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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 ($j \le 1$) 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:

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

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

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):

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

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

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 $[\mathrm{st.dev.}(E)]$ 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 $\mathrm{s}[\mathrm{st.dev.}(E),\ \overline{E}]$ = 9.433 ($P < 0.001$), and (ii) $\mathrm{s}(\overline{D})$ = 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 $\mathrm{s}[\mathrm{st.dev.}(E),\ \overline{E}]$ = 6.115 ($P < 0.001$), and (ii) $\mathrm{s}(\overline{D})$ = 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 $\mathrm{s}[\mathrm{st.dev.}(E),\ \overline{E}]$ = 6.927 ($P < 0.001$), and (ii) $\mathrm{s}(\overline{D})$ = 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 $[\mathrm{st.dev.}(E)]$ 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 $\mathrm{s}[\mathrm{st.dev.}(E),\ \overline{E}]$ = 6.836 ($P = 0.040$), and (ii) $\mathrm{s}(\overline{D})$ = 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 $\mathrm{s}[\mathrm{st.dev.}(E),\ \overline{E}]$ = 2.000 ($P = 0.109$), and (ii) $\mathrm{s}(\overline{D})$ = 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 $\mathrm{s}[\mathrm{st.dev.}(E),\ \overline{E}]$ = 4.227 ($P = 0.033$), and (ii) $\mathrm{s}(\overline{D})$ = 2.251 ($P = 0.011$). Deviance explained (D) by the model are given as percentages on each plot.

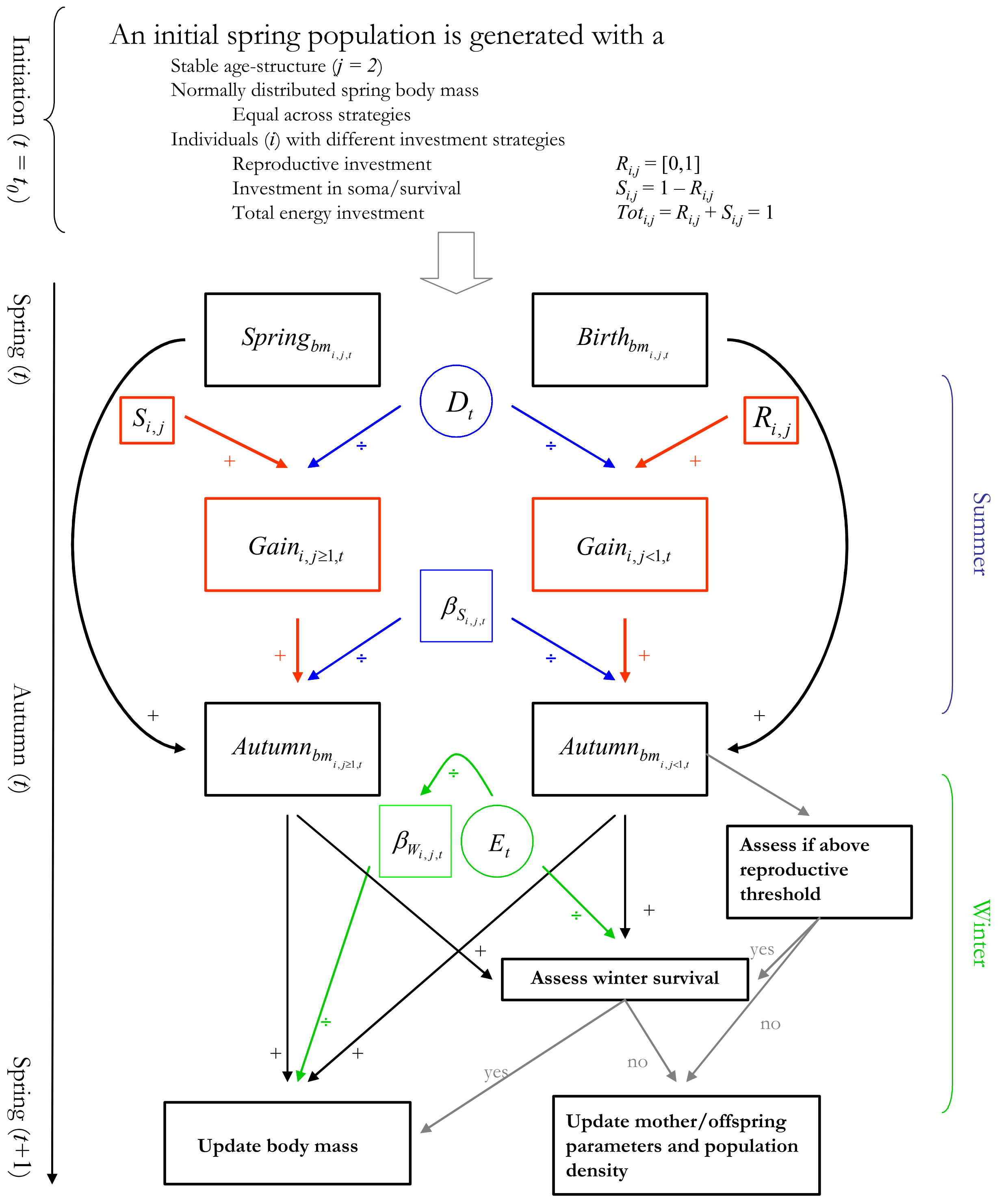

Initiation ($t = t_0$)
An initial spring population is generated with a
Stable age-structure ($j = 2$)
Normally distributed spring body mass
Equal across strategies
Individuals (i) with different investment strategies
Reproductive investment
Investment in soma/survival
Total energy investment
$R_{i,j} = [0,1]$
$S_{i,j} = 1 - R_{i,j}$
$Tot_{i,j} = R_{i,j} + S_{i,j} = 1$
Spring (t)
$Spring_{bm_{i,j,t}}$
$Birth_{bm_{i,j,t}}$
D_t
$S_{i,j}$
$R_{i,j}$
+
÷
$Gain_{i,j\geq1,t}$
$Gain_{i,j<1,t}$
$\beta_{S_{i,j,t}}$
Summer
Autumn (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
Winter
Spring (t+1)
Update body mass
Update mother/offspring parameters and population density

Figure 1.

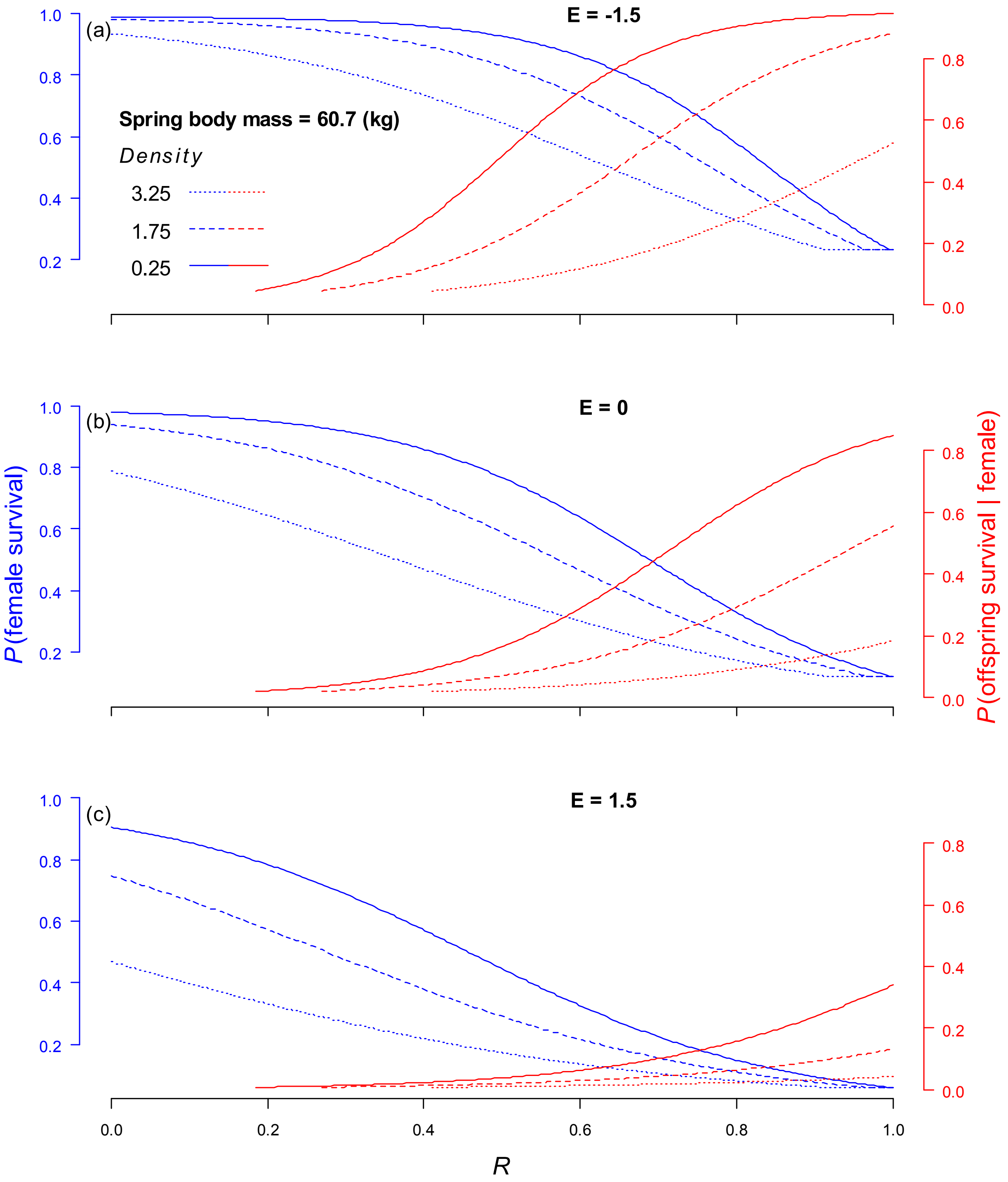

(a)
E = -1.5
Spring body mass = 60.7 (kg)
Density
3.25
1.75
0.25
(b)
E = 0
(c)
E = 1.5
1.0
0.8
0.6
0.4
0.2
0.0
P(female survival)
P(offspring survival | female)
R

Figure 2.

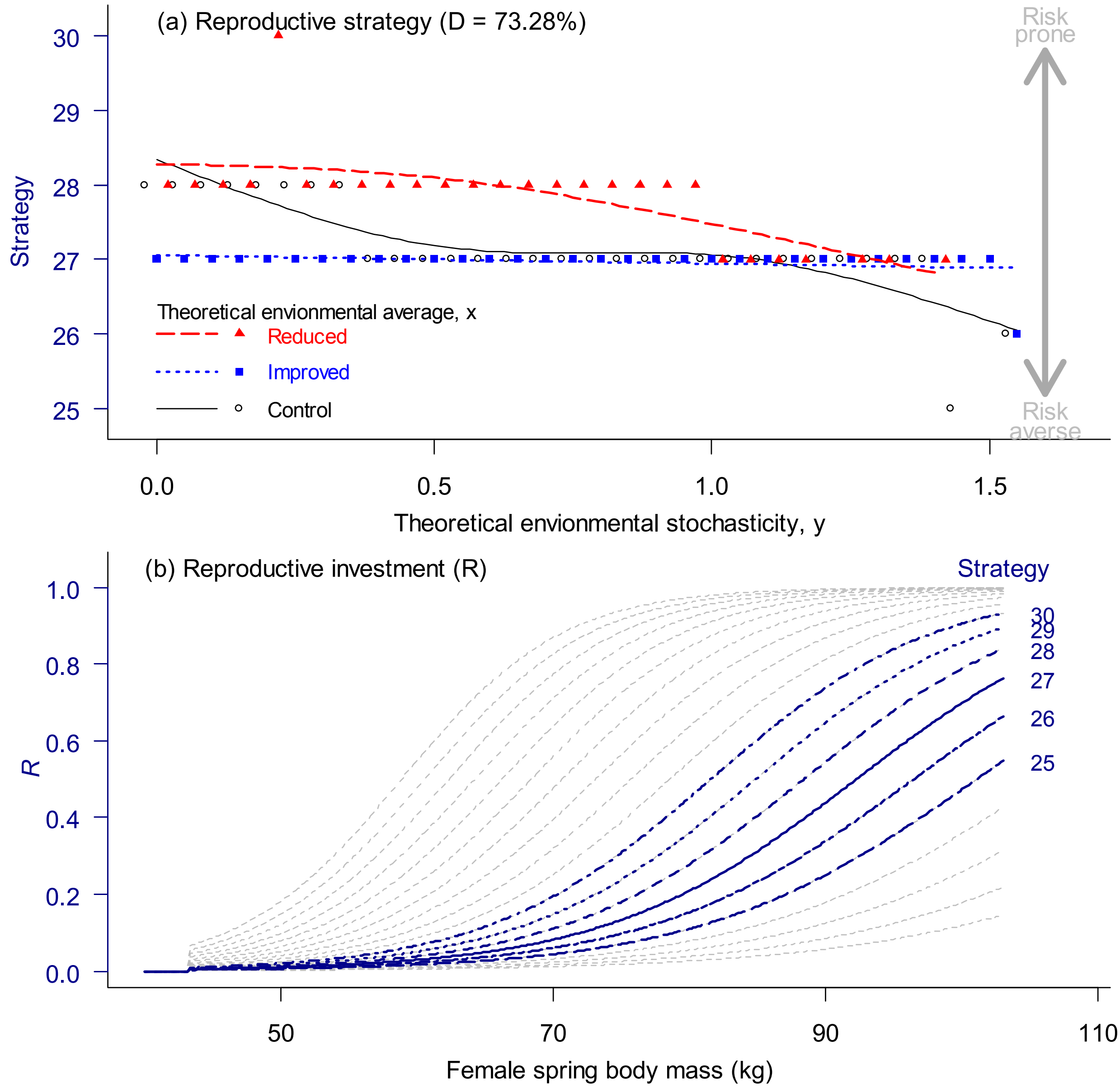

(a) Reproductive strategy (D = 73.28%)
Strategy
30
29
28
27
26
25
Risk prone
Risk averse
Theoretical envionmental average, x
Reduced
Improved
Control
0.0
0.5
1.0
1.5
Theoretical envionmental stochasticity, y
(b) Reproductive investment (R)
Strategy
30
29
28
27
26
25
R
1.0
0.8
0.6
0.4
0.2
0.0
50
70
90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

Figure 3.

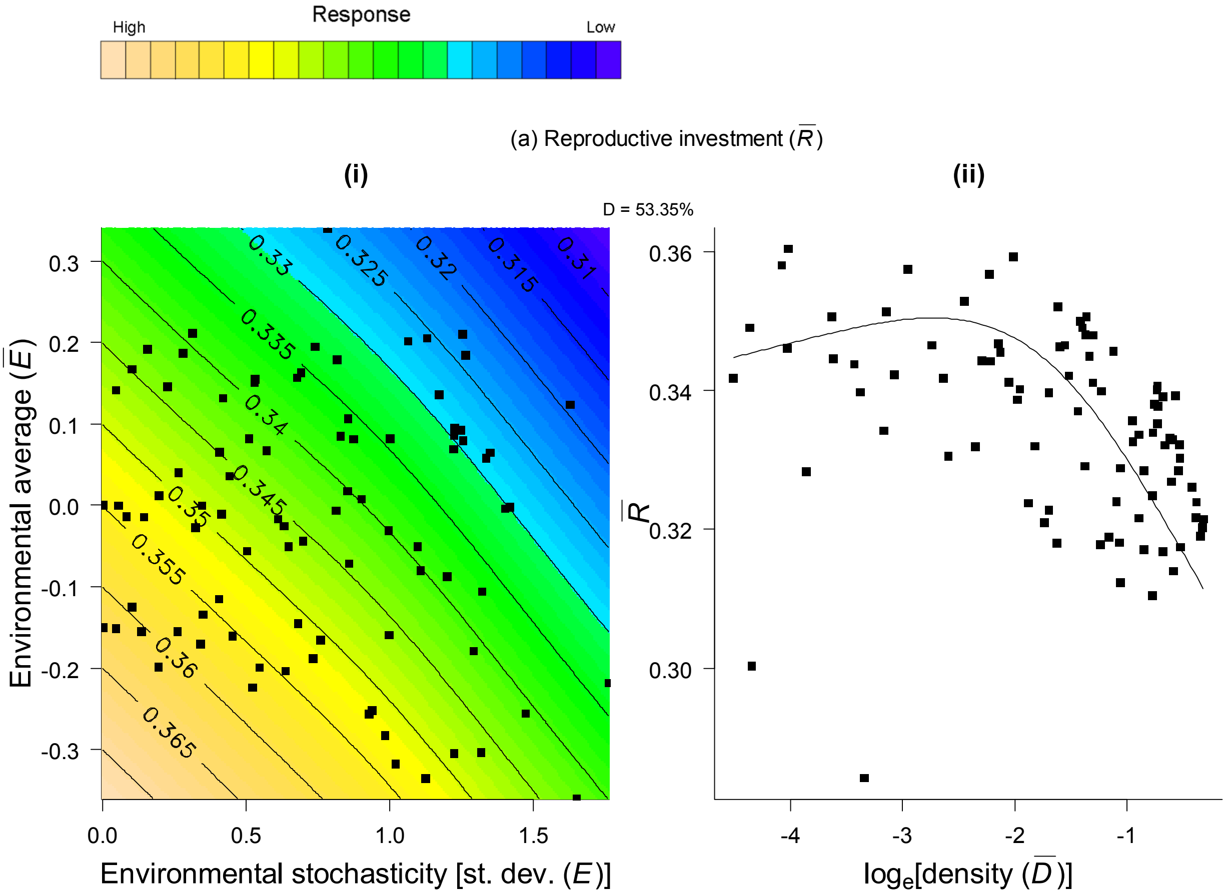

Response
High
Low
(a) Reproductive investment ($\bar{R}$)
(i)
(ii)
D = 53.35%
0.33
0.325
0.32
0.315
0.31
0.335
0.34
0.345
0.35
0.355
0.36
0.365
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
Environmental average ($\bar{E}$)
0.0
0.5
1.0
1.5
Environmental stochasticity [st. dev. (E)]
0.36
0.34
0.32
0.30
$\bar{R}$
-4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

Figure 4.

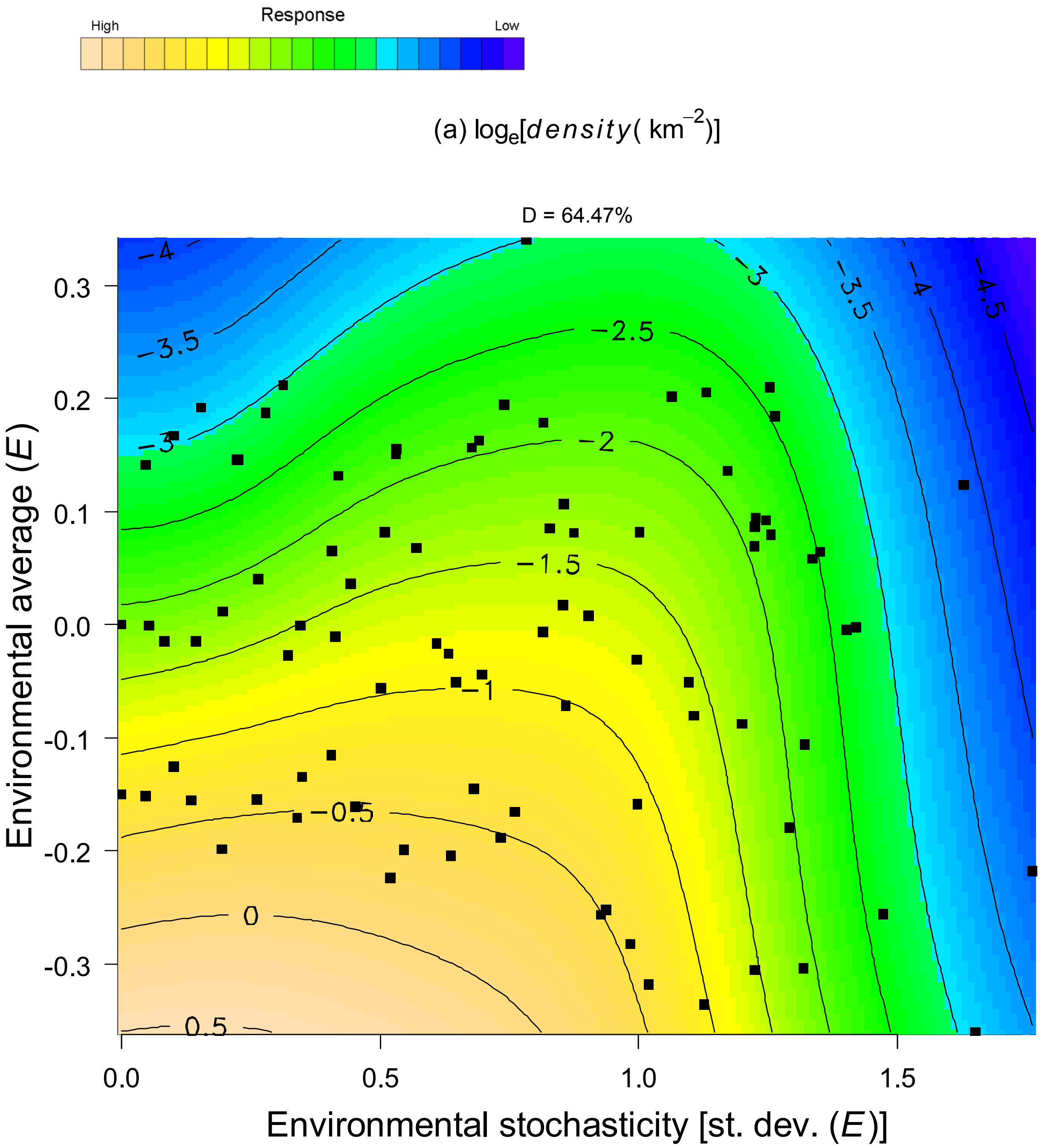
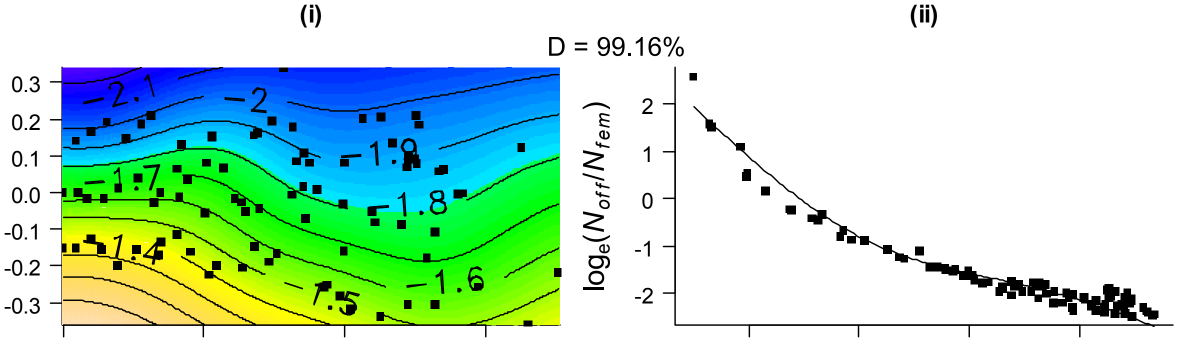
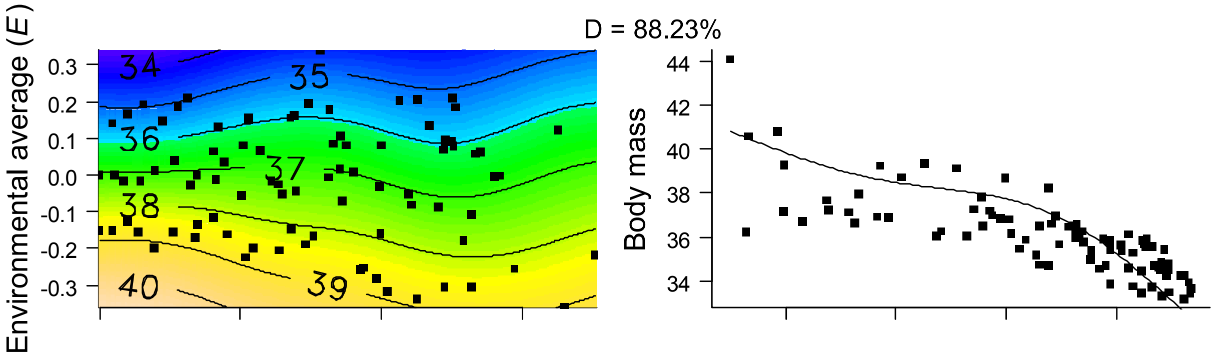

Response
High
Low
(a) log_e[density(km^-2)]
D = 64.47%
Environmental average (Ē)
Environmental stochasticity [st. dev. (E)]
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
0.0
0.5
1.0
1.5
−4
−3.5
−3
−2.5
−2
−1.5
−1
−0.5
0
0.5
−3
−3.5
−4
−4.5

Figure 5.

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



(b) Offspring autumn body mass (kg)



(c) Offspring spring body mass (kg)

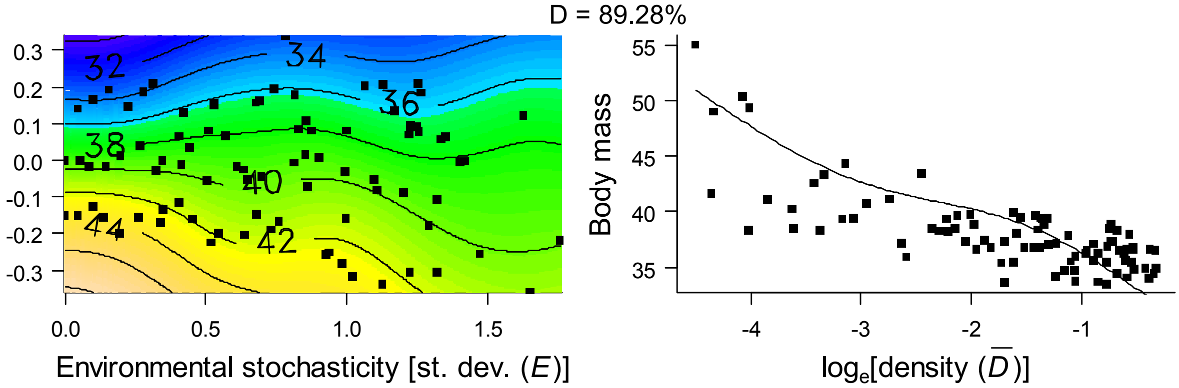


Figure 6.

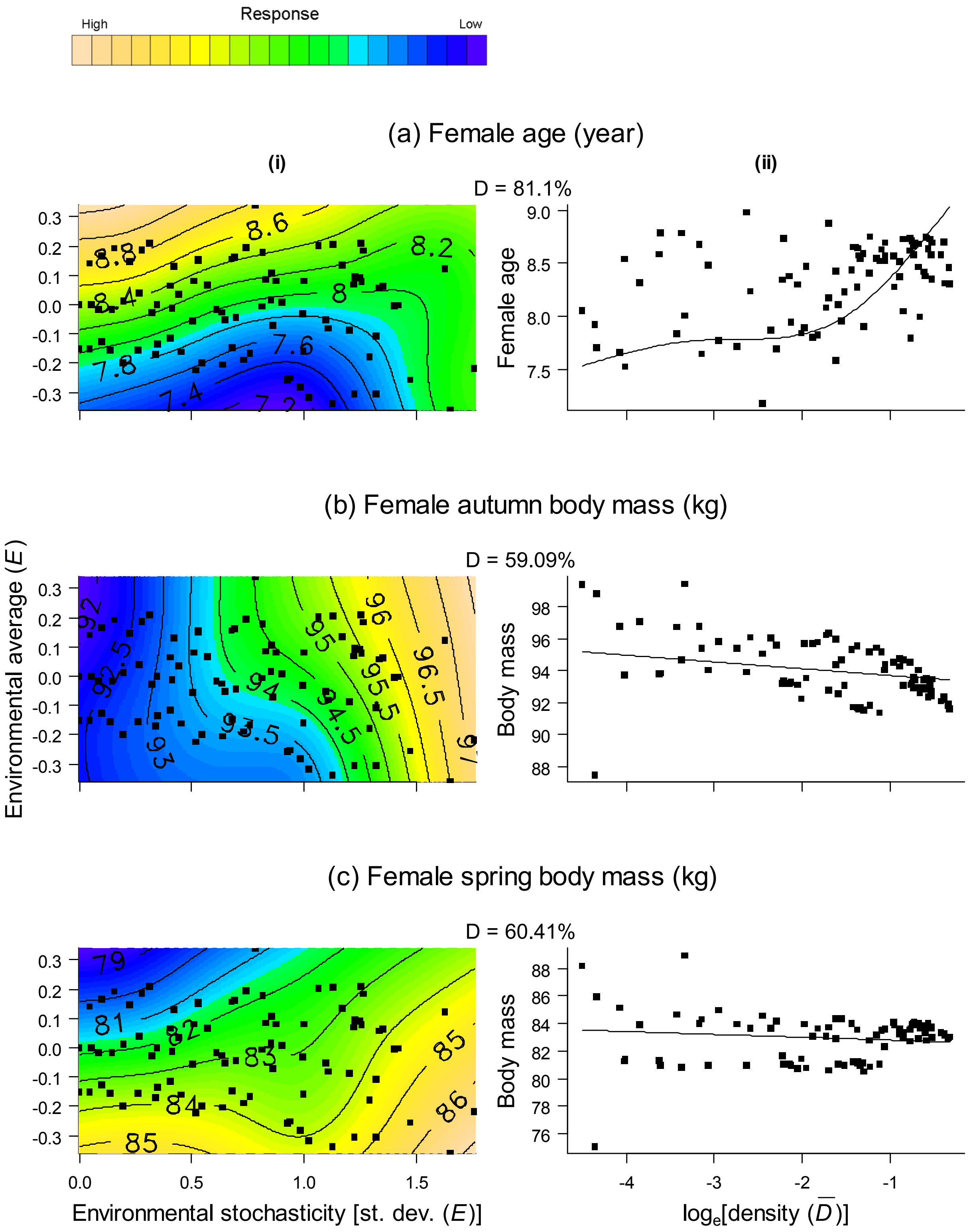

Response
High
Low
(a) Female age (year)
(i)
(ii)
D = 81.1%
8.8
8.6
8.4
8.2
8
7.8
7.6
7.4
7.2
Female age
9.0
8.5
8.0
7.5
(b) Female autumn body mass (kg)
D = 59.09%
92
92.5
93
93.5
94
94.5
95
95.5
96
96.5
97
Environmental average ($\bar{E}$)
Body mass
98
96
94
92
90
88
(c) Female spring body mass (kg)
D = 60.41%
79
81
82
83
84
85
86
Body mass
88
86
84
82
80
78
76
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
0.0
0.5
1.0
1.5
Environmental stochasticity [st. dev. (E)]
-4
-3
-2
-1
log$_e$[density ($\bar{D}$)]

Figure 7.

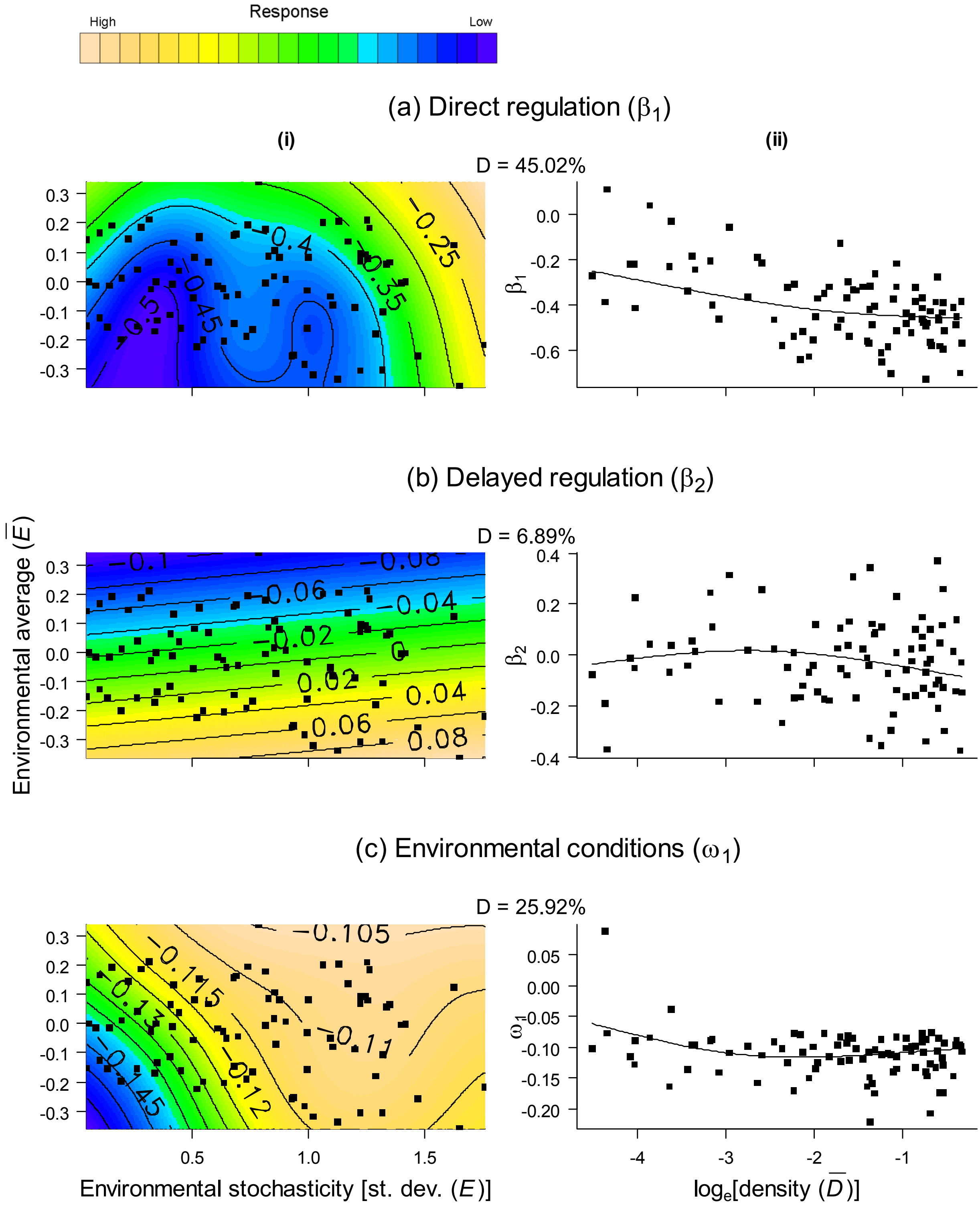

Response
High
Low
(a) Direct regulation (β1)
(i)
(ii)
D = 45.02%
-0.5
-0.45
-0.4
-0.35
-0.25
β1
(b) Delayed regulation (β2)
D = 6.89%
-0.1
-0.08
-0.06
-0.04
-0.02
0
0.02
0.04
0.06
0.08
β2
(c) Environmental conditions (ω1)
D = 25.92%
-0.105
-0.115
-0.13
-0.145
-0.12
-0.11
ω1
Environmental average (Ē)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

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}):

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

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

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

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

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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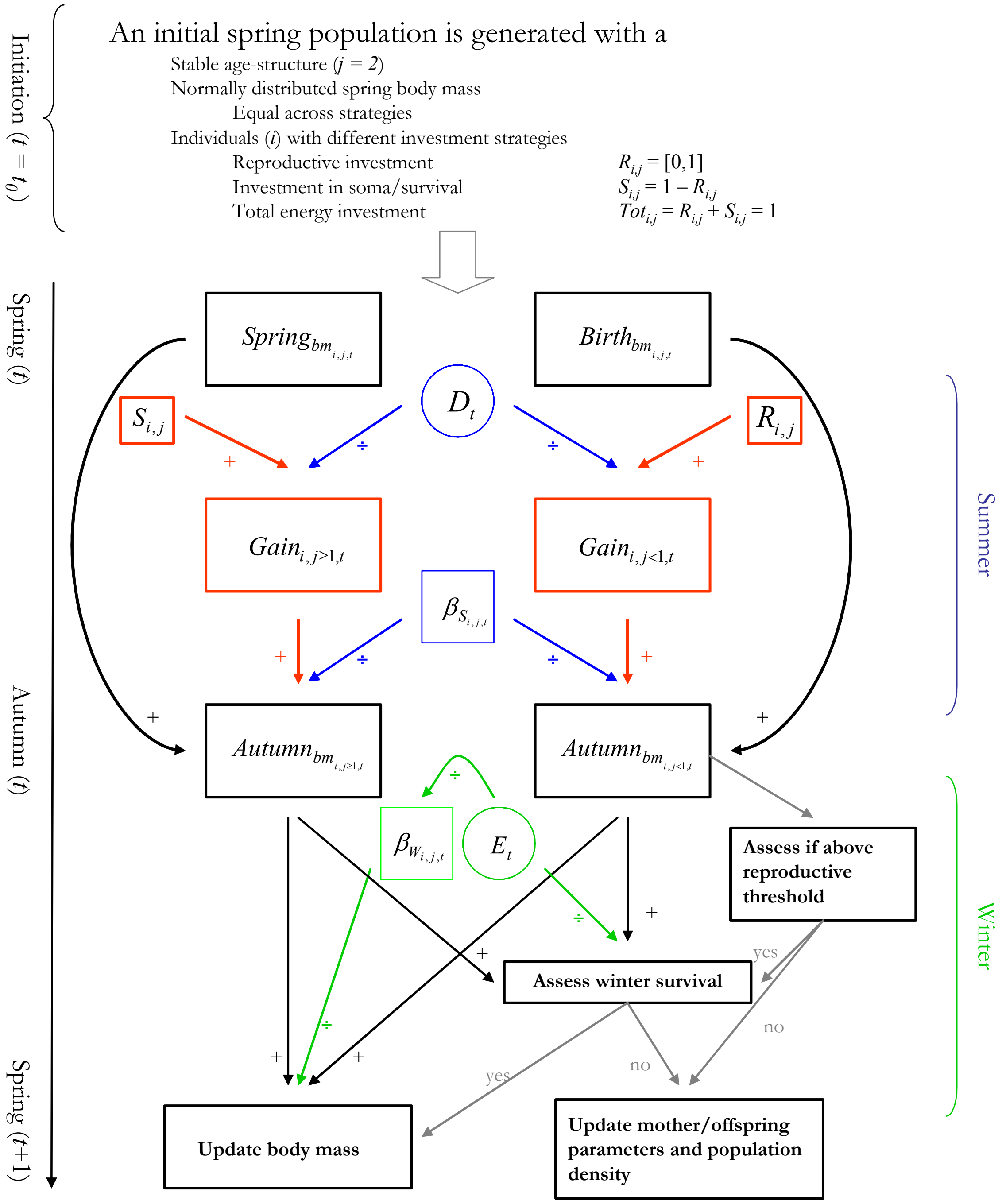


An initial spring population is generated with a
Stable age-structure ($j = 2$)
Normally distributed spring body mass
Equal across strategies
Individuals (i) with different investment strategies
Reproductive investment $R_{i,j} = [0,1]$
Investment in soma/survival $S_{i,j} = 1 - R_{i,j}$
Total energy investment $Tot_{i,j} = R_{i,j} + S_{i,j} = 1$

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).

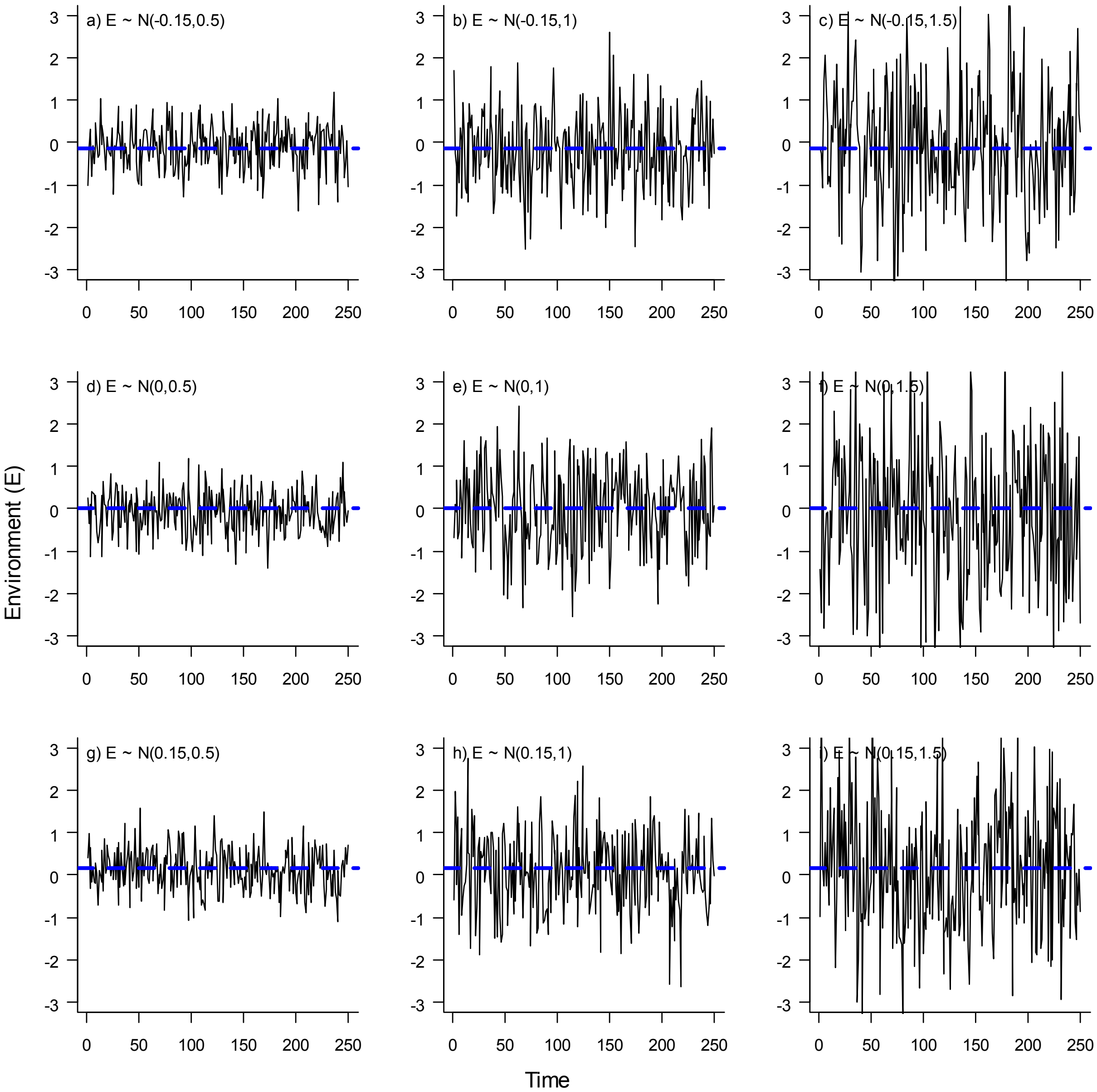


Figure A1.2. Simulated normally distributed environmental conditions (E). Realisation e) [E = ~N(0,1)] mimic the normalized principal components (PC) of climate indexes like AO and *North Atlantic Oscillation Index* (NAO).

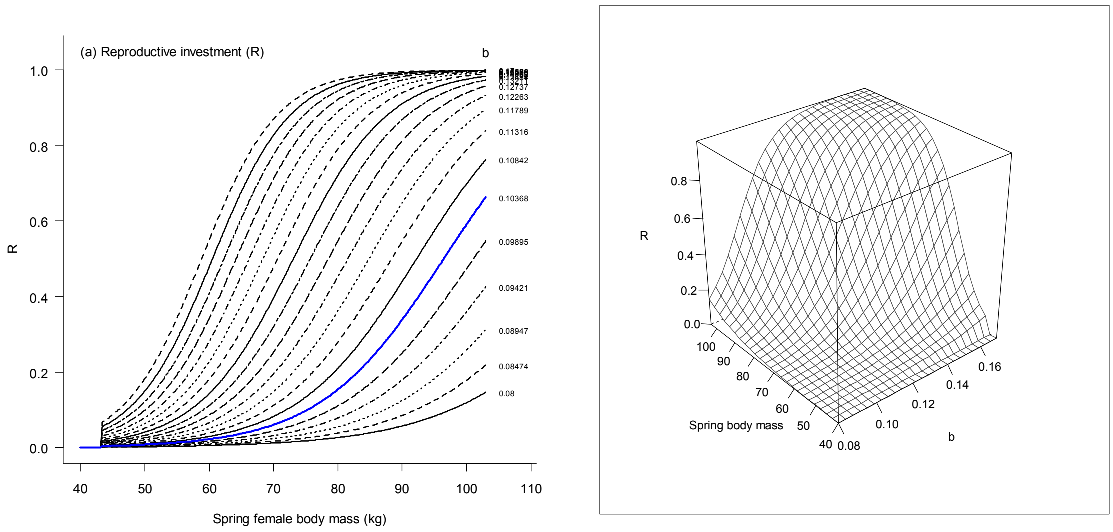
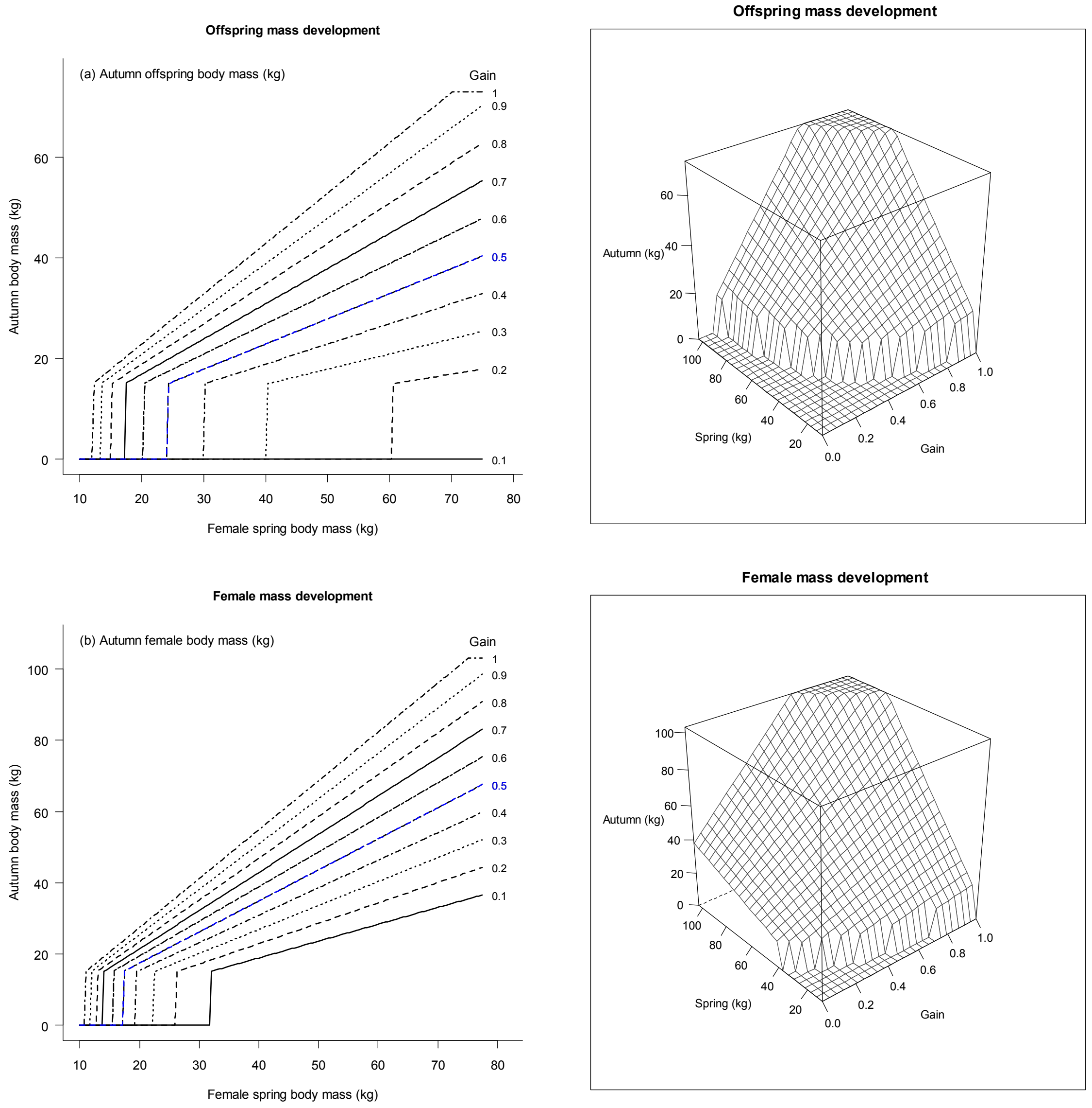


Figure A1.4. Female reproductive allocation (R) as a function of spring body mass for *dynamic state dependent reproductive strategies*. The relationship between reproductive allocation and spring body mass (b_R in eqn A2) is different for different strategies. Individuals will not invest in reproduction 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.



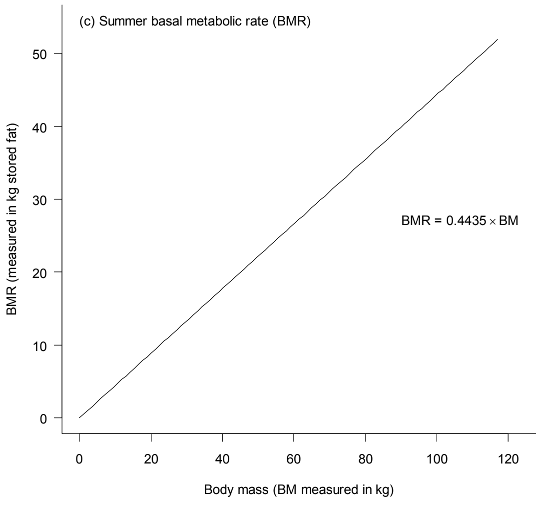


Figure A1.5. Summer mass development for offspring (a) and female (b) as a function of gain (each line representing different values for gain). Gain can be interpreted as allocation in either reproduction (*R*; offspring) or survival (*S*; female) within the limits set by density and a summer metabolic 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.

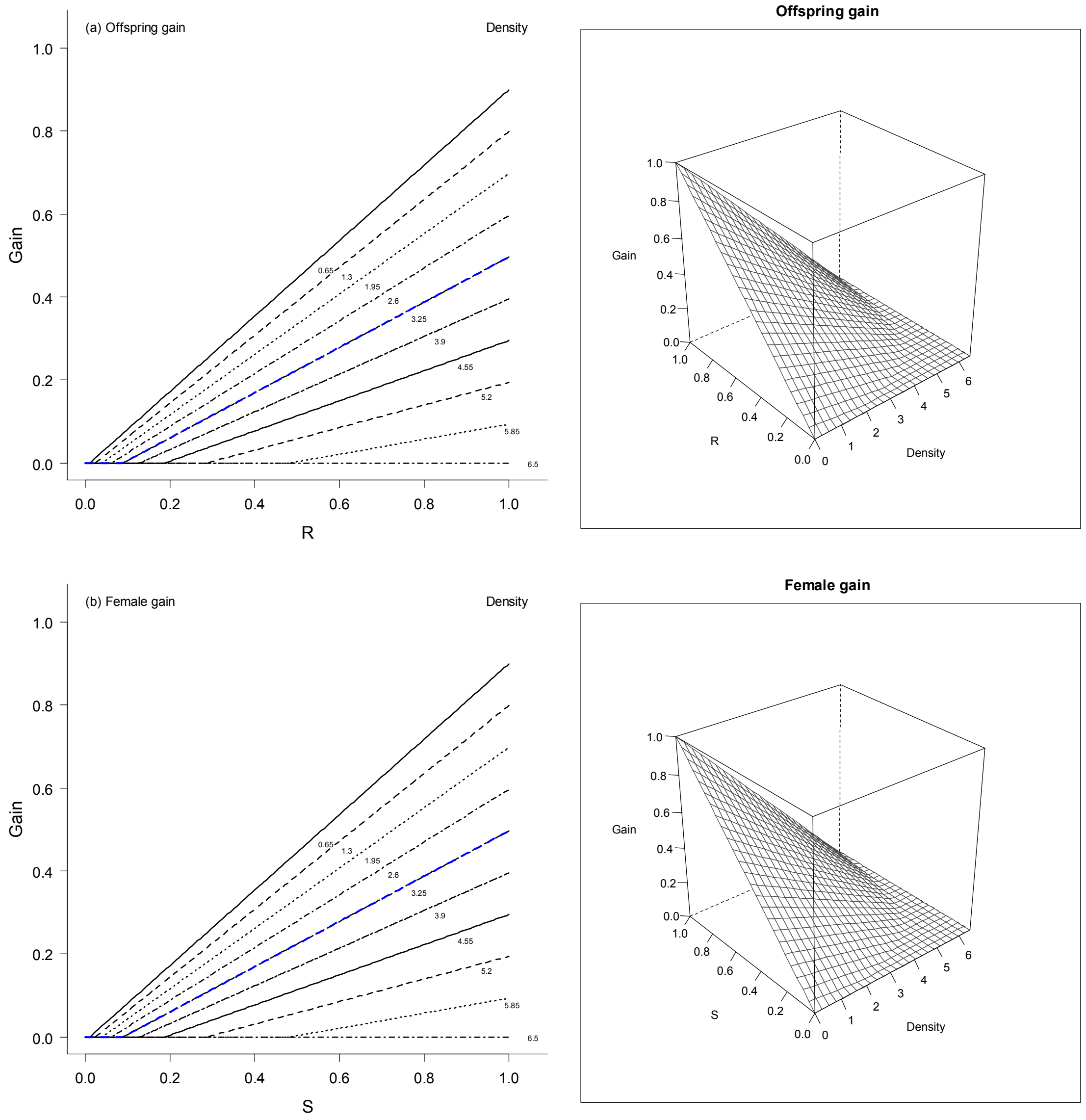


Figure A1.6. Gain in body mass for offspring (a) and female (b) as a function of allocation in either reproduction (*R*; offspring) or survival (*S*; female) and density (different lines). The reward of a fixed allocation will be limited by density; a fixed allocation will lead to lower gain at higher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

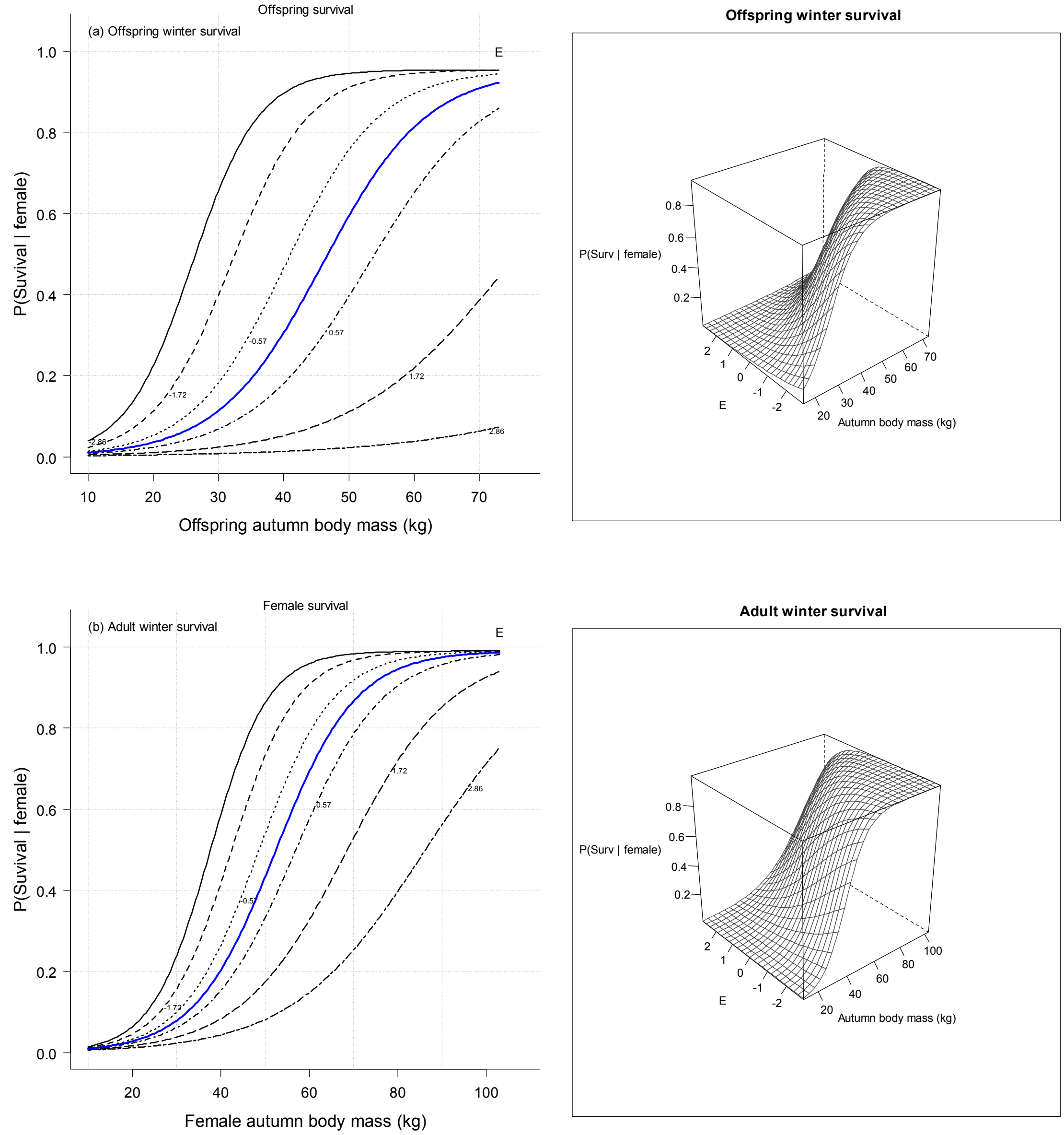


Figure A1.7. Over-winter survival as a function of autumn body mass and environmental conditions for juveniles (a) and adult females (b). Note that the scales on the axes are different for adult females and offspring.

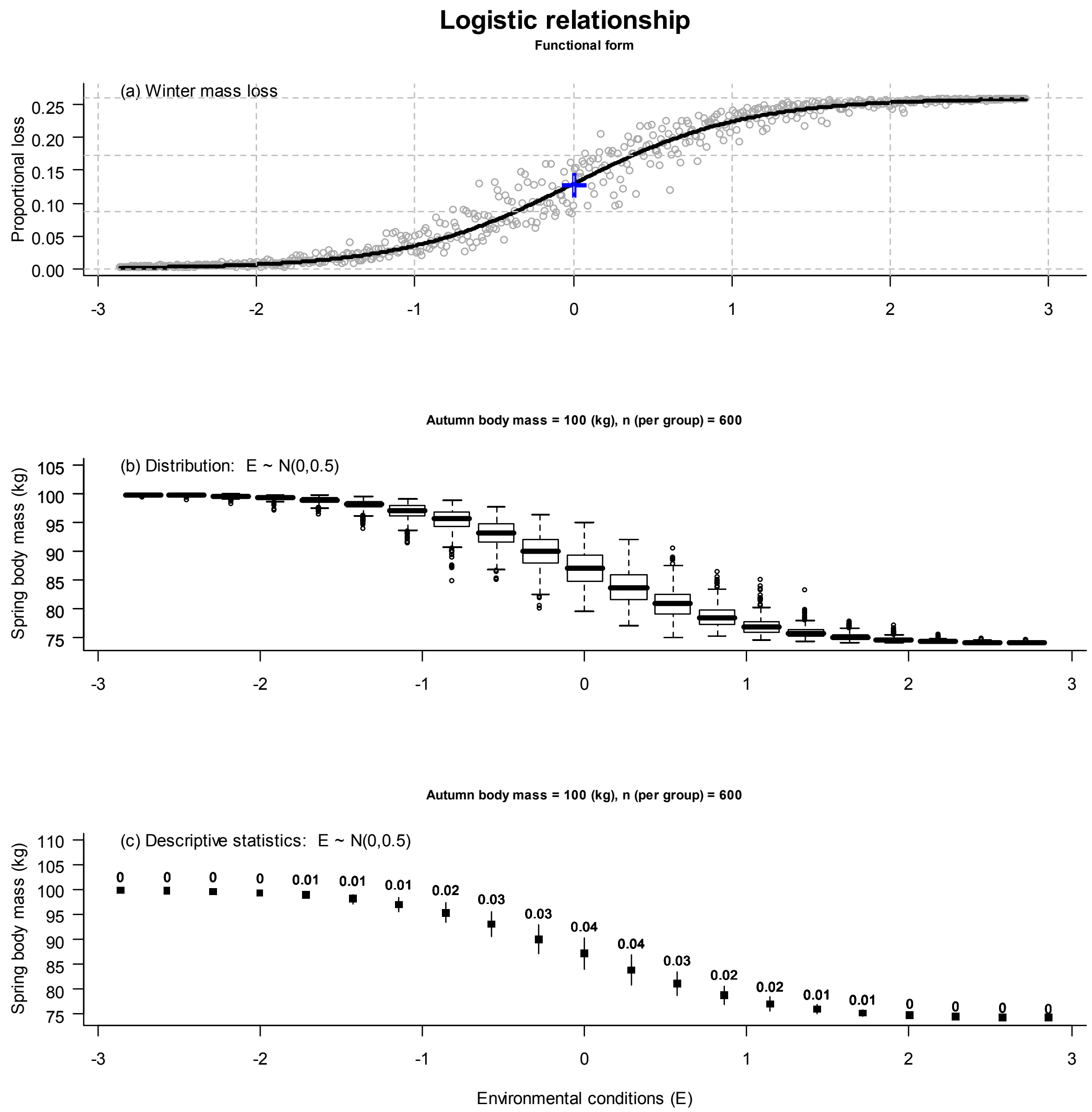


Figure A1.8. (a) Proportional mean loss of (autumn) body mass as a function of environmental conditions (line). Points are generated from the same model except that an error term is now also included. Mean mass loss for $E = 0$ (marked with a cross) are taken from the literature (Table A1.2d). (b) A 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).

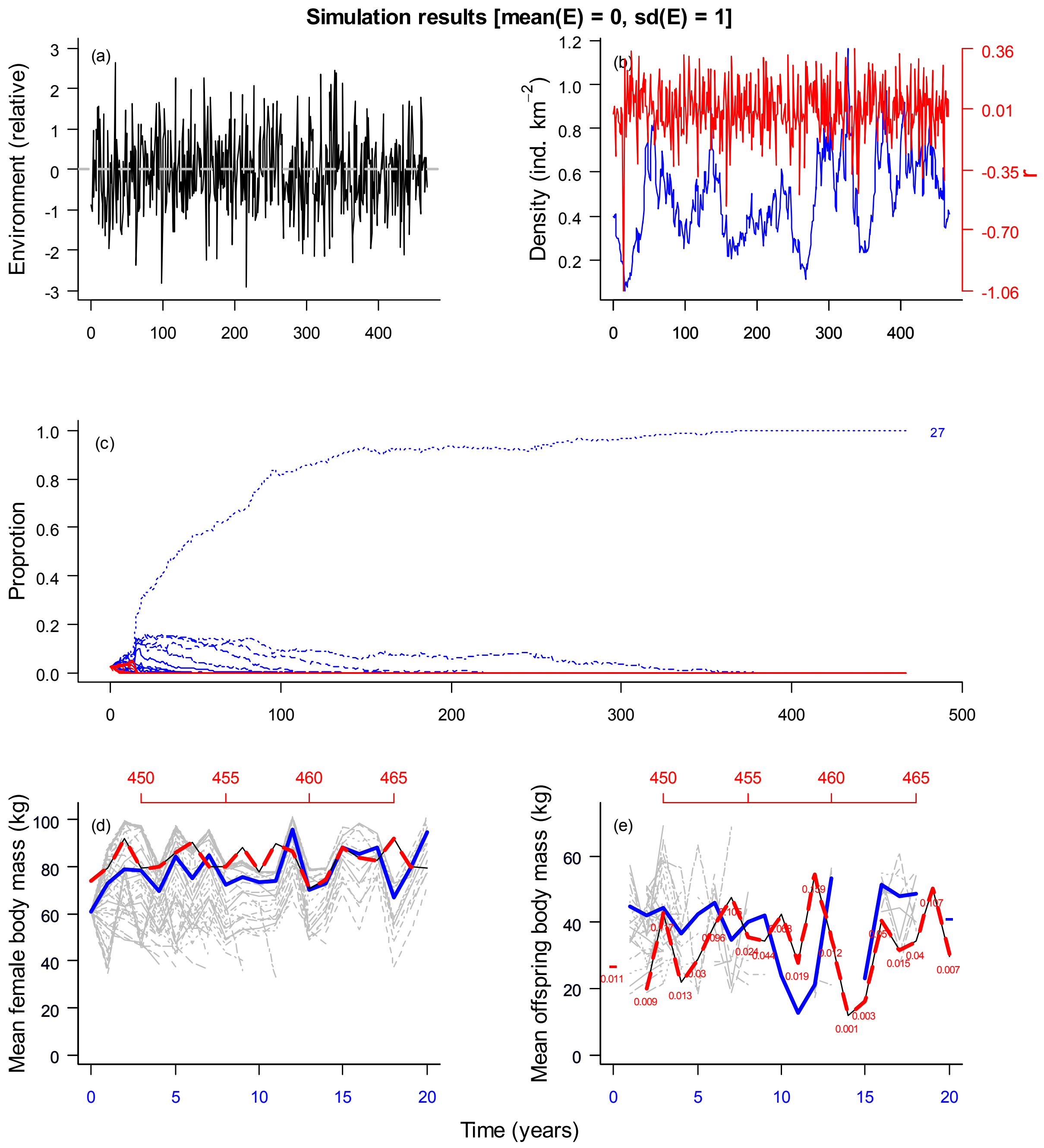

Figure A2. Distribution of (a) winter climatic conditions, (b) population density and growth rates and (c) proportion of individuals in each reproductive investment strategy (blue represent DSDS and red represents FS) from start ($t = t_0$) to the end of the simulation ($t = T$). (d) Average female body 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* ($\overline{E}$)			
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* [$\text{st. dev.}(E)$]			
Intercept	-0.01 (-0.03, 0.03)	-0.09	0.93
y	1.01 (0.97, 1.04)	58.42	<0.01
$R^2 = 0.98$, $F_{5,87} = 3413.00$, $P < 0.01$			