulation models have to trade complexity over generality, where numerous books stress the importance of keeping things as simple as possible without loosing too much realism (e.g. Kokko 2007). This is also the case for our IBM, which is based on numerous assumptions and simplifications. In this section we will not discuss the shape of relationships and the parameters used in each sub-model as this is discussed in A1. First, we have a clearly seasonal model where environmental conditions and population density only have effects during the winter and summer season respectively. Several studies have shown that an interaction between winter climate and density have important effects on population dynamics through their joint effects on adult and juvenile survival (e.g. Grenfell et al. 1998, Coulson et al. 2000). Such interactions were, however, not built in any of the sub-models in the present IBM. Nevertheless, rather complex relationship between summer density and winter climate was present in the statistical models fitted to our output data. The separation of climate and density across seasons can be viewed as a technical issue; including density dependence in both seasons will only increase the interaction between them. This would result in an increased impact of climate in good environments as density would have affected individuals negatively in two seasons instead of just one. Moreover, empirical evidence on Fennoscandian reindeer indicate that density dependence has a negative effect on summer pastures (e.g. Bråthen et al. 2007) and on body mass gain trough the summer but not winter (**Paper 3**). In contrast, winter climatic conditions have important effects on body mass gain in late winter, but this effect disappears at some point during spring and early summer (Fauchald et al. 2004, Bårdsen et al. 2008). The latter results indicate that, with the exception of perhaps extreme winters, individuals do not carry on lagged effects of winter climate when they start to breed in the start of the summer season.

Second, important assumptions and simplifications were also undertaken in how the different reproductive strategies were defined. Real organisms have a much wider behavioral repertoire than the behavioral rules built into our strategies. Individuals who followed a DSDS were, for example, assumed to: (i) give birth to a single offspring every year (after reaching prime-age), all newborns had a constant birth body mass; (ii) have a static reproductive allocation relative to their age, (iii) not the change their allocation during a given summer; and (iv) they all had a constant spring body mass threshold deciding whether to invest in reproduction at all. Numerous studies show that reproductive allocation strategies among female reindeer are not that simple (e.g. Kojola 1993, Adams 2005, Bårdsen et al. 2008, Bårdsen et al. in press), but perhaps the most important limitation for our study is the complete lack of evolution as no strategy changed over time by genetic recombination (as e.g. the IBM by Proaktor et al. 2007).

Reproductive investment

DSDS were superior compared to FS in all simulations. This shows that following a relatively simple strategy can be sufficient to survive even in rather harsh environments. The FS strategies always went extinct, which shows that a too simple strategy did not buffer environmental conditions sufficiently. A higher degree of environmental stochasticity resulted in more *risk* averse *reproductive strategies* for all environmental averages. Moreover, reproductive allocation was negatively related to environmental average and stochasticity as well as population density. Reproductive output, i.e. success and offspring body mass, was also negatively related to environmental average and stochasticity as well as population density. As reproductive allocation occurs during summer it may not come as a surprise that population density was of greater importance compared to winter climate. Moreover, population density was low in generally harsh, i.e. unpredictable and poor, environments (which is a general finding: e.g. Morris and Doak 2002). Consequently, the weak effect that environmental unpredictability had on reproductive output, which was not predicted, was an artefact of density. Finally, in good environments for a given environmental stochasticity, average offspring spring body mass was higher than autumn body mass. This showed that a selection for larger offspring occurred in these environments.

For populations with low harvesting intensities, a higher offspring body mass was found in *poor* compared to good winter climate conditions (Tveraa et al. 2007). Even though Tveraa et al. do not have a clear explanation for this, this fits well with our model as populations experiencing poor environments in their study were also the ones characterized by low and stable densities. The interaction between winter climate and density in the present model, i.e. the combined effect of increased summer gain at low density and the selection for larger offspring body mass in harsh environments, may thus provide an explanation for the findings by Tveraa et al. (2007). This, however, contradicts previous experimental studies on Fennoscandian reindeer where it has been showed that: (1) when females experience a sudden decrease in winter conditions they promptly reduced their reproductive allocation the following summer; and (2) when winter conditions were improved, females were reluctant to change their allocation (Bårdsen et al. 2008). This asymmetric response to improved vs. reduced winter conditions is consistent with *a risk averse reproductive strategy*. Similar findings has been found for Alaskan caribou[8] who restrains their reproductive allocation during severe winters (Adams 2005): females, thus, conserve resources that can be used to either enhance own survival or that can be invested in an offspring if it survives predation beyond a couple of weeks. Additionally, female reindeer also invest less in reproduction when population density increases (**Paper 3**).

Somatic investment

Pseudo-empirical measures of survival and somatic growth were clearly sensitive to environmental unpredictability; females became more risk averse in more stochastic environments as both autumn and spring female body mass increased when winter climatic conditions became more unpredictable. Moreover, increased environmental average had positive effect on autumn body mass, but affected female spring body mass negatively. The relationship between density and body mass was much weaker for females compared to offspring. These findings were expected as: (1) environmental conditions have a direct negative effect on winter body mass development; (2) density has a direct negative effect on summer body mass development; and (3) female survival was insensitive to environmental conditions compared to offspring survival (see A1). As described earlier, reproductive allocation is generally lower in poor and unpredictable environment and during high population density for many long-lived mammals including reindeer. Moreover, allocating resources to reproduction is inversely related to allocation of resources in survival. Our results that a worsening of winter climatic conditions and increased population density lead to more *risk averse reproductive investment* with consequent

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[8] *Rangifer* sp. generally produce small offspring compared to other closely related species (Adams 2005).

increased allocation in own survival relative to reproduction was, thus, in accordance empirical evidence from the literature.

Population dynamics

Both environmental unpredictability and average did have important consequences on the observed population dynamics. Benign environments resulted in the highest density, the highest level of direct regulation and the most apparent negative effects of climatic on population growth rates. Mortality rates, especially for juveniles, are high during extreme winters (Tveraa et al. 2003): populations are, thus, released from negative density-dependence after extreme winters (Aanes et al. 2000). This implies that harsh winters function similar to harvest in relaxing negative density dependence in populations inhabiting benign environments. Our findings was similar to Tveraa et al. (2007) who found that an interaction between density dependence, harvest and climate was affecting population dynamics. Their main findings was that populations with low harvest-intensity living in good environments where the most sensitive to climatic perturbations due to their lack of direct regulation. This was confirmed in our model as we found an interaction between density and climate where high-density populations experiencing benign winter environments where the most sensitive to climate.

Conclusions and future prospects

Our IBM proves that plastic life histories may buffer adverse climatic effects and illustrate how climate interacts with life histories in shaping population dynamics. Future global climate change will most likely result in a shift towards more frequent extreme precipitation events (e.g. Wilby and Wigley 2002, Semmler and Jacob 2004, Tebaldi et al. 2006, Benestad 2007, Sun et al. 2007), a trend that is already empirically evident on several continents (Sun et al. 2007 and references therein). Moreover, many of these climatic scenarios are expected to happen both sooner and more pronounced in the northern hemisphere (e.g. Tebaldi et al. 2006, Benestad 2007). *Rangifer*, which is a northern and circumpolar species, and the northern ecosystems they inhabit, thus, represent suitable modeling systems for assessing impacts of future climate change. Hanssen-Bauer et al. (2005), for example, review several studies predicting how climate will change in Fennoscandia in the future: (i) increased warming rates with distance to the coast, (ii) higher warming rates in winter compared to summer, and (iii) increased precipitation especially during winter. The shifts between warm and cold periods during winter coupled with an year-round increased intensity of precipitation (Hanssen-Bauer et al. 2005), will lead to an increased frequency of wet weather, deep snow and ice crust formation that has negative consequences for large herbivores (e.g. Solberg et al. 2001).

The present model do not, however, include an increased frequency and intensity of precipitation events as we have solely used normally distributed environmental conditions, but this can easily be implemented in the future by using other distributions such as e.g. the skew-normal distribution (Azzalini 2005). Another issue with regard to how climate was implemented in the present model was that we did not included any of the above mentioned weather phenomena (e.g. precipitation and icing events) as we simulated climate using an index. We do not, however, see this as a problem as important climatic events like the ones described above gives clear signatures in existing climatic indexes such as e.g. the NAO (reviewed by e.g. Ottersen et al. 2001, Stenseth et al. 2002, Hurrell et al. 2003). In spite of this, not all predicted changes are believed to have negative effects, which was the rationale for implementing both 'improved' and 'reduced' environmental averages. If we use semi-domestic reindeer in Europe as an example, herding practices along with pasture quality (e.g. an earlier and longer growing season) combined with climate change are predicted to affect the husbandry negatively in Scandinavia, neutral in Finland and positive in Russia (Rees et al. 2008). Even if the future brings improved average climatic conditions compared to the present situation, almost all climate models predicts future winter climatic conditions to be more stochastic than present day for most of the areas inhabited by reindeer. If this prediction is correct, the results from the IBM combined with our previous studies show that such an unpredictable climate will result in reindeer adopting more *risk averse reproductive investment strategies* (even for improved environments). This, along with the potential for buffering harsh winters through reduced reproductive allocation, will again have dramatic negative effects on both population abundance and reproduction.

The ability for individual's to buffer negative climatic effects through plastic life histories have important consequences on how the impacts of future climate change must be understood. For example, many recent analyses of climatic effect signatures in population time series have been used to infer the likely consequences of future climate change (Stenseth et al. 2002). The predicted consequences commonly invoke more frequent population collapses (e.g. Post 2005). Such inferences are based on an underlying assumption that animals have non-plastic life history strategies that are not adequately adaptive to new climate regimes. Contrary to recent studies, such as e.g. the one by Post (2005), our model combined with empirical findings suggest that these changes will more likely results in more risk averse life histories that have the potential of buffering negative effects of climate up to a certain point. We, thus, propose that future studies should focus more on how long-lived organisms, such as large terrestrial herbivores, adjust their life history to counteract climate changes.

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Figure 1. A schematic diagram of the individual-based model of optimal reproductive strategies and population dynamics for a temperate large-herbivore. Grey lines indicate scheduling. And all simulations are started with the same initial conditions. Detailed description of the diagram: (i) *Individual-level processes* (rectangles) represented by females spring ($Spring_{bm_{i,j,t}}$) and autumn body masses ($Autumn_{bm_{i,j,t}}$), investment strategy ($R_{i,j}$ and $S_{i,j}$ which again influence the gain), summer metabolic rate ($\beta_{S_{i,j,t}}$) and proportional winter mass loss ($\beta_{W_{i,j,t}}$). (ii) *Population-level processes* (circles) represented by summer population density (D_t) and winter environmental conditions (E_t).

Figure 2. Cost of reproduction, evaluated over a one year time step, for female reindeer with constant spring body mass of 60.7 kg for three different population densities (D = 1.25, 3.25 & 5.25 individuals km^{-2}) and winter environmental conditions (E = -1.5, 0.0 & 1.5). Note that offspring survival is conditional on an individual being a female so actual survival probability in the model is the above estimates multiplied with 0.5 (assuming a constant 1:1 birth sex ratio).

Figure 3. The winning strategy and the design with respect to environmental conditions (a), and the theoretic relationship between female reproductive investment (R) as a function of spring body mass for *dynamic state dependent reproductive strategies* (b). The relationship between reproductive investment and spring body mass (b_R in eqn. 4) is different across strategies. Individuals will not invest in reproduction if their spring body mass is below a threshold value (τ_{spring}). The thick grey arrow (a) shows the *risk-averse risk-prone* continuum, whereas dotted blue lines shows the range in R-values for different female spring body massed for each winning strategy (25-30). Note that the two most *risk averse* strategies (a; 25-6), is present as the two points with the lowest average female reproductive investment ($\overline{R}$) in all subsequent figures. In some figures (subplot i in Figure 5,6 & 7a) these two points 'force' a curved model to be fitted to the data. If these points are removed more straight line relationships would have occurred. Deviance explained (D) by the model are given in percentage.

Figure 4. GAM model showing that average female reproductive investment ($\overline{R}$) was a function of smoothen (s) interaction between standard deviation [$\text{st. dev.}(E)$] and average ($\overline{E}$) environmental conditions and population density ($\overline{D}$): Intercept = 0.335 (st. err = 0.001, $P < 0.001$), (i) estimated degrees of freedom for s[$\text{st. dev.}(E)$, $\overline{E}$] = 2.651 ($P < 0.001$), and (ii) s($\overline{D}$) = 2.667 ($P < 0.001$). Deviance explained (D) by the model are given in percentage.

Figure 5. GAM model showing average population density ($\overline{D}$) as a function of the smoothen (s) interaction between standard deviation [$\text{st. dev.}(E)$] and average ($\overline{E}$) environmental conditions: Intercept = -1.680 (st. err = 0.075, $P < 0.001$), (i) estimated degrees of freedom for s[$\text{st. dev.}(E)$, $\overline{E}$] = 7.239 ($P < 0.001$). Deviance explained (D) by the model is given as a percentage in the plot.

Figure 6. GAM model showing reproductive investment as a function of the smoothen (s) interaction between standard deviation [$\text{st. dev.}(E)$] and average ($\overline{E}$) environmental conditions as well as average population density ($\overline{D}$): (a) Number of offspring per female (on $\log_e$ scale); Intercept = -1.584 (st. err = 0.010, $P < 0.001$), (i) estimated degrees of freedom for s[$\text{st. dev.}(E)$, $\overline{E}$] = 8.972 ($P < 0.001$), and (ii) s($\overline{D}$) = 2.992 ($P < 0.001$). (b) Offspring autumn body mass; Intercept = 36.083 (st. err = 0.070, $P < 0.001$), (i) estimated degrees of freedom for s[$\text{st. dev.}(E)$, $\overline{E}$] = 7.911 ($P < 0.001$), and (ii) s($\overline{D}$) = 2. 931 ($P < 0.001$). (c) Offspring spring body mass; Intercept = 38.010 (st. err = 0.137, $P < 0.001$), (i) estimated degrees of freedom for s[$\text{st. dev.}(E)$, $\overline{E}$] = 9.689 ($P < 0.001$), and (ii) s($\overline{D}$) = 2.912 ($P < 0.001$). Deviance explained (D) by the model are given as percentages on each plot.

Figure 7. GAM model showing somatic investment as a function of the smoothen (s) interaction between standard deviation $[\text{st. dev.}(E)]$ and average $(\overline{E})$ environmental conditions as well as average population density $(\overline{D})$: (a) Female age; Intercept = 8.337 (st. err = 0.019, $P < 0.001$), (i) estimated degrees of freedom for $\text{s}[\text{st. dev.}(E),\ \overline{E}] = 9.433$ ($P < 0.001$), and (ii) $\text{s}(\overline{D}) = 3.000$ ($P < 0.001$). (b) Female autumn body mass; Intercept = 93.948 (st. err = 0.134, $P < 0.001$), (i) estimated degrees of freedom for $\text{s}[\text{st. dev.}(E),\ \overline{E}] = 6.115$ ($P < 0.001$), and (ii) $\text{s}(\overline{D}) = 1.000$ ($P = 0.017$). (c) Female spring body mass; Intercept = 82.915 (st. err = 0.123, $P < 0.001$), (i) estimated degrees of freedom for $\text{s}[\text{st. dev.}(E),\ \overline{E}] = 6.927$ ($P < 0.001$), and (ii) $\text{s}(\overline{D}) = 1.000$ ($P = 0.212$). Deviance explained (D) by the model are given as percentages on each plot.

Figure 8. GAM model showing population dynamics as a function of the smoothen (s) interaction between standard deviation $[\text{st. dev.}(E)]$ and average $(\overline{E})$ environmental conditions as well as average population density $(\overline{D})$: (a) Direct regulation $(1-\beta_1)$; Intercept = -0.405 (st. err = 0.014, $P < 0.001$), (i) estimated degrees of freedom for $\text{s}[\text{st. dev.}(E),\ \overline{E}] = 6.836$ ($P = 0.040$), and (ii) $\text{s}(\overline{D}) = 1.599$ ($P = 0.009$). (b) Delayed regulation (β_2); Intercept = -0.028 (st. err = 0.118, $P = 0.119$), (i) estimated degrees of freedom for $\text{s}[\text{st. dev.}(E),\ \overline{E}] = 2.000$ ($P = 0.109$), and (ii) $\text{s}(\overline{D}) = 1.767$ ($P = 0.231$). (c) Direct effect of environmental conditions (ω_1); Intercept = -0.111 (st. err = 0.004, $P < 0.001$), (i) estimated degrees of freedom for $\text{s}[\text{st. dev.}(E),\ \overline{E}] = 4.227$ ($P = 0.033$), and (ii) $\text{s}(\overline{D}) = 2.251$ ($P = 0.011$). Deviance explained (D) by the model are given as percentages on each plot.

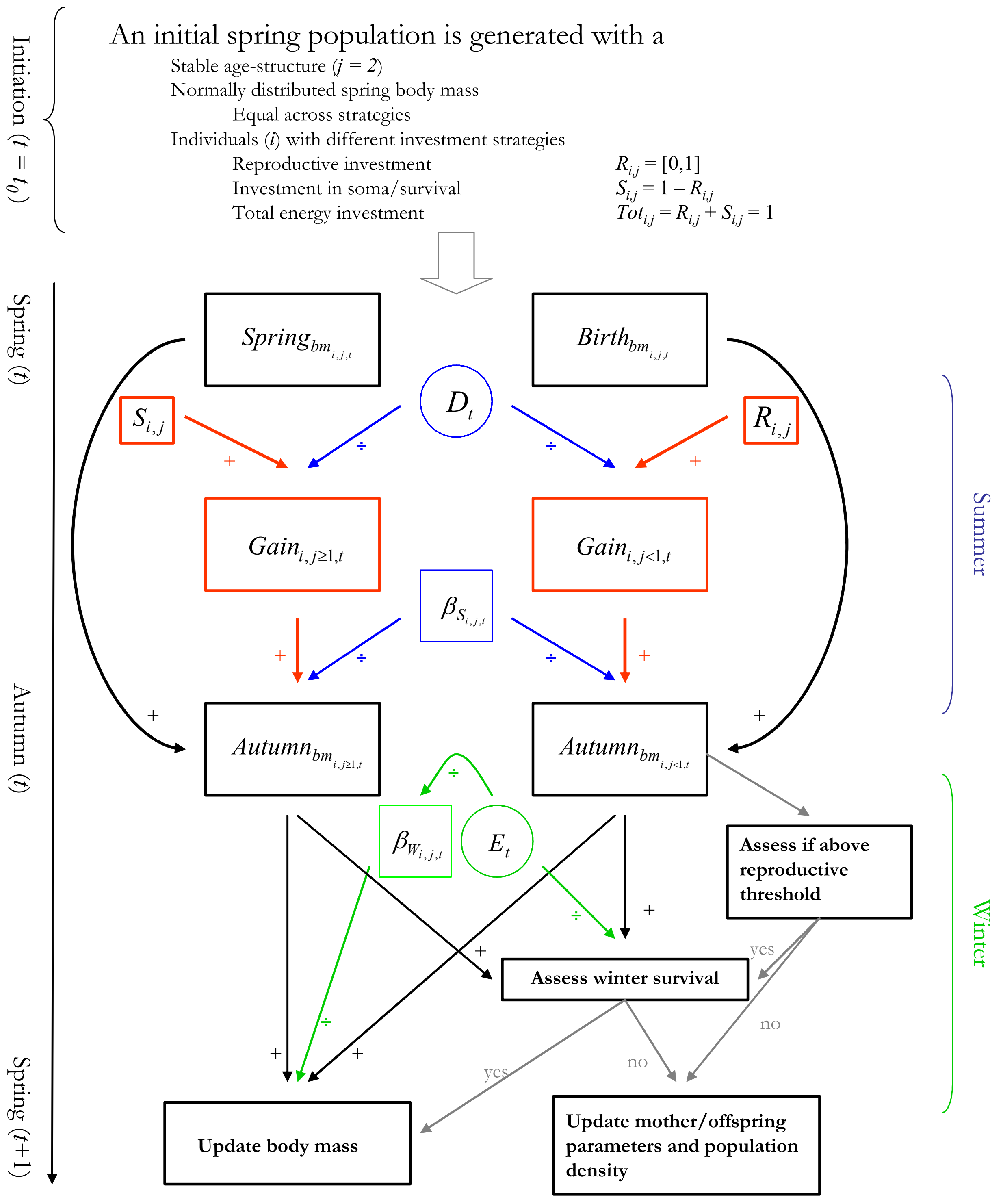

Initiation ($t = t_0$)
An initial spring population is generated with a
Stable age-structure ($j = 2$)
Normally distributed spring body mass
Equal across strategies
Individuals (i) with different investment strategies
Reproductive investment
Investment in soma/survival
Total energy investment
$R_{i,j} = [0,1]$
$S_{i,j} = 1 - R_{i,j}$
$Tot_{i,j} = R_{i,j} + S_{i,j} = 1$
Spring (t)
Autumn (t)
Spring (t+1)
Summer
Winter
$Spring_{bm_{i,j,t}}$
$Birth_{bm_{i,j,t}}$
D_t
$S_{i,j}$
$R_{i,j}$
+
÷
$Gain_{i,j\geq1,t}$
$Gain_{i,j<1,t}$
$\beta_{S_{i,j,t}}$
$Autumn_{bm_{i,j\geq1,t}}$
$Autumn_{bm_{i,j<1,t}}$
$\beta_{W_{i,j,t}}$
E_t
Assess if above reproductive threshold
Assess winter survival
yes
no
Update body mass
Update mother/offspring parameters and population density

Figure 1.

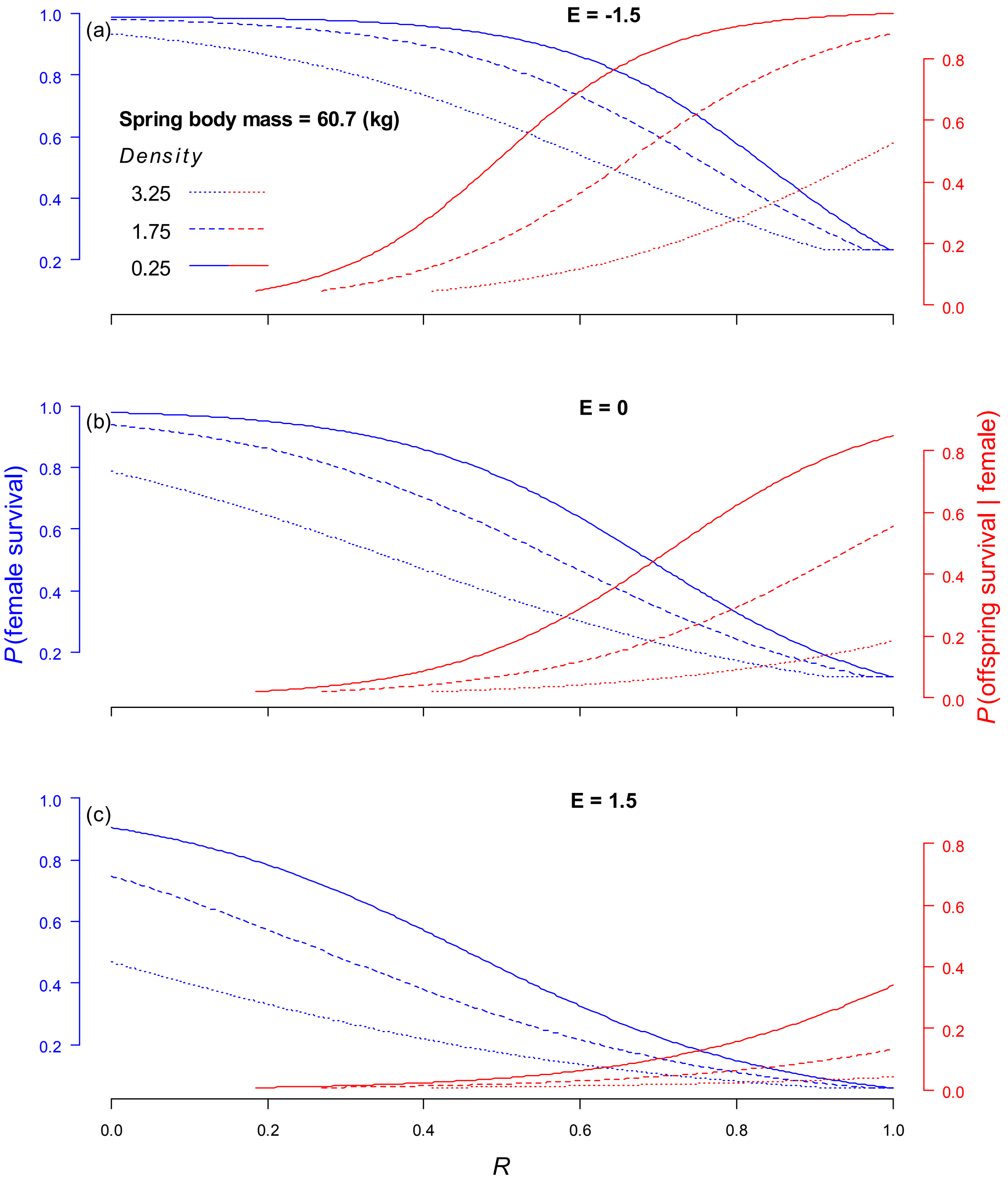

(a)
E = -1.5
Spring body mass = 60.7 (kg)
Density
3.25
1.75
0.25
(b)
E = 0
(c)
E = 1.5
1.0
0.8
0.6
0.4
0.2
0.0
P (female survival)
P (offspring survival | female)
R

Figure 2.

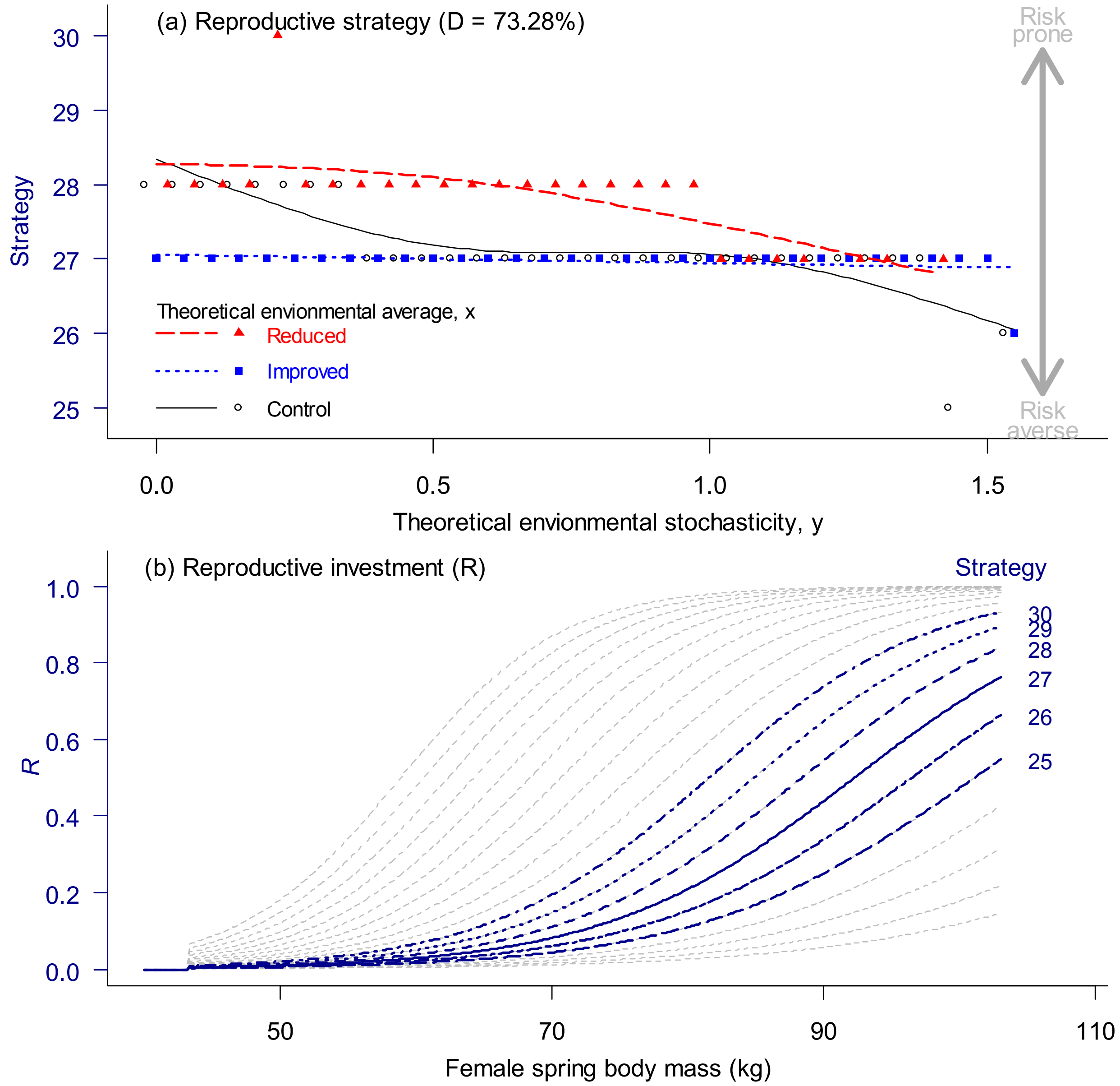

(a) Reproductive strategy (D = 73.28%)
Strategy
30
29
28
27
26
25
Risk prone
Risk averse
Theoretical envionmental average, x
Reduced
Improved
Control
0.0
0.5
1.0
1.5
Theoretical envionmental stochasticity, y
(b) Reproductive investment (R)
R
1.0
0.8
0.6
0.4
0.2
0.0
Strategy
30
29
28
27
26
25
50
70
90
110
Female spring body mass (kg)

Figure 3.

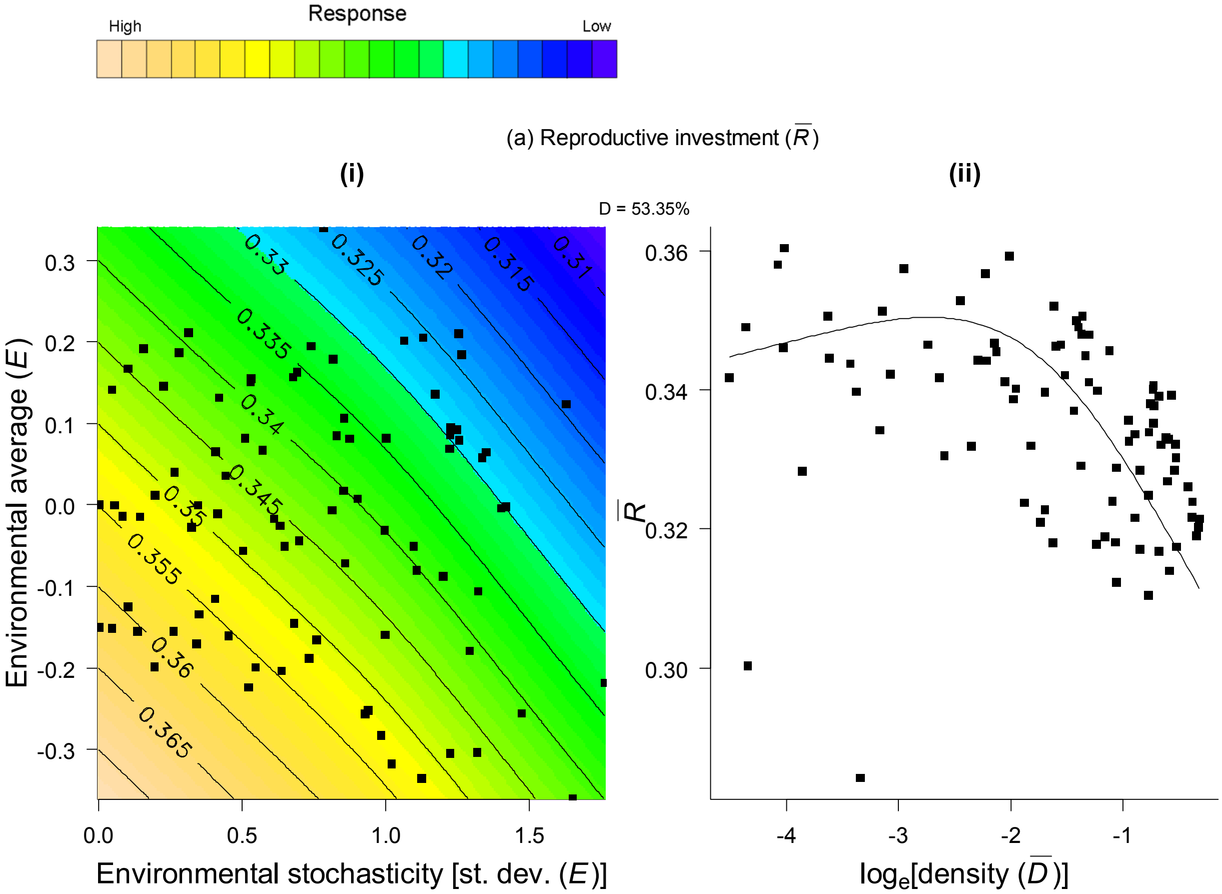

Response
High
Low
(a) Reproductive investment ($\bar{R}$)
(i)
(ii)
D = 53.35%
0.33
0.325
0.32
0.315
0.31
0.335
0.34
0.345
0.35
0.355
0.36
0.365
Environmental average ($\bar{E}$)
Environmental stochasticity [st. dev. (E)]
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
0.0
0.5
1.0
1.5
$\bar{R}$
0.36
0.34
0.32
0.30
-4
-3
-2
-1
log$_e$[density ($\bar{D}$)]

Figure 4.

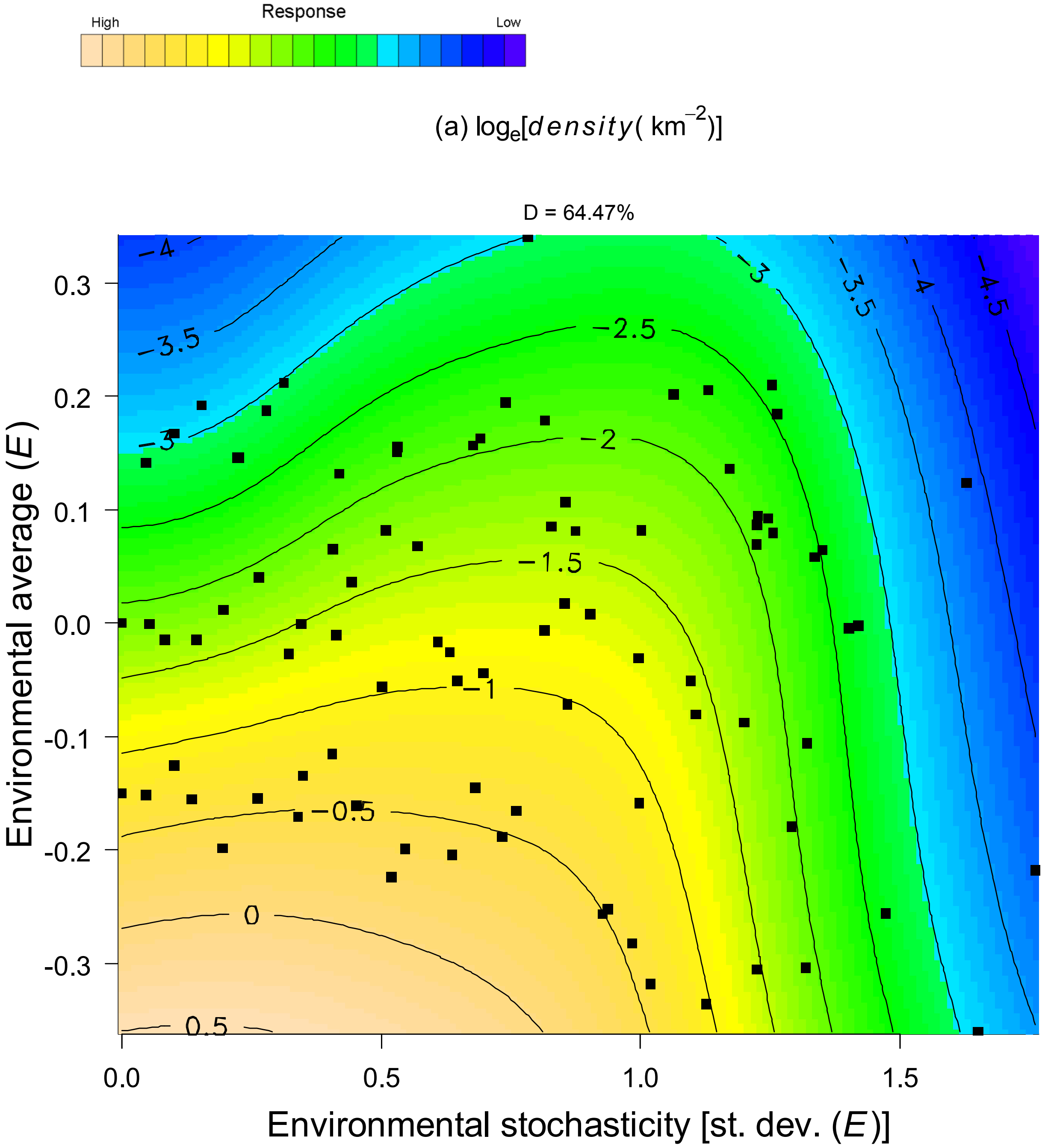
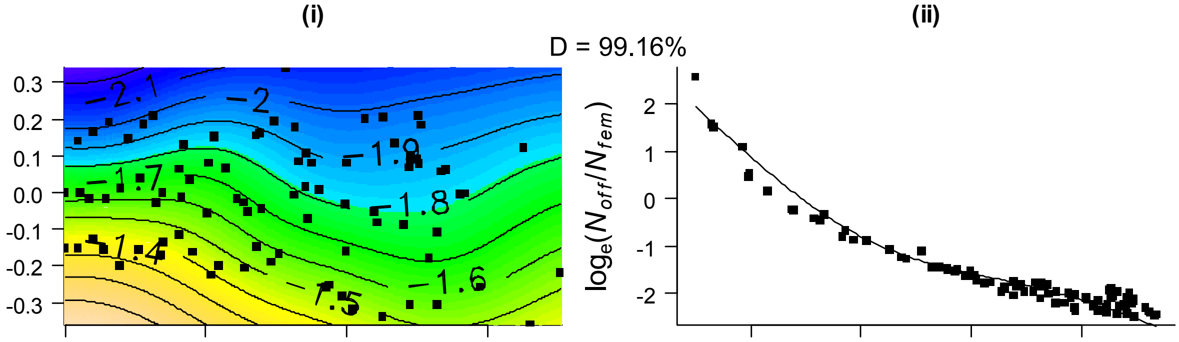
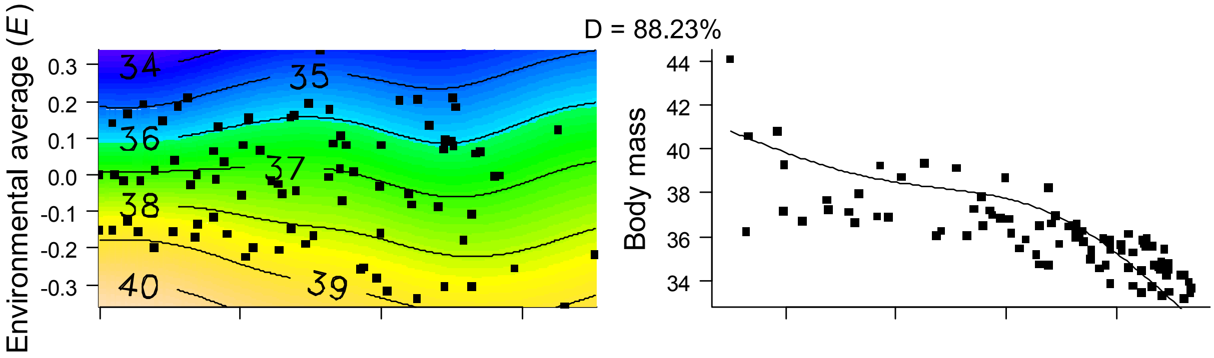

Response
High
Low
(a) $\log_e[density(\text{ km}^{-2})]$
D = 64.47%
Environmental average ($\bar{E}$)
Environmental stochasticity [st. dev. (E)]
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
0.0
0.5
1.0
1.5
−4
−3.5
−3
−2.5
−2
−1.5
−1
−0.5
0
0.5
−3
−3.5
−4
−4.5

Figure 5.

(a) $\log_e(N_{offspring}/N_{female})$



(b) Offspring autumn body mass (kg)



(c) Offspring spring body mass (kg)

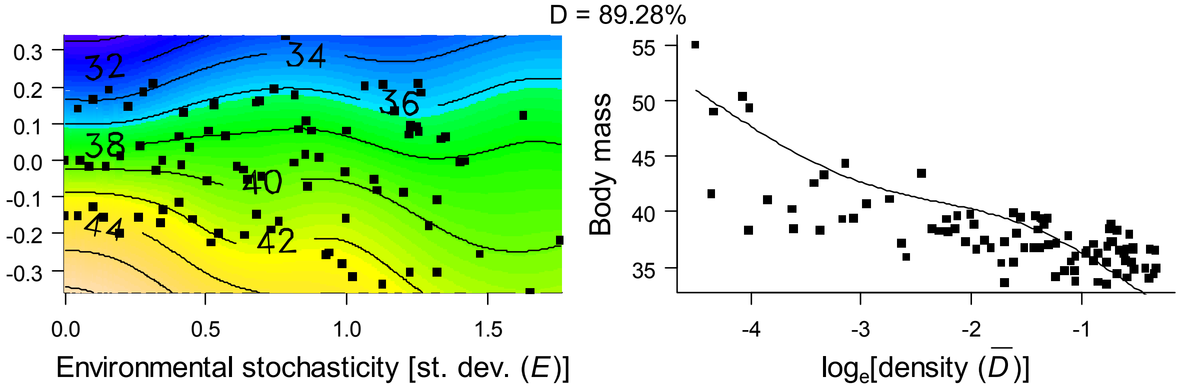
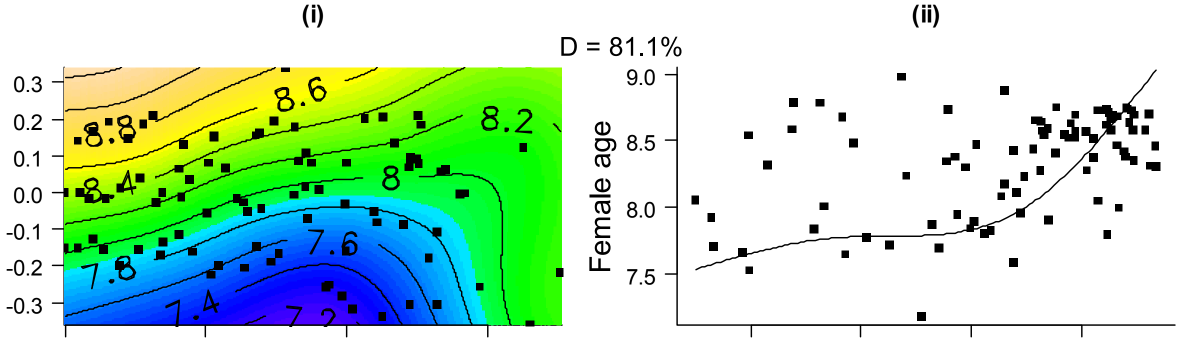
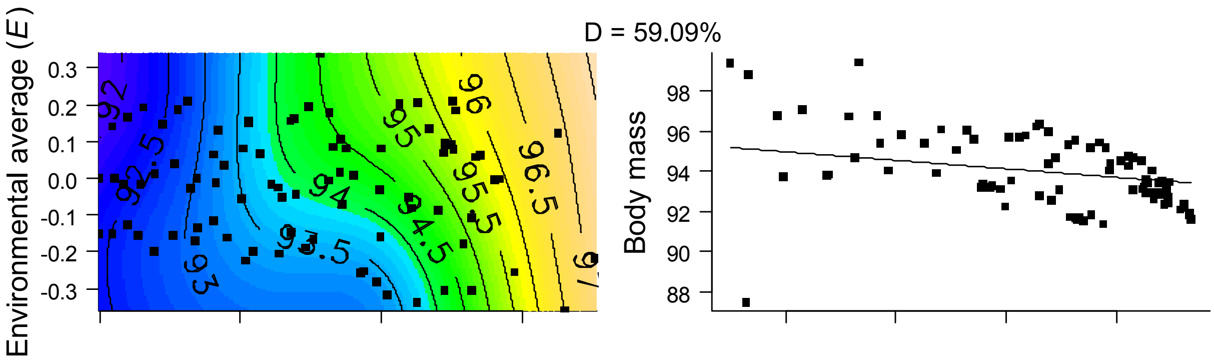


Figure 6.

(a) Female age (year)



(b) Female autumn body mass (kg)



(c) Female spring body mass (kg)

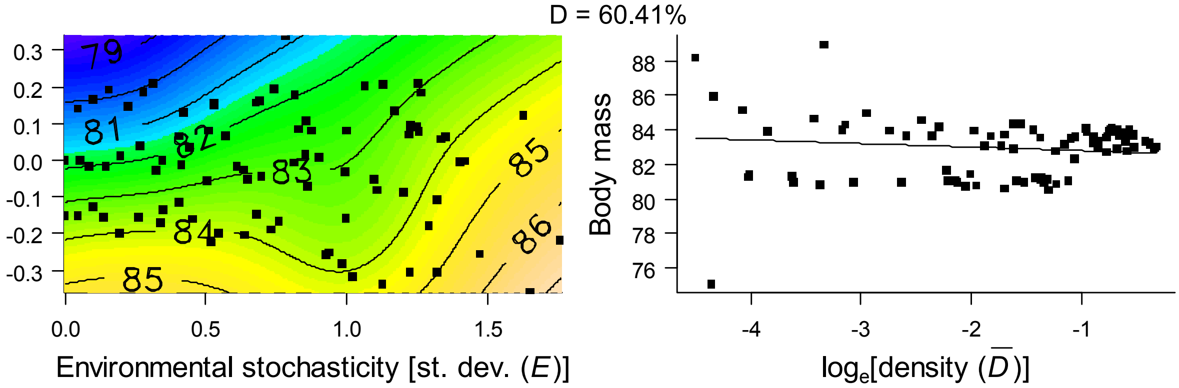


Figure 7.

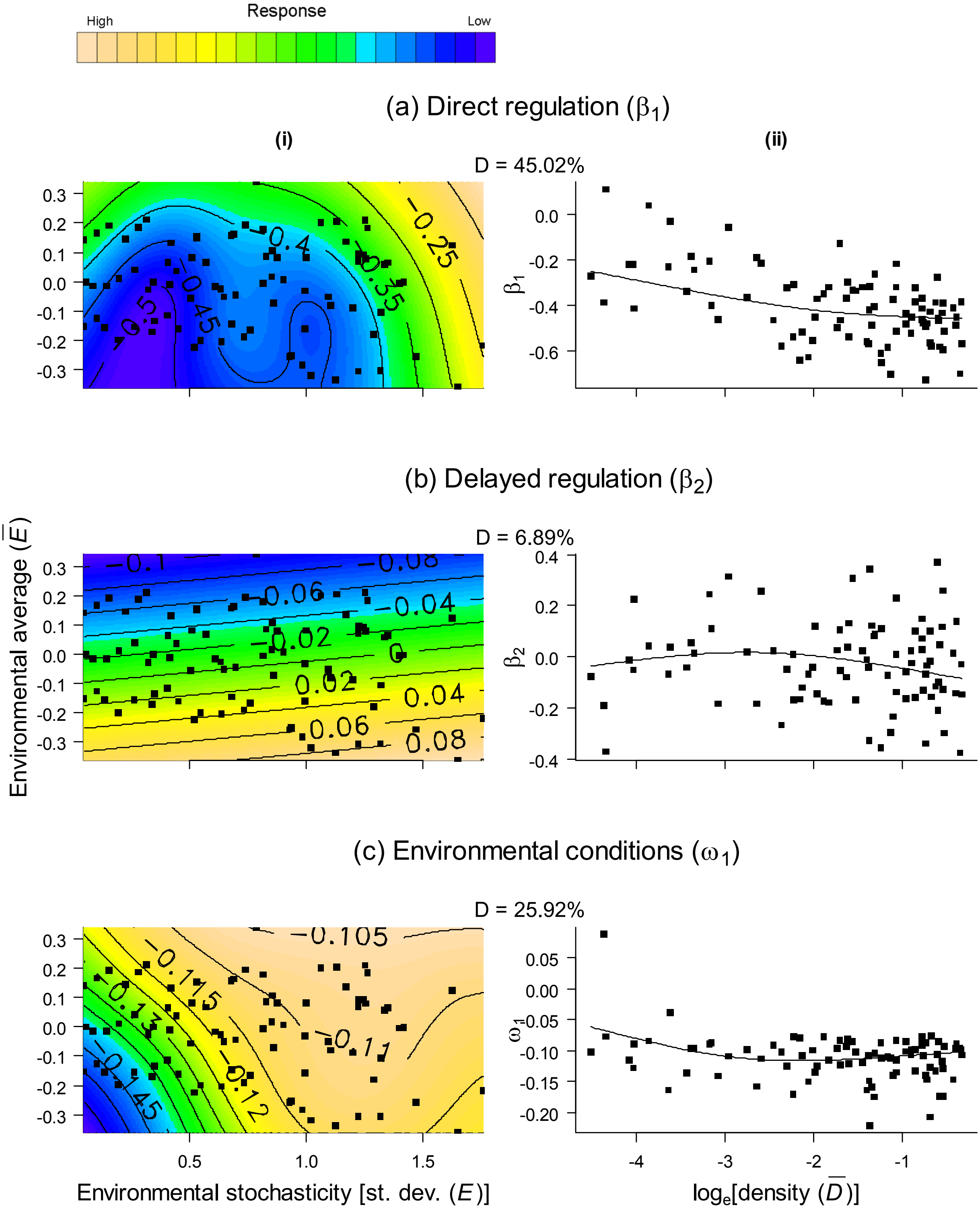

Response
High
Low
(a) Direct regulation (β1)
(i)
(ii)
D = 45.02%
-0.5
-0.45
-0.4
-0.35
-0.25
β1
(b) Delayed regulation (β2)
D = 6.89%
-0.1
-0.08
-0.06
-0.04
-0.02
0
0.02
0.04
0.06
0.08
β2
Environmental average (E)
(c) Environmental conditions (ω1)
D = 25.92%
-0.105
-0.115
-0.11
-0.12
-0.13
-0.145
ω1
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
0.5
1.0
1.5
-4
-3
-2
-1
Environmental stochasticity [st. dev. (E)]
log$_e$[density (D)]

Figure 8.

A1: SPECIFICATION – FORMULATING AN INDIVIDUAL-BASED MODEL (IBM)

This document follows a modified version of the *Overview, Design concepts and Details* (ODD) protocol for IBMs (Grimm and Railsback 2005, Grimm et al. 2006).

I. OVERVIEW

1. PURPOSE

How life history trade-offs are related to environmental stochasticity is poorly understood. However, recent studies suggest a strong impact of winter severity on the cost of reproduction in large herbivores (Clutton-Brock and Pemberton 2004). When reproduction competes with the amount of resources available for survival during an unpredictable non-breeding season, individuals should adopt a risk sensitive regulation of their reproductive allocation (Bårdsen et al. 2008). Temperate large-herbivores face such a trade-off as reproductive allocation competes with acquisition and maintenance of body reserves during summer. For these animals autumn body mass functions as an insurance against stochastic winter climatic severity (Reimers 1972, Skogland 1985, Clutton-Brock et al. 1996, Tveraa et al. 2003, Fauchald et al. 2004). Thus, reproductive allocation during summer should depend on the expected winter conditions (e.g. Tveraa et al. 2007, Bårdsen et al. 2008). As a follow-up to our own empirical studies on reindeer *Rangifer tarandus* (Tveraa et al. 2003, Fauchald et al. 2007, Tveraa et al. 2007, Bårdsen et al. 2008) we will investigate how environmental conditions affect optimal reproductive allocation strategies, and to what extent reproductive allocation strategies affect population dynamics.

Individuals living in a highly unpredictable environment should be on the risk averse side of a risk prone-risk averse continuum (see Bårdsen et al. 2008). For a given distribution of winter conditions, a *risk prone reproductive strategy* involves high reproductive allocation that will result in high reproductive reward during benign winters but high survival cost during harsh winters. A low reproductive allocation will, on the other hand, result in stable winter survival but lower potential reproductive reward. Consequently, this represents a *risk averse reproductive strategy*. *Risk* *averse reproductive strategies* are believed to result in more stable population dynamic, i.e. more or less constant population density, as the individuals buffer their reproductive allocations against a harsh environment. The objective of this study is to develop an IBM that will give us answers to the following research questions:

(1) How does environmental stochasticity affect the optimal reproductive allocation strategy?
(2) How do different reproductive allocation strategies affect population dynamics?

2. STATE VARIABLES AND SCALES

This model consists of three main components and the interaction between them.

Low-level state variables (individual specific states):

(1) *Individual state variables*: age (j ; year) and body mass (kg); assumed known by the individuals.

High-level state variables (population specific states):

(2) *Summer density*: the number of individuals (n_t) per km^2 present during the summer season (D_t); assumed known by the individuals.
(3) *Winter (weather) conditions*: environmental stochasticity (the distribution of winter climatic conditions which may be defined by a distribution's mean, variance and skew). The distribution is assumed known by the individuals whereas its value within each time step (E_t) is not (individuals cannot 'look into the future').

3. PROCESS OVERVIEW AND SCHEDULING

Time (t) is discrete (one step equals one year) with two distinct seasons (summer and winter) per time step. The model will be run for T time steps, i.e. from spring at $t = t_0$ to autumn at $t = t_0 + T$. A key point is that individuals are not assumed to know future winter conditions but they have an 'estimate' of the distribution of this variable. Thus, even though a process that affects individual parameters in one season will have effects in coming seasons (e.g. summer allocation and winter survival) it is crucial that these processes are treated independent over seasons in the model. A schematic overview of processes and scheduling are presented in Figure

A1.1, but below are a verbal presentation of the processes separated by season (summer & winter).

Summer (1 May to 31 October; 184 days).-- An allocation strategy will in any point in time be a scalar representing an individual's allocation of resources (spring body mass) in reproduction vs. somatic growth (a proxy for survival) during summer. An individual can only invest in reproduction (R) and survival (S); i.e. $R+S=1$. The reward for a fixed allocation will be limited by the population's summer density (D). That is, an individual with a fixed reproductive allocation strategy, e.g. $R=0.6$, will collect a higher mean reproductive reward in low- vs. high-density years. The effect of allocation in reproduction and survival will be implemented in two functions (Figure A11): (1) one gain function for females ($Gain$ where S and D are predictors) and (2) one function for offspring (where R and D are predictors). In sum, individual autumn body mass, i.e. summer mass development, depends on: (1) spring body mass (in the first year of life this will be an individual's birth mass), (2) the gain function that represents the increase in body mass per kg spring mass, and (3) a basal summer metabolic rate (β_S).

Winter (1 November to 31 April; 181 days).-- Autumn body mass is a predictor for the three processes that happens in the autumn and during winter: (1) If offspring body mass is below a threshold (τ_{autumn}) it will be removed from further analyses (to ease the implementation of the model, winter survival of offspring with body masses below τ_{autumn} will be set to zero even though the biological rationale for this is that offspring with such a low mass will die during summer). (2) Autumn mass and winter conditions (E) will be a predictor of individual winter survival probability ($P_{Survival}$). (3) If an individual survives, its body mass next spring will depend on its autumn mass as well as a winter loss of body mass (β_W). After these processes have been run time will go one step forward (from t to $t+1$) and the following parameters will be updated; (1) mortality, (2) spring body mass, (3) age and (4) population density.

II. DESIGN CONCEPTS

4. DESIGN CONCEPTS

This part of the ODD is based on concepts described in detail in Grimm and Railsback (2005: chapter 5).

Emergence.-- Population dynamics emerge from the behaviour of individuals. However, individual behaviour is linked to empirical rules. This can be illustrated by the following example: individual autumn body mass is based on spring mass, a built-in allocation strategy (within the limits set by population density) and basal summer metabolic rate.

Adaptation.-- In addition to the individual specific state variables individuals have an built-in strategy, which defines a behavioural rule to follow. Two types of strategies are tested against each other in the present study. First, a *fixed strategy* is defines by a vector looking like e.g. $R_i = [0.0, 0.4, 0.4, 0.4, 0.4]$, which means that this individual will invest zero in reproduction its first year of life, and 0.4 for the rest of its life (this example shows an individual that reaches a maximum age, $j_{\max}$, of 5 years). Second, a *dynamic state dependent strategy* reproductive allocations will in this model depend on spring body mass (state), looking like e.g. $R_i = [0.0, 0.4, 0.7, 0.0, 0.4]$ (see below).

Sensing.-- Within each season, individuals are assumed to know their body mass, age, summer population density and winter environmental condition.

Fitness.-- Fitness, i.e. the long-term performance of alleles and strategies of traits (Coulson et al. 2006 and references therein), will be assessed in this IBM. When evaluating fitness over different strategies, one can say that 'an optimal strategy maximizes the expected number of decedents left far into the future' (e.g. McNamara and Houston 1996, McNamara 1997, 2000). For each scenario (different environments) the model will be run for as many time steps (T) necessarily for the model to converge (see e.g. Proaktor et al. 2007). In the end of a simulation we will have a time series that consists of e.g. the proportion of individuals applying the different strategies, population density and winter conditions. This makes it possible to follow strategies over time.

Prediction.-- Individuals cannot foresee the future. This is the main reason for modelling processes over two distinct seasons.

Interaction.-- Individuals interact indirectly through a shared food resource. This is implemented as the negative density dependence acting on body mass development throughout summer in the gain function. The only positive interaction between individuals is the positive effect of a mother's reproductive allocation on her offspring's autumn body mass.

Stochasticity.-- Winter conditions are drawn from a normal or skew-normal distribution. The empirical distribution, i.e. the actual vectors generated and used in the simulations, is varied by changing important distributional parameters (see *INPUT* section below for details).

Observation.-- Book keeping consists of recording a set of variables per time step.

Low-level state variables (individual-specific):

(1) Body mass of both females and offspring in spring and autumn.

(2) Survival (including survival probability) of both females and offspring.

High-level state variables (population-specific):

(3) The number and proportion of individuals with different allocation strategies.

(4) Summer density.

(5) Winter weather conditions.

III. DETAILS

5. INITIATION & CONVERGENCE

The model will be initiated by creating (n_{t_0}) animals with body masses generated from a normal distribution with a stable age distribution ($j_{t_0} = 2$ year). Moreover, each individual will be provided with different reproductive allocation strategies. The number of different strategies (n_{strat}) give rise to n_{t_0}/n_{strat} number of individuals 'playing' the same strategy. The number of individuals following each strategy and the distribution of body mass will be equal for all allocation strategies irrespectively of the type of strategy. Table A1.1 provides details on initiating the IBM.

A simulation is said to converge when one winning strategy is left alone. After this happened, we ran the simulation for 20 more years as to 'harmonize' the dynamic between the individuals in the population and environmental conditions. Then, we collected data on yearly averages on important output for another 60 years; i.e. 'pseudo-empirical' time-series data from $t = T - 60$ to $t = T$.

6. INPUT

Winter environmental condition (E) is drawn from a normal distribution (Figure A1.2). E is the only variable differing over each simulation. Moreover, the distribution of this variable will be generated based on a real climate variable; the Arctic Oscillation[1] (AO; also known as the Northern Annular Mode).

7. SUBMODELS

Reproductive investment strategies defined on a continuous scale

Investment in reproduction.-- An individual (i) of age (j) and a spring body mass ($Spring_{bm_{i,j,t}}$) will at a given year (t) invest a proportion of its available resources in reproduction ($R_{i,j,t} = [0,1]$):

$$R_{i,j\leq 1,t} = 0 \qquad \text{if } j \leq 1 . \tag{A1}$$

This ensures that juveniles ($j \leq 1$) do not reproduce; they will invest everything in somatic growth. A *fixed strategy* is defined as a scalar between 0 and 1 that represents an allocation rule that an individual will follow throughout its adult life (see *Adaptation* section above for an example of $R_{i,j>1,t} = 0.4$). In a *dynamic state dependent strategy* reproductive allocation will be estimated and updated each year according to the following equations:

$$R_{i,j,t} = \frac{1}{1 + e^{-\left[a_R + \left(b_R \times Spring_{bm_{i,j>1,t}}\right)\right]}} \qquad \text{if } j > 1 \text{ \& if } Spring_{bm_{i,j<1,t}} > \tau_{spring} \tag{A2}$$

$$R_{i,j,t} = 0 . \qquad \text{if } j \leq 1 \text{ or if } Spring_{bm_{i,j<1,t}} \leq \tau_{spring} \tag{A3}$$

Juveniles ($j \leq 1$) and individuals with a spring body mass below a threshold value (τ_{spring}) will not invest in reproduction. Consequently, females in poor condition will skip

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[1] Data and detailed information are freely available: http://www.cgd.ucar.edu/cas/jhurrell/indices.info.html#nam.

reproduction, or have reproductive pauses (e.g. Reimers 1983b, Cameron 1994), in order to invest more in their own soma. Since the intercept (a_R) in this logistical equation will be constant for all strategies (Table A1.1), it is the slope (b_R) of the relationship between reproductive allocation and spring body mass ($Spring_{bm_{i,j,t}}$) that defines different strategies. Thus, a *dynamic state dependent strategy* can in a simplified way be defined as:

$$R_{i,j,t} = \left[0, b_{R_{j=2}}, b_{R_{j=3}}..., b_{R_{j=j\max}}\right] \approx \left[0, b_R\right] \approx b_R \,. \tag{A4}$$

Individuals with a *dynamic state dependent strategy* will initially be given different slope values (b_R), which will be limited within the range of $b_{R_{\min}}$ and $b_{R_{\max}}$ (Table A1.1 & Figure A1.4).

Investment in somatic growth. -- Moreover, allocation in somatic growth, a proxy for survival, is then:

$$S_{i,j,t} = 1 - R_{i,j,t} \,. \tag{A5}$$

Thus, total energy allocation will sum to one ($S_{i,j} + R_{i,j} = 1$), which means that individuals either allocate resources to reproduction or survival and nothing else.

Summer processes

Autumn body mass (Figure A1.5a-b).-- Individual (i) autumn mass ($Autumn_{bm_{i,j,t}} \geq 0$) depends on age (if $j < 1$ an individual will be a juvenile and if $j \geq 1$ it will be defined as an prime-aged/adult), birth mass ($Birth_{bm_{i,t}}$) or spring female body mass ($Spring_{bm_{i,j,t}}$), the gain in mass through summer ($Gain_{i,j,t}$) and a constant basal summer metabolic rate ($\beta_{S_{i,j,t}}$) within the limits set by a threshold body mass (τ_{bm_j}):

$$Autumn_{bm_{i,j<1,t}} = Birth_{bm_{i,t}} + \left(Gain_{i,j<1,t} \times Spring_{bm_{i,j,t}}\right) - \beta_{S_{i,j<1,t}} \qquad \text{if } j < 1 \tag{A6}$$

$$Autumn_{bm_{i,j\geq1,t}} = Spring_{bm_{i,j,t}} + \left(Gain_{i,j\geq1,t} \times Spring_{bm_{i,j,t}}\right) - \beta_{S_{i,j\geq1,t}} \qquad \text{if } j \geq 1 \tag{A7}$$

$$Autumn_{bm_{i,j,t}} = Autumn_{bm_{i,j,t}} \qquad \text{if } Autumn_{bm_{i,j,t}} < \tau_{bm_j} \tag{A8}$$

$$Autumn_{bm_{i,j,t}} = \tau_{bm_j} \qquad \text{if } Autumn_{bm_{i,j,t}} \geq \tau_{bm_j} \,. \tag{A9}$$

Thus, female autumn mass is a function of how much she invests in somatic growth, whereas offspring autumn mass is a function of how much its mother invests in reproduction (Table A1.2a). Basal metabolic rate ($\beta_{S_{i,j,t}}$), based on reported estimates from the literature, was found to be linearly related to body mass (Figure A1.5c; see also Table A1.2a for details):

$$\beta_{S_{i,j,t}} = a_\beta + \left(b_\beta \times Spring_{bm_{i,j,t}}\right) \qquad \text{if } j < 1 \qquad \text{(A10)}$$

$$\beta_{S_{i,j,t}} = a_\beta + \left(b_\beta \times Birth_{bm_{i,t}}\right) \qquad \text{if } j \geq 1\,. \qquad \text{(A11)}$$

Gain function (Figure A1.6).-- This function determines the per capita gain in body mass (i.e. 'per kilo' females spring mass) over the summer ($Gain_{i,j,t} \geq 0$). Gain depends on an individual's allocation strategy, and it is different for juveniles ($j < 1$) and adults ($j \geq 1$):

$$Gain_{i,j<1t} = b_{G\,j<1}(\mathrm{R}_{i,j}) + c_G(D_t) + d_G(\mathrm{R}_{i,j} \times D_t) \qquad \text{if } j < 1 \qquad \text{(A12)}$$

$$Gain_{i,j\geq 1,t} = b_{G\,j\geq 1}(S_{i,j}) + c_G(D_t) + d_G(S_{i,j} \times D_t) \qquad \text{if } j \geq 1\,. \qquad \text{(A13)}$$

Offspring autumn body mass will thus depend on how much their mothers invest in reproduction ($R_{i,j}$), whereas female autumn mass will depend on how much she invests in somatic growth ($S_{i,j} = 1 - R_{i,j}$) under the constraints that density (D_t) represents (Table A1.2b).

'Summer survival' (Figure A1.5a & A1.7a).-- If autumn body mass is below a threshold value (τ_{autumn_j}) it will be set to zero:

$$Autumn_{bm_{i,j,t}} = 0 \qquad \text{if } Autumn_{bm_{i,j,t}} < \tau_{autumn_j} \qquad \text{(A14)}$$

$$Autumn_{bm_{i,j,t}} = Autumn_{bm_{i,j,t}} \qquad \text{if } Autumn_{bm_{i,j,t}} \geq \tau_{autumn_j}\,. \qquad \text{(A15)}$$

The rationale for setting mass to zero is to mimic summer survival. In order to avoid one loop in the programming code survival is only modelled in the winter season (Table A1.2).

Winter processes

Winter survival (Figure A1.7).-- Individual winter survival conditional of being a female, $P\left(Survival_{i,j,t+1} \mid female\right) = [0,1]$, depends on autumn body mass. We follow the female segment of the population only so offspring survival probability will be multiplied with 0.5. Survival is negatively related to environmental conditions (E_t) and it follows a logistical form (with an asymptote of I_{W_j}):

$$P\left(Survival_{i,j,t+1} \mid female\right) = I_{W_j} \times \left\{ \frac{1}{1 + e^{-\left[a_{W_j} + \left(b_{W_j} \times Autumn_{bm_{i,j,t}} \right) + \left(c_{W_j} \times E_t \right) + \left(d_{W_j} \times E_t \times Autumn_{bm_{i,j,t}} \right) \right]}} \right\}. \quad \text{(A16)}$$

This function is different for adult females and offspring as discussed in the literature (Table A1.2c).

Spring body mass (Figure A1.8).-- If an individual survives, its body mass next spring ($t+1$) will depend on autumn body mass as well as a proportional loss of body reserves during winter ($\beta_{W_{i,j,t}}$):

$$\beta_{W_{i,j,t}} = I_{Loss} \times \left\{ \frac{1}{1 + e^{-\left[a_{Loss} + \left(b_{Loss} \times E_t \right) + e_{i,j,t} \right]}} \right\} \qquad \text{if } P_{Survival_{i,j,t+1}} = 1 \qquad \text{(A17)}$$

$$Spring_{bm_{i,j+1,t+1}} = Autumn_{bm_{i,j,t}} \times \left(1 - \beta_{W_{i,j,t}}\right) \qquad \text{if } P_{Survival_{i,j,t+1}} = 1 . \qquad \text{(A18)}$$

Winter losses increases with increasing environmental conditions (E_t), and this relationship has a logistical form: smaller values the scaling parameter (ϑ_{Loss}) gives a higher degree of curvature (highly sigmoid shape) compared to lager values of ϑ_{Loss} (see Table A1.2d for details). The absolute loss of body mass will be larger for large individuals (eqn. A18), but the proportional loss of body reserves are equal for lager and smaller individuals. Moreover, we have added individual stochasticity ($e_{i,j,t}$) to winter loss of body mass in order model chance operating on individual performance during winter (Table A1.2d).

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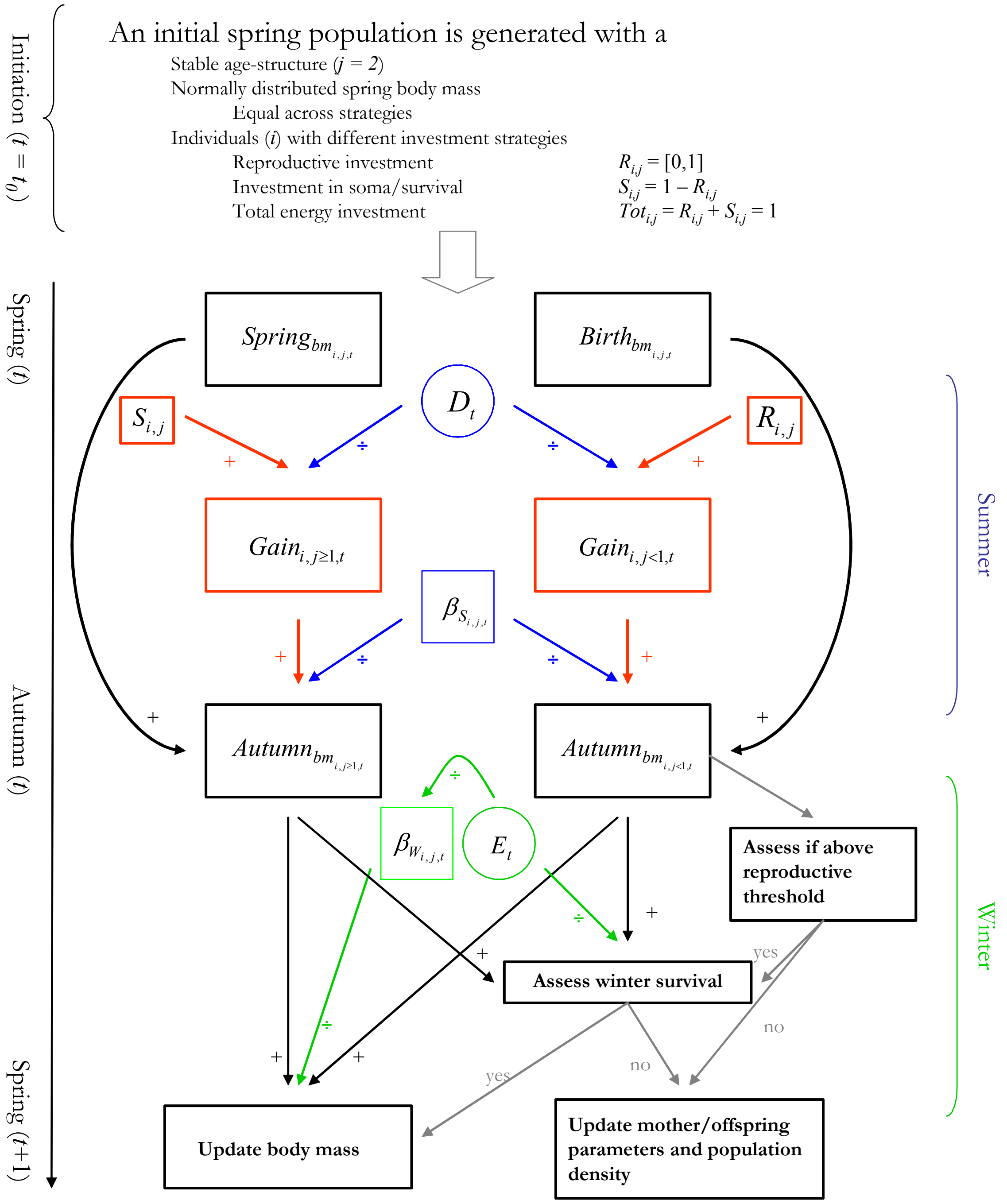


Figure A1.1. A schematic diagram of the individual-based model of optimal reproductive strategies and population dynamics for a temperate large-herbivore. Grey lines indicate scheduling. Detailed description of the diagram: (i) *Individual-level processes* (rectangles) represented by females spring ($Spring_{bm_{i,j,t}}$) and autumn body masses ($Autumn_{bm_{i,j,t}}$), allocation strategy ($R_{i,j}$ and $S_{i,j}$ which again influence the gain), summer metabolic rate ($\beta_{S_{i,j,t}}$) and proportional winter mass loss ($\beta_{W_{i,j,t}}$). (ii) *Population-level processes* (circles) represented by summer population density (D_t) and winter environmental conditions (E_t).

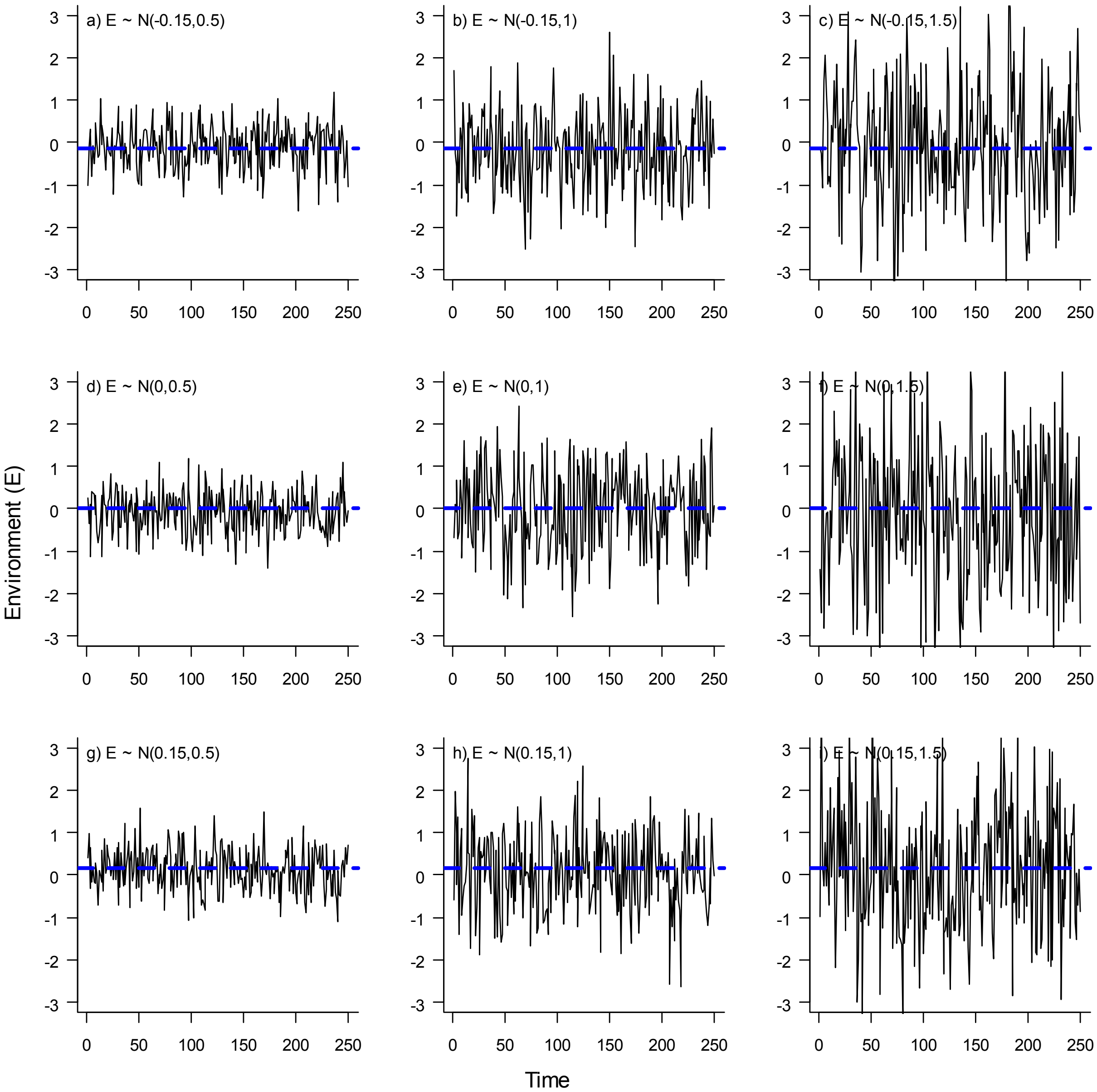


Figure A1.2. Simulated normally distributed environmental conditions (E). Realisation e) [E = ~N(0,1)] mimic the normalized principal components (PC) of climate indexes like AO and *North Atlantic Oscillation Index* (NAO).

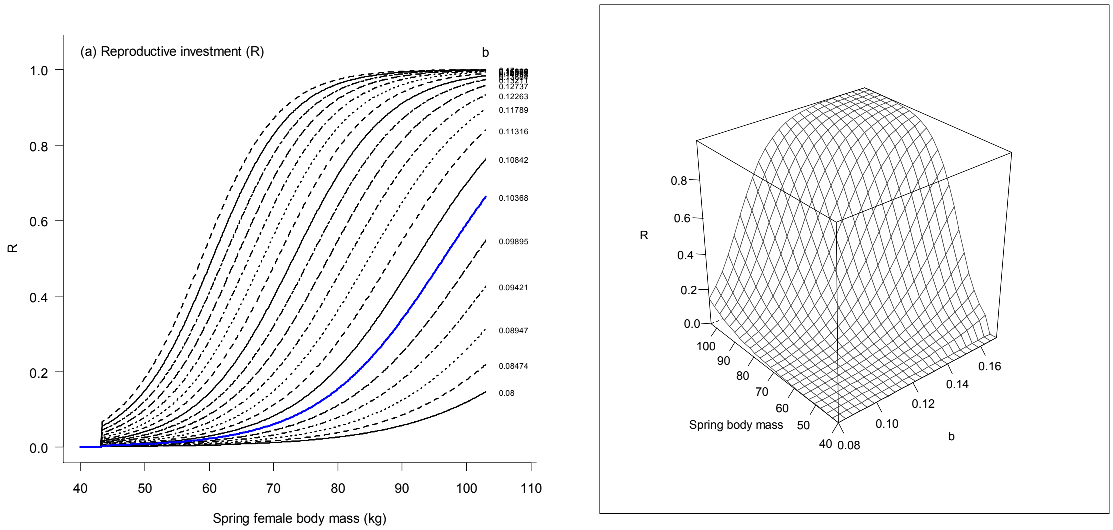
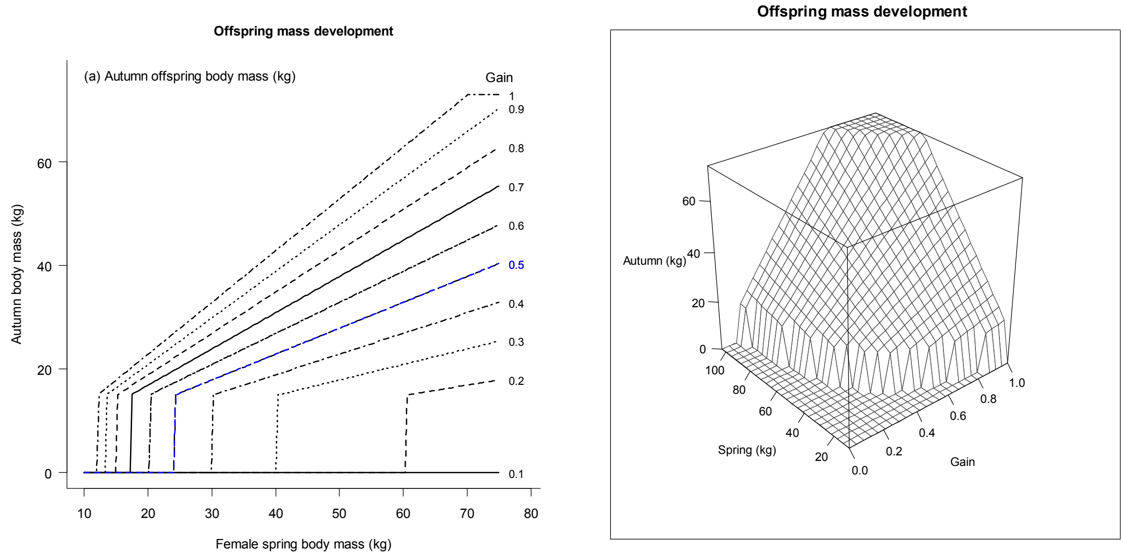
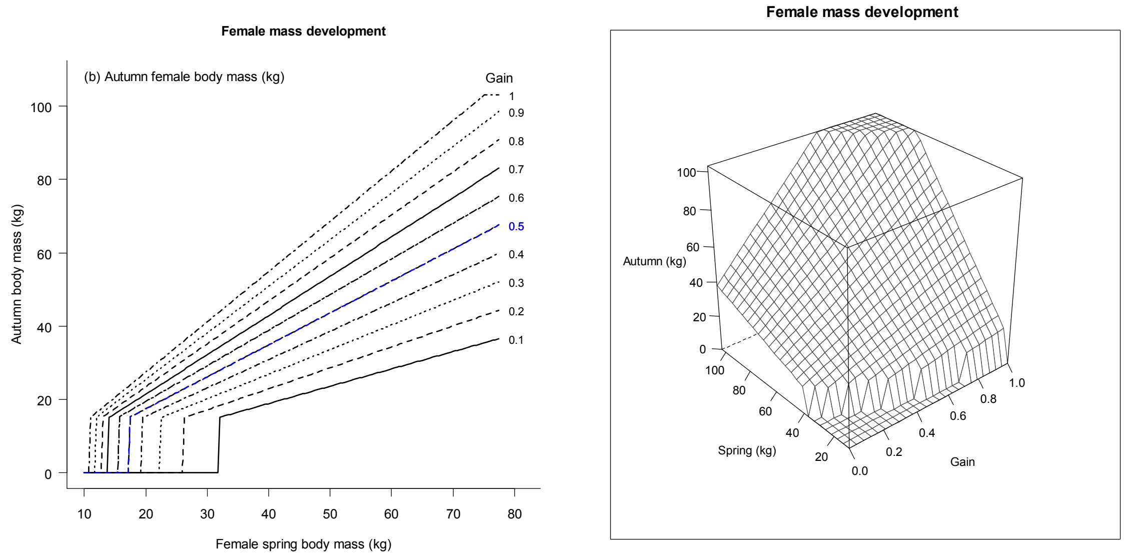


Figure A1.4. Female reproductive allocation (R) as a function of spring body mass for *dynamic state dependent reproductive strategies*. The relationship between reproductive allocation and spring body mass (b_R in eqn A2) is different for different strategies. Individuals will not invest in reproduction if their spring body mass is below a threshold value (τ_{spring}). Note that the scale of the axis containing spring body mass is different across figures.





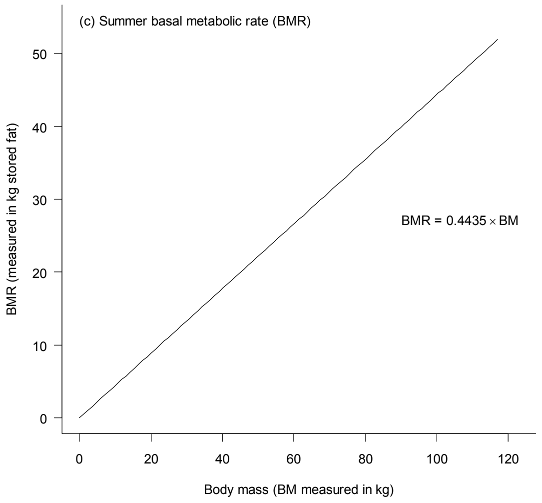


Figure A1.5. Summer mass development for offspring (a) and female (b) as a function of gain (each line representing different values for gain). Gain can be interpreted as allocation in either reproduction (*R*; offspring) or survival (*S*; female) within the limits set by density and a summer metabolic rate (Table A1.2a; Figure A1.6). The angle on the lines representing lines with a gain <0.4 (a) is due to the fact that live offspring are supposed to have an autumn body mass above a threshold value (τ_{autumn}). (c) Summer resting metabolic rate as a function of spring body mass. Note that the x-axis is different between the plots.

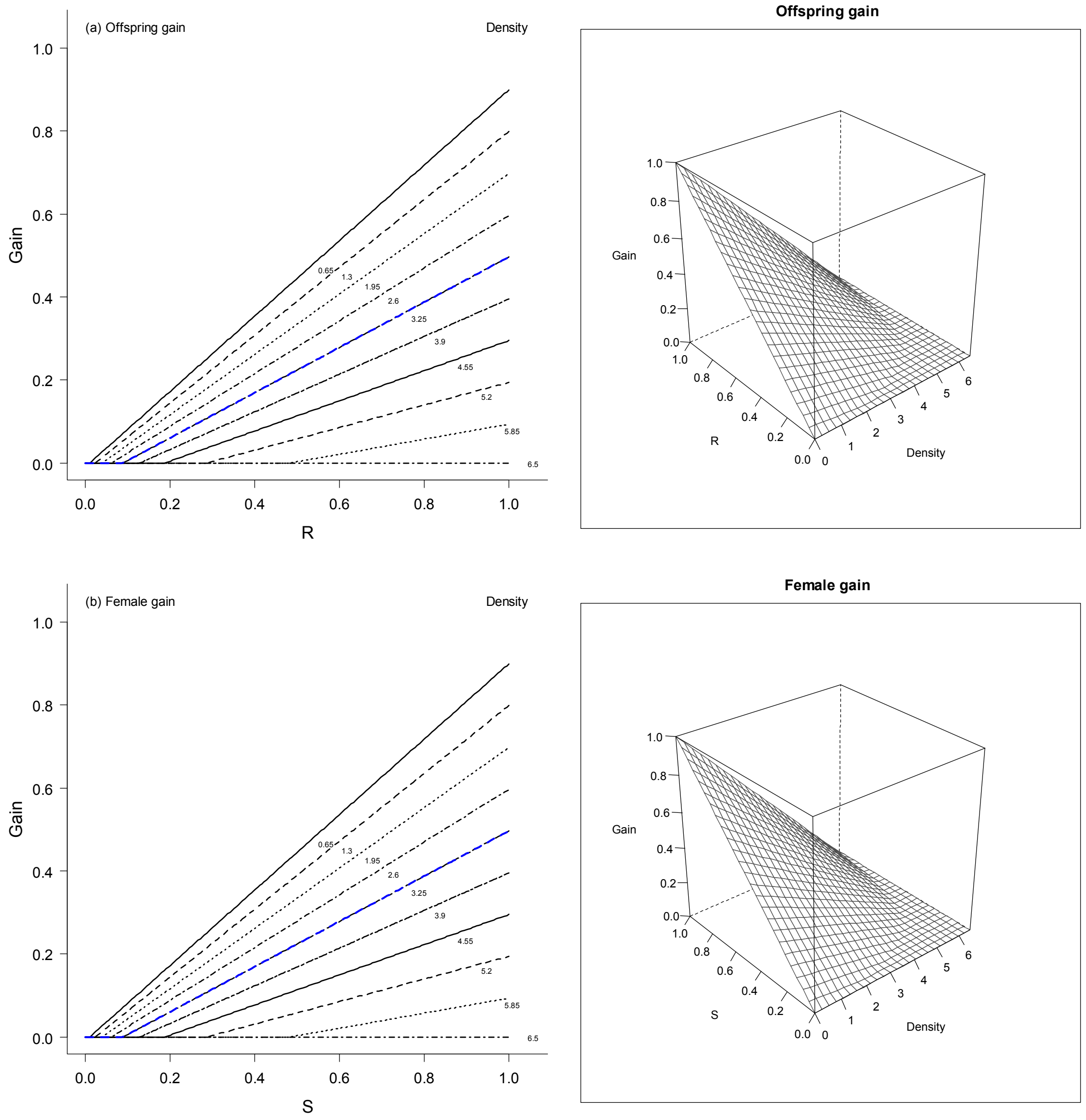


Figure A1.6. Gain in body mass for offspring (a) and female (b) as a function of allocation in either reproduction (*R*; offspring) or survival (*S*; female) and density (different lines). The reward of a fixed allocation will be limited by density; a fixed allocation will lead to lower gain at higher compared to lower densities.

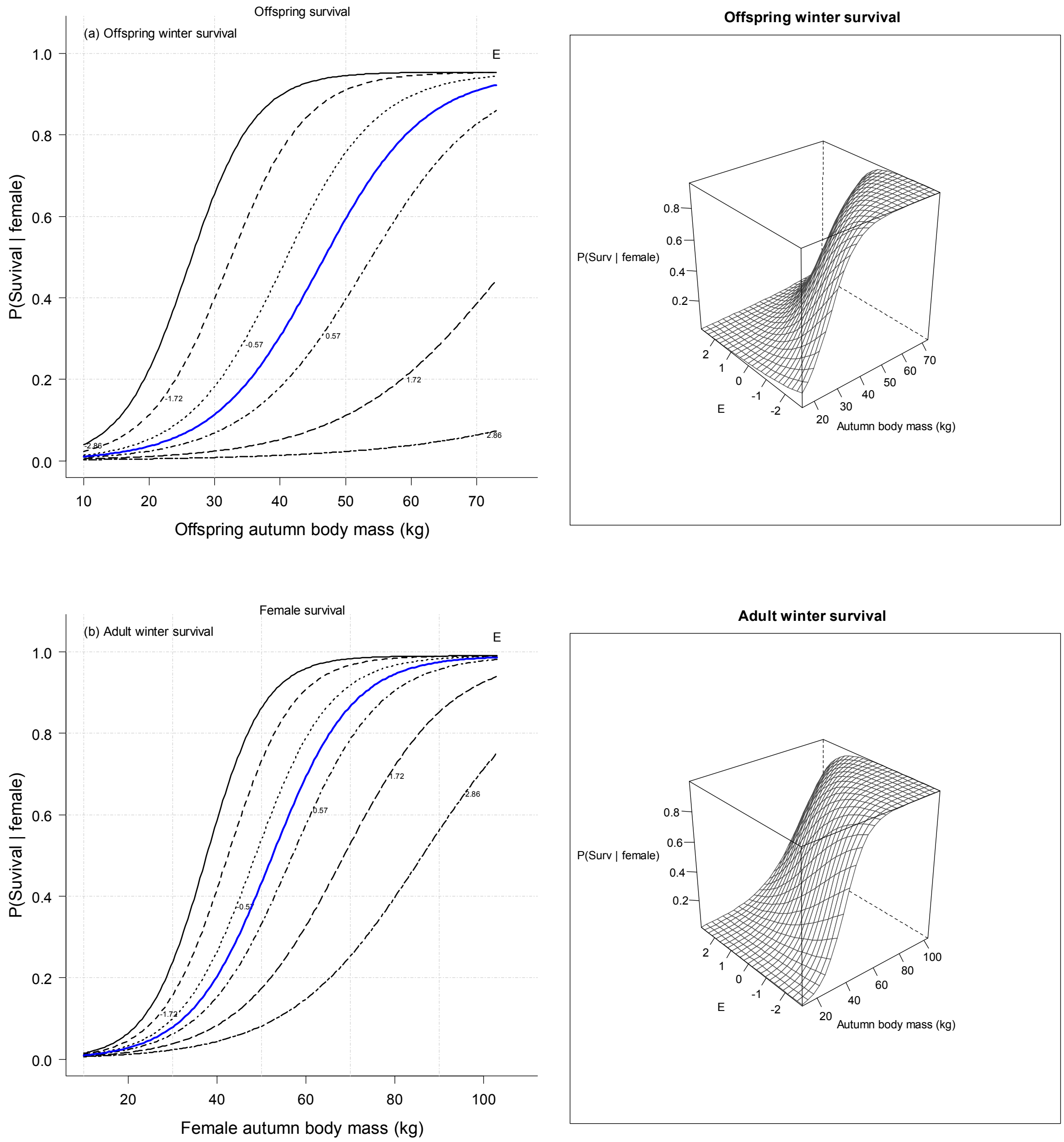


Figure A1.7. Over-winter survival as a function of autumn body mass and environmental conditions for juveniles (a) and adult females (b). Note that the scales on the axes are different for adult females and offspring.

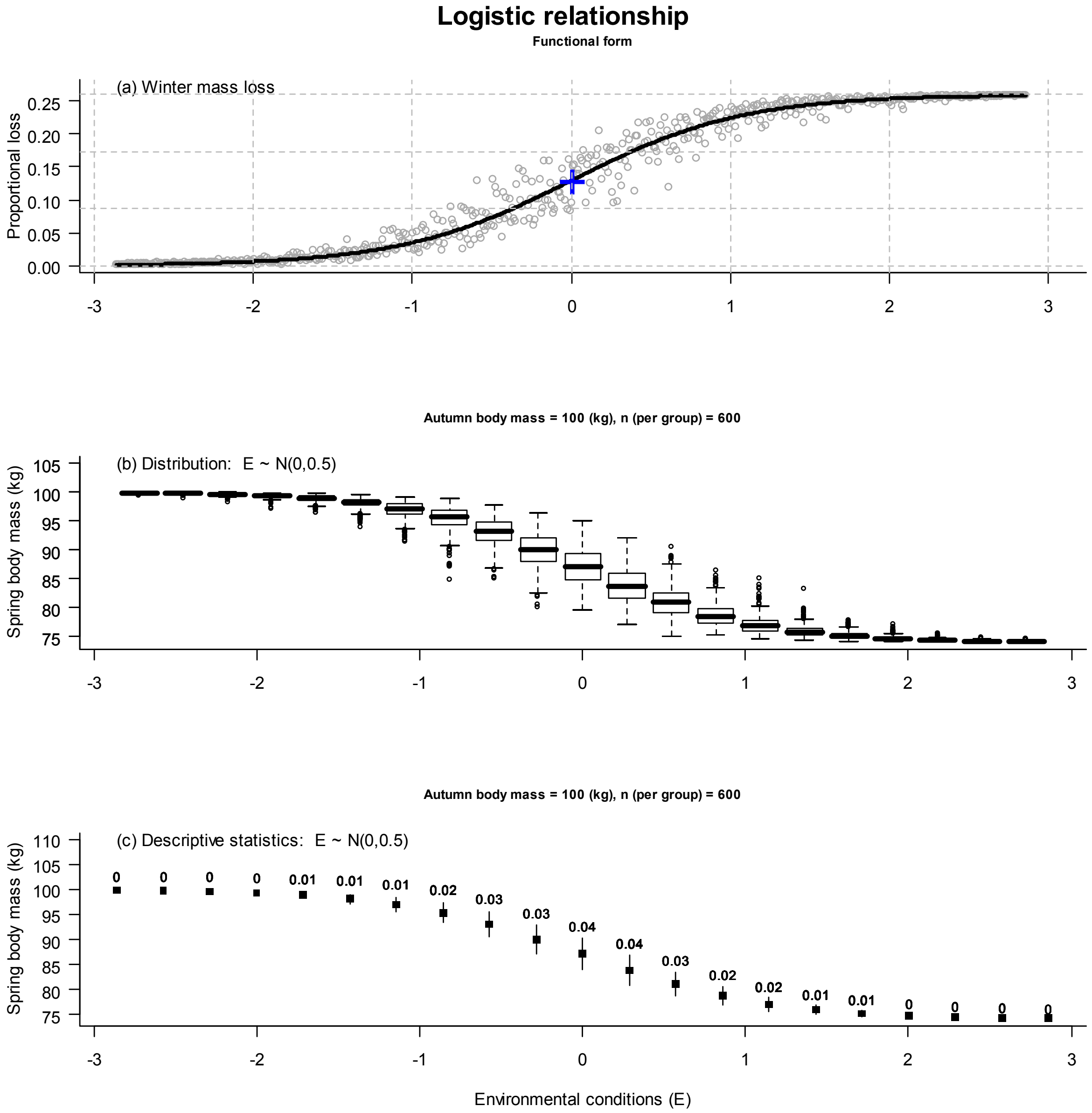


Figure A1.8. (a) Proportional mean loss of (autumn) body mass as a function of environmental conditions (line). Points are generated from the same model except that an error term is now also included. Mean mass loss for $E = 0$ (marked with a cross) are taken from the literature (Table A1.2d). (b) A boxplot showing the distribution (median, 75% and 25% quartiles and outlying observations as points) for 600 constant autumn masses. (c) Descriptive statistics, i.e. means with standard deviations (bars) and coefficient of variations (text), for several environmental values (groups) using the same realisation as in the previous plot (see Table A1.2d for details).

Table A1.1. Values used for the initiation of the model.

Parameter	**Explanation**	**Value (scale)**	**Source/Notes**
(a) Initiation (Figure A1.2-A1.4 & Expression A1-A5)			
t_0	Initial time (spring)	0 (year)	——
A	Study area	2000 (km^2)	——
n_{t_0}	Number of females present at t_0	800 (number)	——
n_{strat}	The number of different strategies at t_0	40 (number)	——[a]
n_{t_0}/n_{strat}	The number of individuals within each strategy stratum at t_0	20 (number)	——
$Spring_{bm_{t_0,i}}$	Initial spring body mass generated from a normally distribution with a given mean (x) and standard deviation (y): $\approx N(x,y)$	$x = 60.70$ (kg) $y = 5.00$ (kg)	(Fauchald et al. 2004: Table 2b)[b,c]
j_{t_0}	Initial age similar for all individuals	2 (year)	(Crête et al. 1994, Fancy et al. 1994, Albon et al. 2002)
$j_{\max}$	Maximum (max) possible age	16 (year)	Personal communication[d]
τ_{spring}	Reproductive spring mass threshold in the *dynamic state dependent strategy* (DSDS)	43.20 (kg)	Tveraa et. al (unpul. data)[e]
a_R	Intercept in the equation defining the DSDS	-10.00 (constant)	——
$b_{R\min}$	Minimum (min) slope (b_R) in the equation defining the DSDS	0.08 (constant)	——
$b_{R\max}$	Max slope (b_R) in the equation defining the DSDS	0.17 (constant)	——

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[a] This gives rise to 20 *fixed* (equally spaced reproductive allocation strategies between 0 and 1) and 20 *dynamic state dependent strategies* (equally spaced values of b_R between $b_{R\min}$ and $b_{R\max}$).

[b] These estimate is based on subtracting the reported body masses for a female on natural pasture with the mean body mass of a newborn calf of 7.8 kg (their Table 2).

[c] The standard deviation is found by comparing the reported quartiles[b] in Fauchald et al. (2004) with a generated normal distribution using their mean value[b] following function `quantile(rnorm(mean = 68.5-7.8, sd = x, n = 1000))[c(2, 4)]` in the software *R* (R Development Core Team 2007). By testing different values of `x` we found that `x` = 5 gave approximately similar quartiles as reported by Fauchald et al. (2004).

[d] Heikki Törmänen, *Reindeer Research Station*, *Finnish Game and Fisheries Research Institute*, Kaamanen, Finland: data from 1993, experimental reindeer herd in Kutuharju, Finland.

[e] T. Tveraa, P. Fauchald, K. Langeland & B.-J. Bårdsen: data from 16C (a reindeer herding district in Finnmark, Northern Norway), collected on the 24th of May 2003.

Table A1.2. Parameters used in the model.

Parameter	Explanation	Value (scale)	Source/Notes
(a) Autumn body mass (Figure A1.5 & Expression A6-A11, A15-A16)			
$Birth_{bm_{i,t}}$	Mean birth mass ($j<1$)	7.8 (kg)	(Valkenburg et al. 2003, Adams 2005)
τ_{autumn_j}	Threshold for min. mass: offspring ($j<1$)	15.0 (kg)	______
	female ($j\geq 1$)	15.0 (kg)	______
$Spring_{bm_{i,j,t}}$	Spring body mass ($j\geq 1$)	Estimate (kg)	______
τ_{bm_j}	Threshold for max. mass: offspring ($j<1$)	73.0 (kg)	Personal communication[a]
	female ($j\geq 1$)	103.0 (kg)	(Holand et al. 2004)
a_β	Intercept for summer basal metabolic rate	0.000 (constant)	(Nilssen et al. 1984, Schmidt-Nielsen 1997)[c]
$b_\beta = \frac{(\beta_{s_{\max}} - 0)}{(\tau_{bm_{j=2}} - 0)}$	Constant for spring body mass	0.628 (constant)	
(b) Gain (Figure A1.6 & Expression A12-A13)			
D_t	Density; n_t/A	Estimate (n km^{-2})	(Tveraa et al. 2007)[d]
b_G	Constant for allocation: $S_{i,j}$ or $R_{i,j}$	1.000 (constant)	______
c_G	Constant for density	-0.150 (constant)	______
d_G	Constant for interaction	-0.140 (constant)	______

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[a] Heikki Törmänen, *Reindeer Research Station*, *Finnish Game and Fisheries Research Institute*, Kaamanen, Finland: data from the experimental reindeer herd in Kutuharju, Finland.

[b] This is based on the lowest autumn (December) female reindeer dressed body mass in Reimers (1983b: Figure 2). In order to 'transform' dressed body mass it into live mass we multiplied the dressed body mass by 1.92 as suggested by Reimers (1983a).

[c] This is based on a summer basal metabolic rate (BMR) of 2.36 W (J s^{-1}) kg^{-1} for Norwegian and Svalbard reindeer (Nilssen et al. 1984: average summer and autumn resting metabolic rates presented in their Table 1). Total summer BMR was calculated on a daily basis, i.e. assuming a constant daily BMR, summed over 184 days (length of the summer season). Total summer BMR was based on spring body mass, i.e. birth mass for offspring, as starting conditions. Maximum possible summer BMR ($\beta_{s_{\max}}$) is the summer BMR for the largest possible female body mass (defined by $\tau_{bm_{j=2}}$). Daily BMR was estimated according to well-known physiological relationships and by converting Joule (J) to calories using the following constants: 1 J = 0.239 cal, 1 kcal = 1000 cal & 1 kcal = 0.1011 g or 0.00011 kg stored fat (Schmidt-Nielsen 1997).

[d] Maximum density, which limits the gain function (gain will then be zero), is set to 6.5 individuals km^{-2} (Tveraa et al. 2007: Figure 4a).

Table A1.2. Continued.

Parameter	**Explanation**	**Value (scale)**	**Source/Notes**
(c) Winter survival (Figure A1.7 & Expression A16)			
$I_{W\,j}$	Asymptote for survival; offspring ($j < 1$)	0.954 (prob.)	(Rødven 2003)[e]
	female ($j \geq 1$)	0.990 (prob.)	(Albon et al. 2002)[e]
$a_{W\,j}$	Intercept: offspring ($j < 1$)	-5.750 (constant)	______[f]
	female ($j \geq 1$)	-5.750 (constant)	
b_{Wj}	Constant for autumn mass: offspring ($j < 1$)	0.125 (constant)	______[f]
	female ($j \geq 1$)	0.110 (constant)	
c_{Wj}	Constant for environment: offspring ($j < 1$)	-0.225 (constant)	______[f]
	female ($j \geq 1$)	-0.005 (constant)	
d_{Wj}	Constant for interaction: offspring ($j < 1$)	-0.025 (constant)	______[f]
	female ($j \geq 1$)	-0.015 (constant)	
(d) Spring body mass (Figure A1.8 & Expression A17-A18)			
I_{Loss}	Max. proportional body mass loss (converted from proportional to logit[g] scale)	0.260 (prop.)	(Bergerud 1974, Dauphiné 1976, Bradshaw et al. 1998)
$e_{i,j,t}$	error term: $\approx N(0,x)$	0.500 (logit)	______
ϑ_{Loss}	Scaling parameter used when estimating a_{Loss}	0.005 (prop.)	______
$E_{\min} / E_{\max}$	Max./min. environmental value	-2.860/2.860	Mimics AO[h]
$a_{Loss} = \text{logit}[(1-\vartheta_W)/2]$	Intercept	Estimate (logit)	(Bradshaw et al. 1998 and referenced therein)[i]
$b_{Loss} = \dfrac{[\text{logit}(1-\vartheta_W) - \text{logit}(\vartheta_W)]}{(E_{\max} - E_{\min})}$	Constant for environment	Estimate (logit)	______[j]

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[e] The upper 95% confidence interval (CI) for prime-aged survival is taken as asymptote for adults (Albon et al. 2002), whereas the we estimated this from the maximum yearly mean (1.60 on logit scale) and 0.74 standard error (SE) for survival 4-16 months from Rødven (2003: his table 3).

[f] The general finding in the literature is that adult female survival varies little from year-to-year relative to juvenile survival, which is highly variable (reviewed by e.g. Gaillard et al. 2000). Different coefficients for the two age classed are chosen to take this into account (Figure A1.7). However, even adult survival has been found to decrease for reindeer experiencing extreme winter conditions (Tveraa et al. 2003). Thus, during extreme environmental conditions even adult survival will be affected in this model (Figure A1.7b).

[g] Logit, or log-odds of proportions/probabilities, of x is defined as: $\text{logit}(x) = \log(x/1-x)$. The antilogit, i.e. transformation from logit to proportion/probability scale, is defined as: $\text{antilogit}(x) = I \times 1/[1 + (1/e^x)]$, where the asymptotic value (I) usually is set to 1.

[h] Based on data available at http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#nam. The minimum/maximum is the maximum absolute value of normalized PC values of the annual *Artic Oscillation Index* from 1899 until 2007). The minimum and maximum values must be symmetrical as the estimated intercept will be wrong if unsymmetrical values are chosen.

[i] Average loss of autumn body mass during winter for *Rangifer tarandus* have been reported to be 12.5% (Bradshaw et al. 1998). Thus, we tuned the models so that (*i*) during an average year (E = 0) average loss of body reserves is ~0.125, (*ii*) at an extremely god year (E = -2.85) average loss is ~0 and (*iii*) during an extremely harsh year (E = 2.85) loss is ~0.26 on average (Bergerud 1974).

[j] I_{Loss} ensures that mass loss goes towards zero (spring mass ~ autumn mass) for extremely god years (as E goes towards -2.85) and towards I_{Loss} for extremely bad years (as E goes towards 2.85) on a probability scale (0 and I_{Loss} are the asymptotes in the logistic relationships). The intercept, slope, and st. dev. are logits as all calculation are performed on logit scale.

A2: FIGURE OF IMPORTANT OUTPUT AS A FUNCTION OF TIME FOR THE STANDARD NORMALLY DISTRIBUTED ENVIRONMENT

Important output of details associated with one example simulation (Figure A2.1).

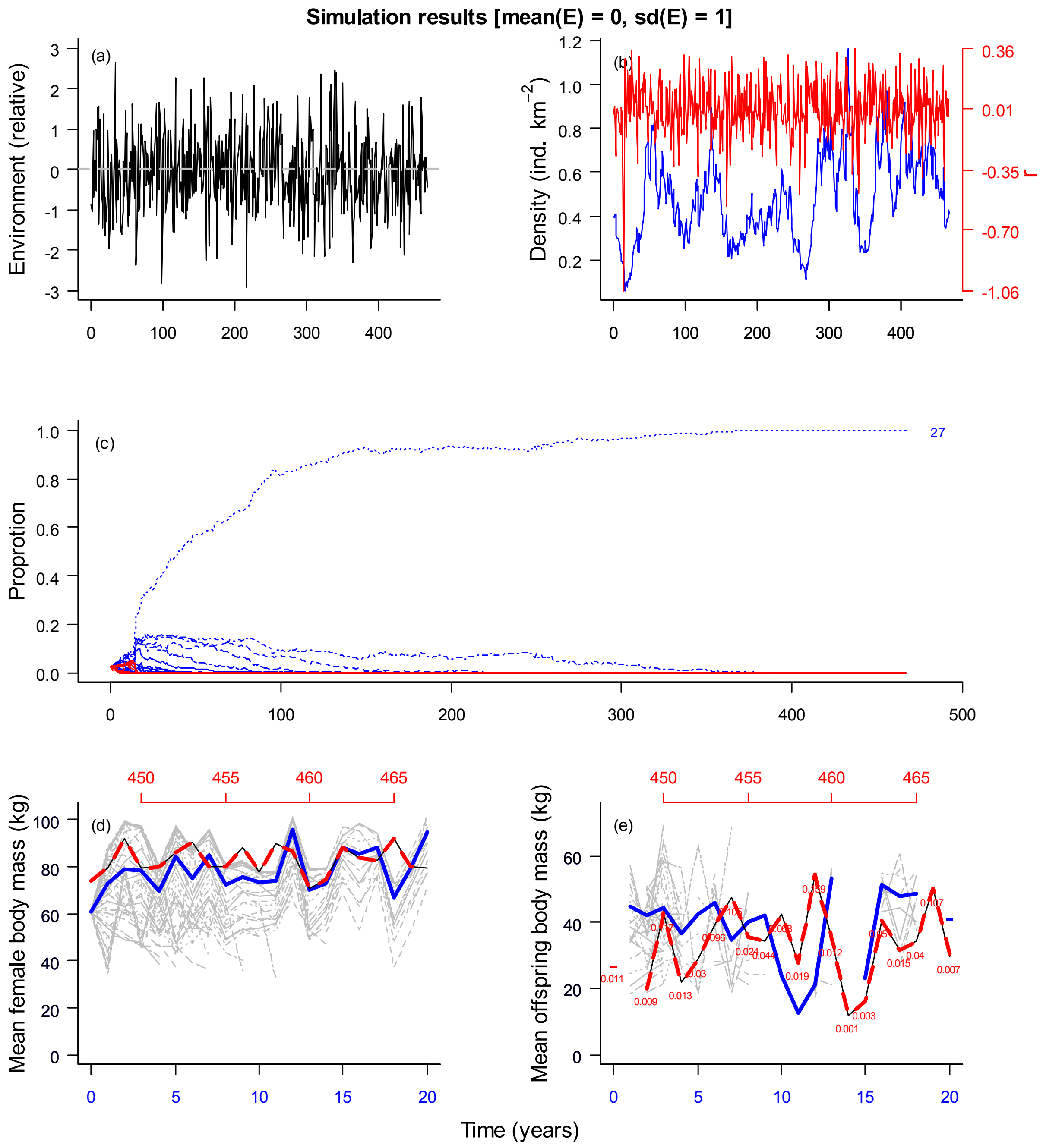


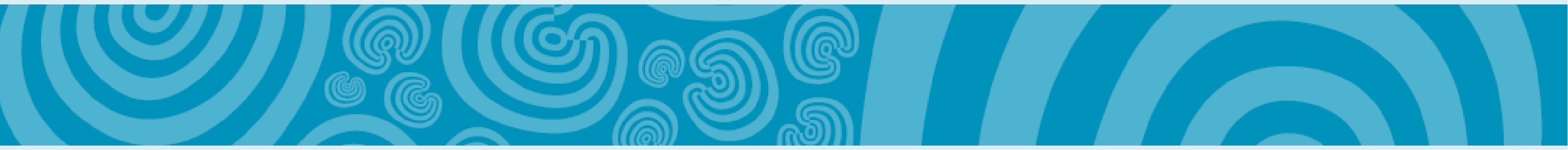
Figure A2. Distribution of (a) winter climatic conditions, (b) population density and growth rates and (c) proportion of individuals in each reproductive investment strategy (blue represent DSDS and red represents FS) from start $(t = t_0)$ to the end of the simulation $(t = T)$. (d) Average female body mass for the first (t_0 to $t = 20$; blue) and last 20 years ($t = T - 20$ to $t = T$; red). Grey lines represent the average body mass for each strategy present within the first 20 years. (e) Shows the same as figure d except that this shows the same trend for offspring body mass. Numbers for the red labelled line indicated the proportion of females breeding successfully within each year.

A3: TERMINAL TIME AND A TEST OF THE DESIGN: ENVIRONMENTAL INPUT VALUES

The relationship between terminal time (T) and estimated distributional parameters of the two input variables; i.e. the theoretic average (x) and the theoretic standard deviation (y) for environmental conditions (Table A3.1). These results are based on data from the 60 years preceding T.

Table A3.1. Estimates from linear models (*LM*) relating final time (a), environmental average and (b) as well as (c) environmental stochasticity to the theoretic input values for the environment [theoretical averages (x) and theoretical standard deviations (y)]. The intercept shows average body mass for; (1) the level 'Control' for the factor environmental conditions. The other coefficients are the estimated difference between the intercept, or the main effect for y, for each level of the other included factors.

Parameter	Value (95% CI)	*t*-value	*P*-value
(a) *Terminal time* (T)			
Intercept	1120.32 (873.72, 1366.92)	9.03	<0.01
Average environment (x) [Improved]	-539.74 (-886.38, -193.09)	-3.10	<0.01
Average environment (x) [Reduced]	-902.75 (-1261.39, -544.12)	-5.01	<0.01
Standard deviation for environment (y)	-473.13 (-754.63, -191.63)	-3.34	<0.01
x [Improved] $\times y$	421.89 (31.79, 811.99)	2.15	0.03
x [Reduced] $\times y$	926.92 (487.03, 1366.81)	4.19	<0.01
$R^2 = 0.25$, $F_{5,84} = 5.49$, $P < 0.01$			
(b) *Environmental average* ($\bar{E}$)			
Intercept	-0.01 (-0.04, 0.04)	-0.07	0.93
x [Improved]	-0.14 (-0.20, -0.08)	-4.68	<0.01
x [Reduced]	0.11 (0.05, 0.17)	3.57	<0.01
$R^2 = 0.44$, $F_{5,87} = 33.29$, $P < 0.01$			
(c) *Environmental stochasticity* [st. dev.(E)]			
Intercept	-0.01 (-0.03, 0.03)	-0.09	0.93
y	1.01 (0.97, 1.04)	58.42	<0.01
$R^2 = 0.98$, $F_{5,87} = 3413.00$, $P < 0.01$			



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