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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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Key words: climate change; dynamic optimization; environmental stochasticity; individual-based model (IBM); phenotypical plasticity; *Rangifer tarandus*.

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Abstract: Empirical work suggest that long-lived organisms have adopted risk sensitive reproductive strategies where individuals trade the amount of resources spent on reproduction vs. survival according to expected future environmental conditions. Earlier studies also suggest that climate affects population dynamics indirectly through long-term changes in individual life histories and through directly limitations acting on population vital rates. We found support for this as: (1) Dynamic strategies were needed to buffer climate effects. (2) Females in poor and unpredictable climatic regimes adopted strategies involving low reproductive allocations. These strategies mainly resulted in high expected female age and adult body mass. (3) Strong negative density dependence on offspring body mass and survival, along with a generally low population density in poor and unpredictable environments, resulted in no clear negative climatic effects on empirically relevant measures of reproductive allocation. (4) Time series analyses of populations growth rates revealed that populations inhabiting benign environments were most sensitive to climatic perturbations as high density prohibited an effective buffering of adverse climatic effects. Similarly, populations inhabiting harsh environments were least sensitive to climatic perturbations. Regularly occurring harsh winters 'harvested' these populations releasing them from negative density dependence, which resulted in high rewards for a given resource allocation.

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; Williams 1966). 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 for long-lived organisms who are known for favoring own survival over reproduction [birds (e.g. Lindén and Møller 1989; Ricklefs 2000); fish (e.g. Winemiller and Rose 1992); mammals (e.g. Brown and Sibly 2006; Ellison 2003; Gaillard et al. 2000; Gaillard and Yoccoz 2003); reptiles (Shine 2005)].

Many organisms inhabit highly unpredictable environments caused by temporal variation in abiotic weather conditions and/or biotic factors such as population density (e.g. Clutton-Brock et al. 1996; Coulson et al. 2001; McNamara et al. 1995; 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. Bårdsen et al. 2008; McNamara et al. 1995). If, for example, the winter season represents a bottleneck for survival and winter weather conditions are highly variable, individuals should ensure that they retain sufficient reserves during summer in order to survive the coming winter (e.g. Bårdsen et al. 2008; Clutton-Brock et al. 1997; Clutton-Brock et al. 1996; Erikstad et al. 1998; Festa-Bianchet et al. 1998; Skogland 1985). Formally, this means that strategic decisions, e.g. whether to reproduce or not or how many resources to allocate to an offspring, have 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 (Bårdsen 2009; Bårdsen et al. 2008; Kacelnik and Bateson 1996; Stephens

and Krebs 1986 and references therein provide a discussion of the concept of risk sensitivity).

For many organisms in northern and clearly seasonal environments, autumn body mass functions as an insurance against stochastic winter climatic severity (e.g. Bårdsen et al. 2008; Clutton-Brock et al. 1996; Fauchald et al. 2004; Reimers 1972; Skogland 1985). Thus, 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 (sensu Bårdsen et al. 2008). Similarly, a 'risk-averse' reproductive strategy results in stable winter survival, but lower potential reproductive reward.

The quantity and quality of studies using climate models, especially 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 average, 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; Sun et al. 2007; Tebaldi et al. 2006). How organisms will respond is unclear empirical results are based on climatic effects given the current distribution of climate variables, but some predictions have been made. For example, on a population-level, predicted consequences of future climate change invoke more frequent population collapses (e.g. Post 2005; Tyler et al. 2008). Such predictions are problematic as they generally assume a non-plastic life history in the sense that organisms cannot adapt to new climatic regimes (see e.g. Benton et al. 2006; Bårdsen et al. 2008 for discussions). 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 reduce their reproductive allocation in order to buffer adverse climatic effects (Bårdsen et al. 2008; Tveraa et al. 2007). Within the concept of risk sensitivity it is the variance in environmental variables that is

important (sensu Bårdsen 2009). 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 (e.g. Kacelnik and Bateson 1996; Stephens and Krebs 1986).

The present model was built as a tool for assessing how different environments can affect optimal reproductive strategies in long-lived mammals, and how interactions between these optimal strategies and environmental conditions can shape population dynamics. The model is parameterized for reindeer (or caribou; *Rangifer tarandus*), which represents a suitable model organism for these questions (see Appendix A1). Our model is general in design and structure, but due to the necessity of incorporating known information of mechanisms and processes affecting individual life histories this model was developed for a specific species (a modeling philosophy similar to e.g. De Roos et al. 2009). The present study use a state-dependent individual-based model (IBM) to investigate how females should optimize their reproductive allocation in a stochastic environment with density dependent processes. The specific aim for this study was to answer the following questions: (1) How the average and variance in environmental conditions affected the optimal reproductive allocation; and (2) how different reproductive allocation strategies affected individual life histories and population dynamics for a given environment?

THE INDIVIDUAL-BASED MODEL (IBM)

MODEL OVERVIEW

We model the female segment of a population over several years; time (t) is discrete (one step equals one year), where each step is divided in two distinct seasons: summer, with density dependent competition over a shared food resource; and winter, where stochastic environmental conditions affect survival and body mass losses. 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 large positive values represents harsh conditions, similar to climatic indexes like AO and NAO (see e.g. Hurrell et al. 2003; Ottersen et al. 2001; Stenseth et al. 2002)]. A key point in this model is that individuals do not know the state of the coming winter conditions during summer 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. As our research questions cannot be easily answered within an analytical framework we chose to apply an individual-based simulation model where we take advantage of available information on known processes and mechanisms affecting individuals (sensu Benton et al. 2006). A detailed model description, which follows the ‘overview, design concepts and details’ (ODD) protocol developed by Grimm et al. (2006) and Grimm & Railsback (2005) is found in Appendix A1. Formalities, like model equations, rules and tables presenting the model parameters, are presented in the ODD protocol. 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

An allocation strategy will at any point in time be a scalar representing an individual’s allocation of resources (eqn. A1-5) to reproduction (R) vs. somatic growth (S), which is a proxy for survival, during summer. The reward for a given allocation will be limited by the population’s summer density (D): an individual with a given allocation will collect a higher average reward during low- vs. high-density. The reward for allocating resources in R and S , within the limitations set by D , was implemented using two gain functions (eqn. A12-13): (1) one function for females where S was a predictor, and (2) one function for offspring where R was a

predictor. In sum, individual autumn body mass depended on (Figure 1): (1) spring body mass (females) or birth body mass (offspring), (2) the gain function that represents the increase in body mass per kg spring body mass, and (3) a basal summer metabolic rate. The implemented relationship was generated from knowledge about the physiology of *Rangifer* using a set of equations that were modified from Proaktor et al. (2007) (Figure A1.5).

Winter

Autumn body mass is a predictor of three processes during autumn and winter: (1) If autumn body mass is below a threshold the individual is assumed dead during summer and is removed from further analyses (eqn. A14). (2) However, if autumn body mass is above this threshold, it will act as a state variable as autumn body mass together with winter environmental conditions predict individual winter survival probability (eqn. A16-17). (3) Moreover, if an individual survives the winter, body mass in the coming spring will depend on its previous autumn body mass loss of body mass during winter (eqn. A18-19). 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; (2) spring body mass; (3) age; and (4) population density (see A1: 'Process overview and scheduling' for details).

MODELLING REPRODUCTIVE ALLOCATION 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 follows. An individual will in a given time (t) allocate a proportion of its available resources in reproduction (R). Juveniles do not allocate resources to reproduction

($R = 0$), but to somatic growth (details are provided in A1: ‘Reproductive allocation strategies defined on a continuous scale’). As total energy allocation sums to one ($S = 1 - R$), individuals either allocate resources to reproduction or survival (eqns. A1-5). The model contains no true senescence (as e.g. the IBM by Proaktor et al. 2007), but age as an individual-level state ensures that juveniles do not reproduce (eqn. A1) and that females do not become unrealistically old (eqn. A16). The cost and benefit, assuming a constant female body mass, for different R as a function of density and winter weather is shown in Figure 2. Two types of strategies were tested against each other in the simulations.

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. $R_{i,j} = [0.0, 0.4, 0.4, 0.4, \dots]$, which means that this individual (i) will allocate nothing in reproduction its first year of life ($j = 1$), and then 0.4 for the rest of the time ($j > 1$). As body mass is an important predictor for survival and reproductive output for female *Rangifer* (Bårdsen et al. 2008; Fauchald et al. 2004; Kojola 1993; Kojola 1997; Tveraa et al. 2003) it is natural that spring body mass acts as a state variable in the model. Thus, in a *dynamic state dependent reproductive strategy* (DSRS) an individual (i) with age (j) will have a reproductive allocation vector ($R_{i,j}$) being determined and updated each year according to (see A1 for details):

$$R_{i,j} = \frac{1}{1 + e^{-[a_R + (b_R \times \text{Spring}_{bm,i,j})]}} \quad \text{if } j > 1 \text{ \& if } \text{Spring}_{bm,i,j} > \tau_{\text{spring}} \quad \text{eqn. 1}$$

$$R_{i,j} = 0. \quad \text{if } j \leq 1 \text{ or if } \text{Spring}_{bm,i,j} \leq \tau_{\text{spring}} \quad \text{eqn. 2}$$

To allocate in reproduction, an adult individual (i) must be older than the juvenile stage ($j > 1$) and must have a spring body mass ($\text{Spring}_{bm,i,j}$) above a lower threshold value (τ_{spring}). The intercept (a_R) in the equation is constant among strategies so that a DSRS can be defined by the parameter b_R (A1). A lower body mass threshold for reproduction has firm empirical support: red deer *Cervus elaphus* (Albon et al. 1983), moose *Alces alces* (Sæther et al. 1996; Sæther and

Haagenrud 1983), bighorn sheep *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 the reproductive allocation vector for an DSDS may end up looking like e.g.

[0.0, 0.4, 0.7, 0.0, ...].

DESIGN AND DATA ANALYSIS

We run the model under normally distributed environmental conditions [$E \approx N(x, y)$], generated using the `rnorm` function in the software *R*, characterized by different theoretical averages (x) and theoretical standard deviations (y ; synonymous to unpredictability) (Figure A1.2). We applied three different theoretical averages ($x = 0.00, -0.15, 0.15$): 'control'; 'improved'; and 'reduced'. Moreover, 41 different possible theoretical standard deviations ($y = 0.00, 0.05, 0.10, \dots, 2.00$) was also applied. 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.

Dynamic optimization: reproductive strategies

A simulation is said to converge when one winning strategy is left alone (see Appendix A1). After convergence, we ran the simulation for 80 more years when terminal time (T) was reached. For the last 60 years, i.e. from $t = T - 60$ to $t = T$, we recorded the following data: (1) the type of strategy present; (2) the average reproductive allocation coefficient (\bar{R}); and (3) how \bar{R} was related to both average population density (\bar{D}) and environmental conditions (see below).

Pseudo-empirical statistical analyses

We collected 'pseudo-empirical' data on important output during the last 60 years of each simulation (see A2 for an example). T for each simulation was dependent on both x and y

(A3). The estimated values of \bar{x} (hereafter termed \overline{E}) and \bar{y} [hereafter termed $\overline{sd(E)}$] were, however, only depended on their respective theoretic input values (x & y ; A3).

Allocation of resources to 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 (\bar{R} & \bar{S}). We analysed these generated datasets by standard statistical approaches. First, within each simulation 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 from the ‘within simulations analyses’ above as responses in an ‘across simulation analyses’. We then used the smoothed interaction between both environmental characteristics [i.e. $\overline{sd(E)}$ & \overline{E}] and smoothed \bar{D} 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). Frequently used empirical measures of reproduction allocation include: the number of offspring per female (on log_e scale; hereafter termed reproductive success); autumn; and spring offspring body mass, whereas expected female age; autumn; and spring female body have been used as empirical measures of parental allocation (used in our previous studies: Bårdsen et al. in press; Bårdsen et al. 2008; Fauchald et al. 2004; Tveraa et al. 2003).

⁶ *Within simulation analyses.*-- In R each yearly value (*t*) was modelled as follows: ‘lm (value_{*t*} ~ I ($E_t - \overline{E}$))’. Centring of environmental conditions means that the intercept 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 (intercept ~ s (st.dev.(E), \overline{E} , bs = "tp", k = k*3) + s (\bar{D} , bs = "tp", k = k))’ where ‘k’ equals 4.

Population dynamics: 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. Cryer and Chan 2008; Shumway and Stoffer 2006). 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. Cryer and Chan 2008; Ripley 2002; Shumway and Stoffer 2006); E as a covariate was included via the *xreg* argument]. We, thus, estimated the first-order AR coefficient ($1 + \beta_1$), 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 of results (Figure 4-8) with respect to the interaction between $\overline{sd(E)}$ and \overline{E} were performed using the `vis.gam` function [plot i shows both environmental predictors for average density], whereas plotting of \overline{D} (plot ii) was shown for the average value of both environmental predictors (see Wood 2008 for details).

RESULTS**DYNAMIC OPTIMIZATION**

An important finding was that *dynamic stated dependent reproductive strategies* (DSDS) were superior to *fixed strategies* (FS) for all environmental conditions, but the selected DSDS varied among different environments. Even though the range in strategies selected across all analyses was low (a total of only 5 different strategies where 2 strategies did win in 96% of all simulations) increasing levels of

environmental stochasticity resulted in more risk averse reproductive strategies for all environmental averages (Figure 3a). This relationship was, however, weakest for improved environmental conditions. Additionally, reindeer experiencing good environments adopted a more risk averse strategy relative to the other environmental averages even for low environmental stochasticity.

A similar but more clear-cut conclusion was found when average female reproductive allocation (\bar{R}) was predicted as a function of environmental stochasticity [$\overline{\text{sd}(E)}$] and environmental average (\bar{E}): (i) improved \bar{E} and increased $\overline{\text{sd}(E)}$ both had negative effects on \bar{R} (Figure 4,i); and (ii) increased population density (\bar{D}) had a negative effect on \bar{R} (Figure 4,ii). As \bar{R} was clearly negatively related to \bar{D} , we tested and found that \bar{D} was negatively related to both $\overline{\text{sd}(E)}$ and \bar{E} (Figure 5).

PSEUDO-EMPIRICAL STATISTICAL ANALYSES

Reproductive allocation: reproductive success and offspring body mass

Reproductive allocation depended on environmental conditions. First, reproductive success was practically unaffected by environmental stochasticity until a certain threshold was reached, after which reproductive success decreased as $\overline{\text{sd}(E)}$ increased. This threshold was reached earlier in good vs. poor environments (Figure 6a,i; the effect of $\overline{\text{sd}(E)}$ was practically unimportant for large \bar{E}). Second, the relative strength of \bar{E} and $\overline{\text{sd}(E)}$ was generally similar with respect to both offspring autumn and spring body mass, even though the negative effect of $\overline{\text{sd}(E)}$ was stronger in the analysis of spring body mass (Figure 6i,b-c). Third, the negative effect of \bar{E} was stronger compared to the negative effect of $\overline{\text{sd}(E)}$ in all analyses.

The above relationships must be understood in relation to \bar{D} as density was negatively related to $\overline{\text{sd}(E)}$ (Figure 5). Larger \bar{D} lead to lowered reproductive success and offspring body mass in both autumn and spring (Figure 6ii,a-c). These findings were surprising as this happened

even though higher $\overline{\text{sd}(E)}$ clearly resulted in more risk averse reproductive strategies (Figure 3a) and as increased values of \overline{D} , \overline{E} and $\overline{\text{sd}(E)}$ resulted in lowered \overline{R} (Figure 4). 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 allocation: expected females age and female body mass

Allocation of resources to somatic growth also depended on environmental conditions. First, female age was positively related to $\overline{\text{sd}(E)}$ and negatively related to \overline{E} (Figure 7a,i). Second, female autumn body mass was not strongly affected by $\overline{\text{sd}(E)}$ until a certain threshold again was reached. After this threshold, body mass increased rapidly as $\overline{\text{sd}(E)}$ increased. This threshold value was affected by \overline{E} as the positive relationships between autumn body mass and $\overline{\text{sd}(E)}$ seemed to be linear for high values of \overline{E} . Additionally, female autumn body mass was positively related to \overline{E} (Figure 7b,i) at least for intermediate values of $\overline{\text{sd}(E)}$. Third, female spring body mass was also positively related to $\overline{\text{sd}(E)}$, which also seemed to be stronger after reaching a threshold value (Figure 7c,i). Relative to the analyses of autumn body mass we did find a rather strong negative effect of \overline{E} as generally good conditions gave the highest spring body mass.

The relationships involving female body mass may, as in the analysis of reproductive allocation, be more or less confounded with \overline{D} . Large \overline{D} did for instance result in an increased expected female age (Figure 7a,ii), which means that increased density lead to increased allocation in own survival (see also Figure 4a,ii). Density did also have a statistically significant 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 increased $\overline{\text{sd}(E)}$ or \overline{E} , lead to an increased allocation soma or survival.

Population dynamics: time series analyses

Changes in life histories caused by environmental conditions as reported above had important effects on the observed population dynamics. First, we found the strongest direct negative density dependence ($1 + \beta_1$) in good and predictable environments; i.e. at low values for both \bar{E} and $\overline{\text{sd}(E)}$ (Figure 8a,i). Not surprisingly, \bar{D} did have a negative effect on $1 + \beta_1$ 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 $\overline{\text{sd}(E)}$ and \bar{E} was purely additive: increased \bar{E} , decreased $\overline{\text{sd}(E)}$ and increased \bar{D} resulted in increased delayed regulation, but neither effects were statistically significant (Figure 8b). Third, in the analysis of environmental conditions (ω_1), the largest negative effect of environmental conditions was present in good and predictable environments (Figure 8c,i). This negative environmental effect decreased until a threshold was achieved, then this threshold flattened (Figure 8c,i). Moreover, increased \bar{D} resulted in a higher impact of ω_1 on population growth rates (Figure 8c,ii). In sum, we conclude that 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 had large effects on the amount of resources that virtual female reindeer should allocate to reproduction vs. survival, which has significant effects on population vital rates and dynamics. First, the part of the study assessing dynamic optimization found that DSDS were superior compared to FS in all simulations as the FS strategies always went extinct. This clearly shows that plastic strategies are needed in order to buffer adverse climate. Second, predictions from the theory of risk sensitive life histories was supported as 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. This finding was,

however, not as strong as expected as two closely related strategies were winning in most simulations. Nevertheless, \bar{R} clearly followed our predictions as individuals inhabiting harsh environments allocated least to reproduction. Third, populations inhabiting benign winter conditions experienced the highest density and were most sensitive to occasional climatic perturbations. This was a result of negative density dependence as density had a clear negative effect on reproduction compared to the minor effect 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 of low reproductive allocation and low density. Low density lead to a higher reward for a given allocation compared to high density. High density would, 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 causing a lowered density. Fifth, increased density caused increased negative impacts of occasional harsh winters and increased the strength of direct regulation of populations.

LIMITATIONS 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 losing 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. Coulson et al. 2000; Grenfell et al. 1998). Such interactions were, however, not included 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. Moreover, 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 (Bårdsen 2009: 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 (Bårdsen et al. 2008; Fauchald et al. 2004). The latter results indicate that, with the exception of perhaps extreme winters, individuals do not carry lagged effects of winter climate at the onset of the next breeding 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: (1) give birth to a single offspring every spring (after reaching prime-age), all newborns had a constant birth body mass; (2) have a static reproductive allocation relative to their age, (3) not change their allocation during a given summer; and (4) they have a constant spring body mass threshold deciding whether to allocate in reproduction at all.

Numerous studies show that reproductive allocation strategies among female reindeer are not that simple (e.g. Adams 2005; Bårdsen et al. in press; Bårdsen et al. 2008; Kojola 1993), but perhaps the most important limitation for our study is the complete lack of evolution as no strategy change over time by genetic recombination (as e.g. the IBM by Proaktor et al. 2007).

Finally, the present model do not include 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 include 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. Hurrell et al. 2003; Ottersen et al. 2001; Stenseth et al. 2002).

DYNAMIC OPTIMIZATION

The FS strategies always went extinct, which shows that 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 even though the range of strategies that did win in each simulation was limited. More or less the same strategy was optimal for all kind of environments. This came as a surprise as we included such a wide range of simulated environments in the study. However, average reproductive allocation (i.e., the reward for a strategy combined with a given spring body mass for DSDS) was negatively related to environmental average and stochasticity as well as population density. The latter finding of reduced reproductive allocation in harsh environments was in accordance with our predictions.

PSEUDO-EMPIRICAL STATISTICAL ANALYSES

Reproductive allocation: reproductive success and offspring body mass

Reproductive output, i.e. success and offspring body mass, was also negatively related to environmental average and stochasticity as well as population density. This is further supported empirically by the fact that many organisms buffer their reproductive allocation according to environmental conditions: mammals: e.g. humans *Homo sapiens* (e.g. Bronson 1995; Lycett and Dunbar 1999; Quinlan 2007), moose (Sand 1996; Sæther et al. 1996); *Rangifer* (Adams 2005; Bårdsen et al. 2008; Tveraa et al. 2007), bighorn sheep (Festa-Bianchet and Jorgenson 1998); and

Weddell's seals *Leptomychotes weddellii* (Hadley et al. 2007), long-lived birds: e.g. puffin *Fratercula arctica* (Erikstad et al. 1997); common eider *Somateria mollissima* (Bustnes and Erikstad 1991; Hanssen et al. 2003); and Antarctic petrels *Thalassoica antarctica* (Varpe and Tveraa 2005), fish (review: Klemetsen et al. 2003; van den Berghe 1992) and plants (review: Obeso 2002). As reproductive allocation occurs during summer it may not come as a surprise that population density was of greater importance compared to winter climate in the present study. Moreover, population density was low in generally harsh, i.e. unpredictable and poor, environments (which is a general finding: e.g. Caswell 2001; 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 during winter occurred in these environments. For populations with low harvesting intensities, a higher offspring body mass was found in poor compared to good environments (Tveraa et al. 2007). Even though Tveraa et al. did not have a clear explanation for this, their findings 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). In sum, we found a moderate effect of environmental conditions relative to density. This rather surprising result was due to the fact that negative density dependence was clearly effecting offspring autumn body mass (eqn. A12), which again affected both survival and body mass in the coming winter and spring (eqns. A16-19, see also Wilmers et al. 2007).

Somatic allocation: expected females age and female body mass

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. This was expected as long-lived organism with many potential breeding attempts are not willing to jeopardize own survival over reproduction during an given breeding attempt (Bårdsen 2009). Late winter conditions have profound effects on survival and reproduction for temperate large herbivores in clearly seasonal environments (e.g. Coulson et al. 2001; Coulson et al. 2000; DelGiudice et al. 2002; Patterson and Messier 2000; Tveraa et al. 2003). Autumn body mass, which represents an insurance against harsh late winter conditions, is then traded against the resources a female can allocate to her offspring during summer as accumulation of fat reserves during summer might compete with lactation (Clutton-Brock et al. 1989; Clutton-Brock et al. 1996; Fauchald et al. 2004; Festa-Bianchet and Jorgenson 1998; Reimers 1972; Skogland 1985). Within the context of the present IBM this was expected as an increased autumn body mass was predicted due to the combined effect of lowered density finding and as more risk averse reproductive strategies was optimal in harsh winter environmental conditions.

The relationship between density and body mass was much weaker for females compared to offspring, which is expected for large mammalian herbivores (e.g. Clutton-Brock et al. 1992; Festa-Bianchet and Jorgenson 1998). These findings were also 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 relative to offspring survival (A1). The finding that reindeer have adopted a risk sensitive reproductive strategy is in accordance with 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). Similar findings has been found for Alaskan caribou⁸ 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 allocated in an offspring if it survives predation beyond a couple of weeks. Additionally, female reindeer also allocates less in reproduction when population density increases (Bårdsen 2009: paper 3).

Population dynamics: time series analyses

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 (Wilmers et al. 2007; 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.

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

CONCLUSIONS AND FUTURE PROSPECTS

Future global climate change will most likely result in a shift towards more frequent extreme precipitation events (e.g. Benestad 2007; Semmler and Jacob 2004; Sun et al. 2007; Tebaldi et al. 2006; Wilby and Wigley 2002), 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. Benestad 2007; Tebaldi et al. 2006). *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: (1) increased warming rates with distance to the coast, (2) higher warming rates in winter compared to summer, and (3) 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).

In spite of this, not all predicted changes are believed to have negative effects, which was the rationale for modeling both improved and reduced climatic scenarios. 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 allocation strategies (even for improved environments). 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, Wilmer et al.'s (2007) model show that highly fecund species, i.e. those that lack the ability for buffering reproduction according their environment, are more likely to exhibit pronounced populations fluctuation and consequent crashes than less fecund species. 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 where extinction is inevitable. 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. As observational and experimental study protocols alone cannot unravel the complex relationship between life histories and population dynamics (De Roos et al. 2009), we believe that the development of proper models can be a sound first step towards achieving a better understanding of this. In that respect we agree with Benton et al. (2006:1178, which is in accordance with De Roos et al. 2009) who state that: "The complexity of causation in population dynamics that is being identified in empirical work, along with the insights from theory that different mechanisms can give rise to dynamics with similar characteristics, should provide a challenge to develop modeling approaches that can incorporate sufficiently detailed mechanism".

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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. All simulations are started with the same initial conditions. The model contain: (i) individual-level processes (rectangles) represented by female body mass in spring ($Spring_{bm_{i,j}}$) and autumn ($Autumn_{bm_{i,j}}$), allocation strategy ($R_{i,j}$ and $s_{i,j}$ which again influence gain), summer metabolic rate ($\beta_{s_{i,j}}$) and proportional winter mass loss ($\beta_{w_{i,j}}$), and (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 (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. Survival probability in the model is therefore 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 allocation (R) as a function of spring body mass for *dynamic state dependent reproductive strategies* (b). The relationship between reproductive allocation and spring body mass (b_R in eqn. 1) is different across strategies. 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 masses for each winning strategy (25-30). Note that the two most *risk averse* strategies (a; 25 and 26) are present as the two points with the lowest average female reproductive allocation (\bar{R}) in all subsequent figures. Deviance explained (D) by the model are given in percentage.

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

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

Figure 6. GAM model showing reproductive allocation as a function of the smoothen (s) interaction between standard deviation [$\overline{\text{sd}(E)}$] and average (\bar{E}) environmental conditions as well as average population density (\bar{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 $s[\text{st.dev.}(E), \bar{E}] = 8.972$ ($P < 0.001$), and (ii) $s(\bar{D}) = 2.992$ ($P < 0.001$). (b) Offspring autumn body mass; Intercept = 36.083 (st. err = 0.070, $P < 0.001$), (i) estimated degrees of freedom for $s[\text{st.dev.}(E), \bar{E}] = 7.911$ ($P < 0.001$), and (ii) $s(\bar{D}) = 2.931$ ($P < 0.001$). (c) Offspring spring body mass; Intercept = 38.010 (st. err = 0.137, $P < 0.001$), (i) estimated degrees of freedom for $s[\overline{\text{sd}(E)}, \bar{E}] = 9.689$ ($P < 0.001$), and (ii) $s(\bar{D}) = 2.912$ ($P < 0.001$). Deviance explained (D) by the model are given as percentages on each plot.

Figure 7. GAM model showing somatic allocation as a function of the smoothen (s) interaction between standard deviation [$\overline{\text{sd}(E)}$] 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 $s[\overline{\text{sd}(E)}, \overline{E}] = 9.433$ ($P < 0.001$), and (ii) $s(\overline{D}) = 3.000$ ($P < 0.001$). (b) Female autumn body mass; Intercept = 93.948 (st. err = 0.134, $P < 0.001$), (i) estimated degrees of freedom for $s[\overline{\text{sd}(E)}, \overline{E}] = 6.115$ ($P < 0.001$), and (ii) $s(\overline{D}) = 1.000$ ($P = 0.017$). (c) Female spring body mass; Intercept = 82.915 (st. err = 0.123, $P < 0.001$), (i) estimated degrees of freedom for $s[\overline{\text{sd}(E)}, \overline{E}] = 6.927$ ($P < 0.001$), and (ii) $s(\overline{D}) = 1.000$ ($P = 0.212$). 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 [$\overline{\text{sd}(E)}$] 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 $s[\overline{\text{sd}(E)}, \overline{E}] = 6.836$ ($P = 0.040$), and (ii) $s(\overline{D}) = 1.599$ ($P = 0.009$). (b) Delayed regulation (β_2); Intercept = -0.028 (st. err = 0.118, $P = 0.119$), (i) estimated degrees of freedom for $s[\overline{\text{sd}(E)}, \overline{E}] = 2.000$ ($P = 0.109$), and (ii) $s(\overline{D}) = 1.767$ ($P = 0.231$). (c) Direct effect of environmental conditions (ω_1); Intercept = -0.111 (st. err = 0.004, $P < 0.001$), (i) estimated degrees of freedom for $s[\overline{\text{sd}(E)}, \overline{E}] = 4.227$ ($P = 0.033$), and (ii) $s(\overline{D}) = 2.251$ ($P = 0.011$). Deviance explained (D) by the model are given as percentages on each plot.

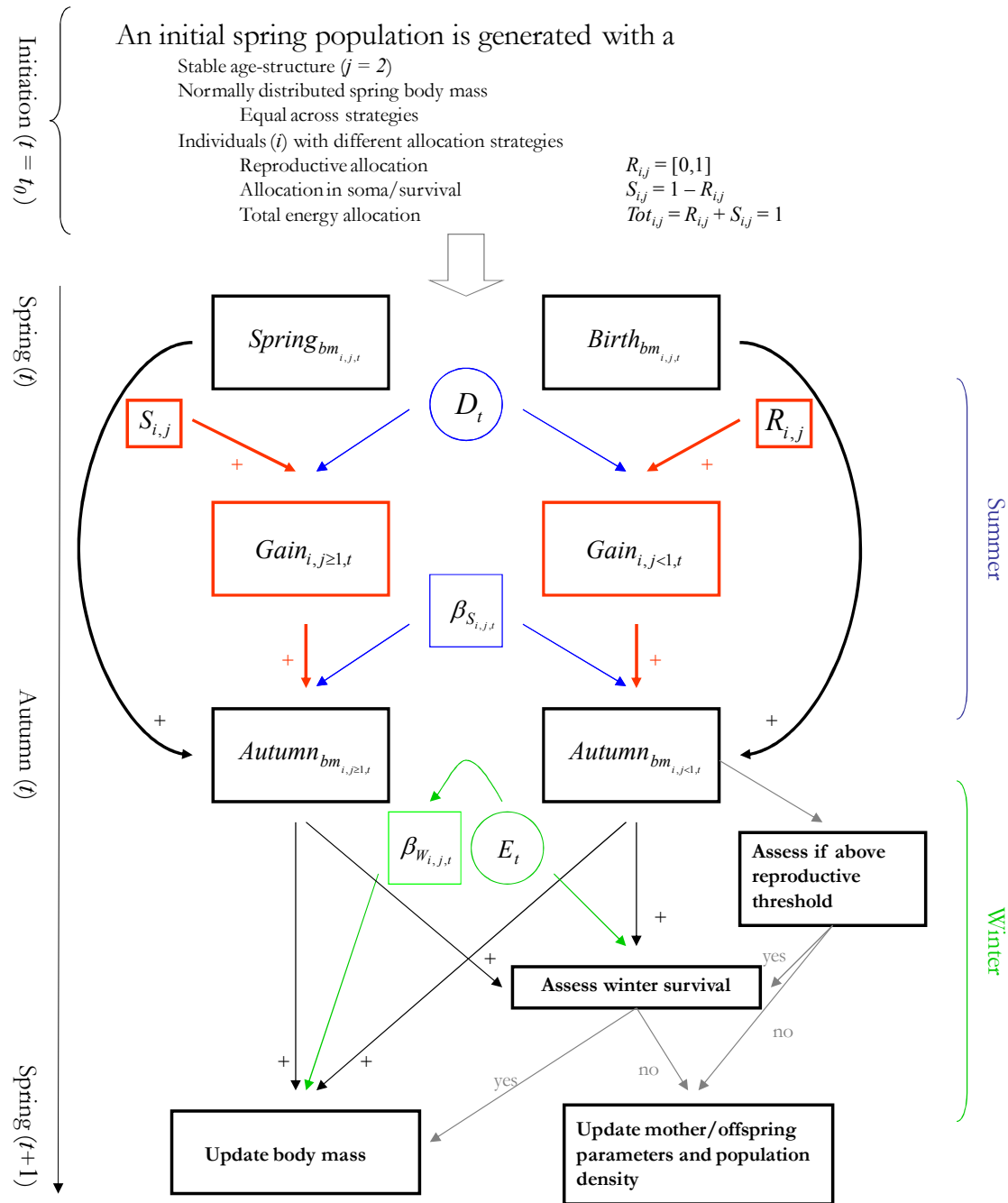


Figure 1.

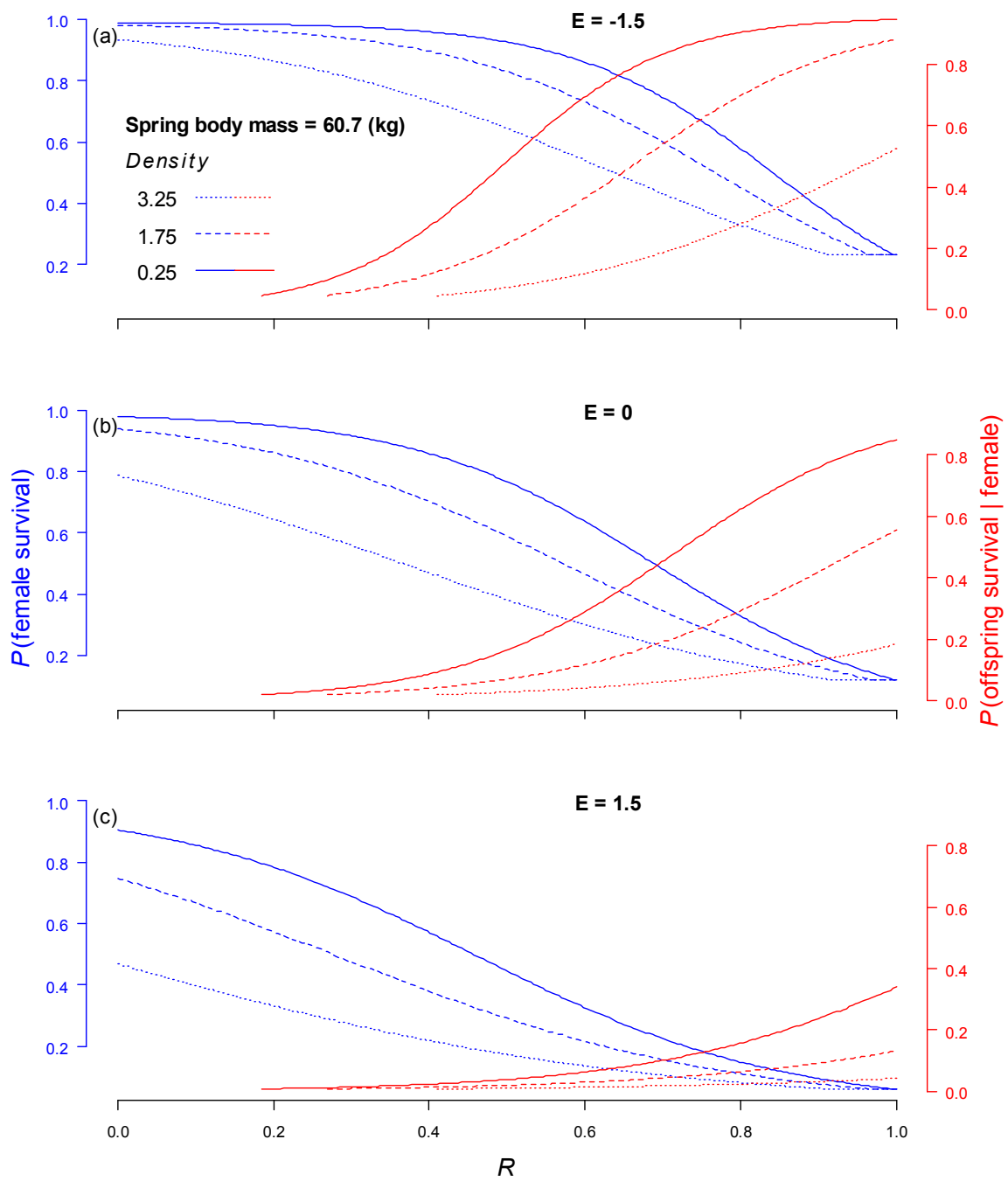


Figure 2.

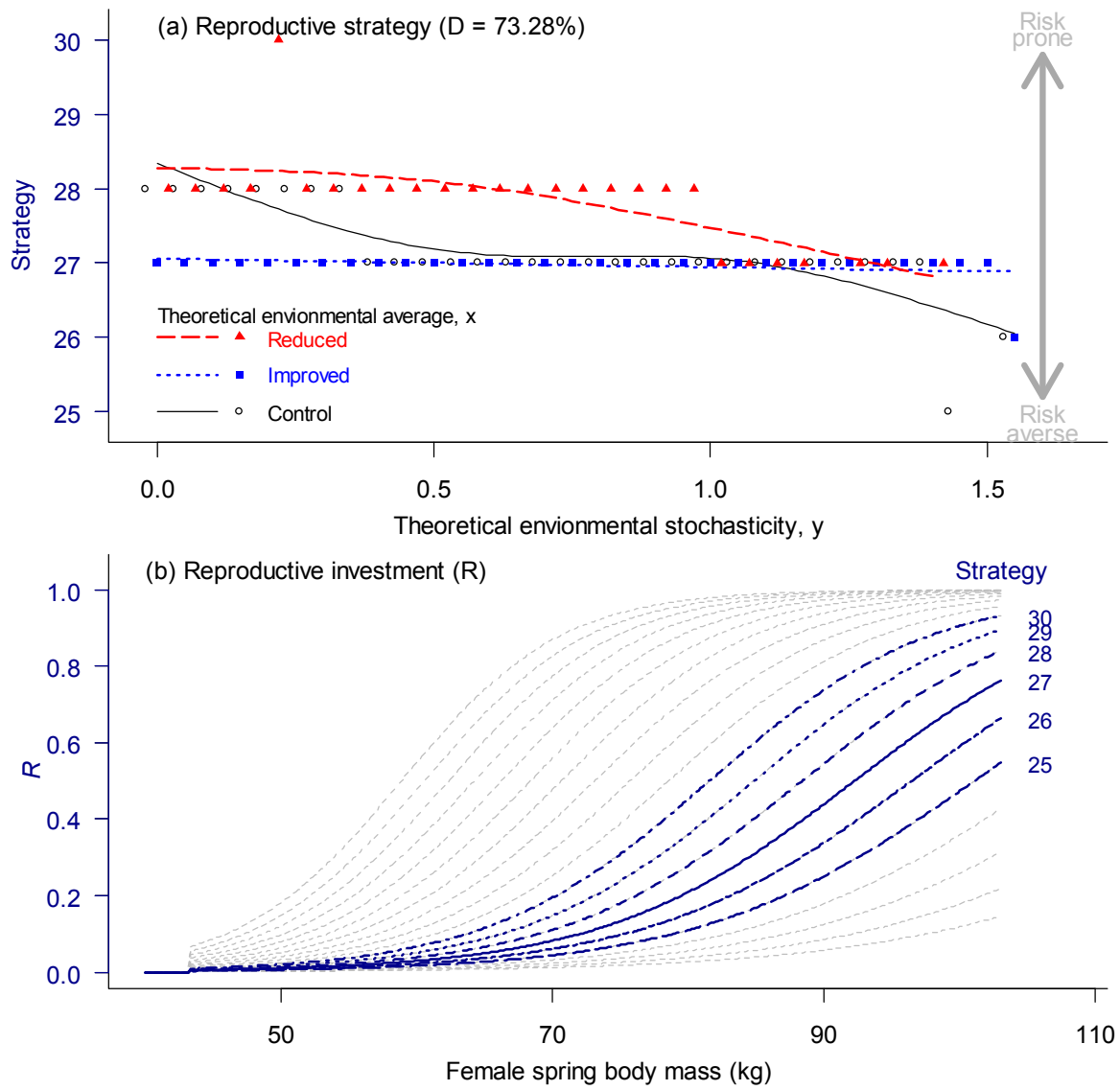


Figure 3.

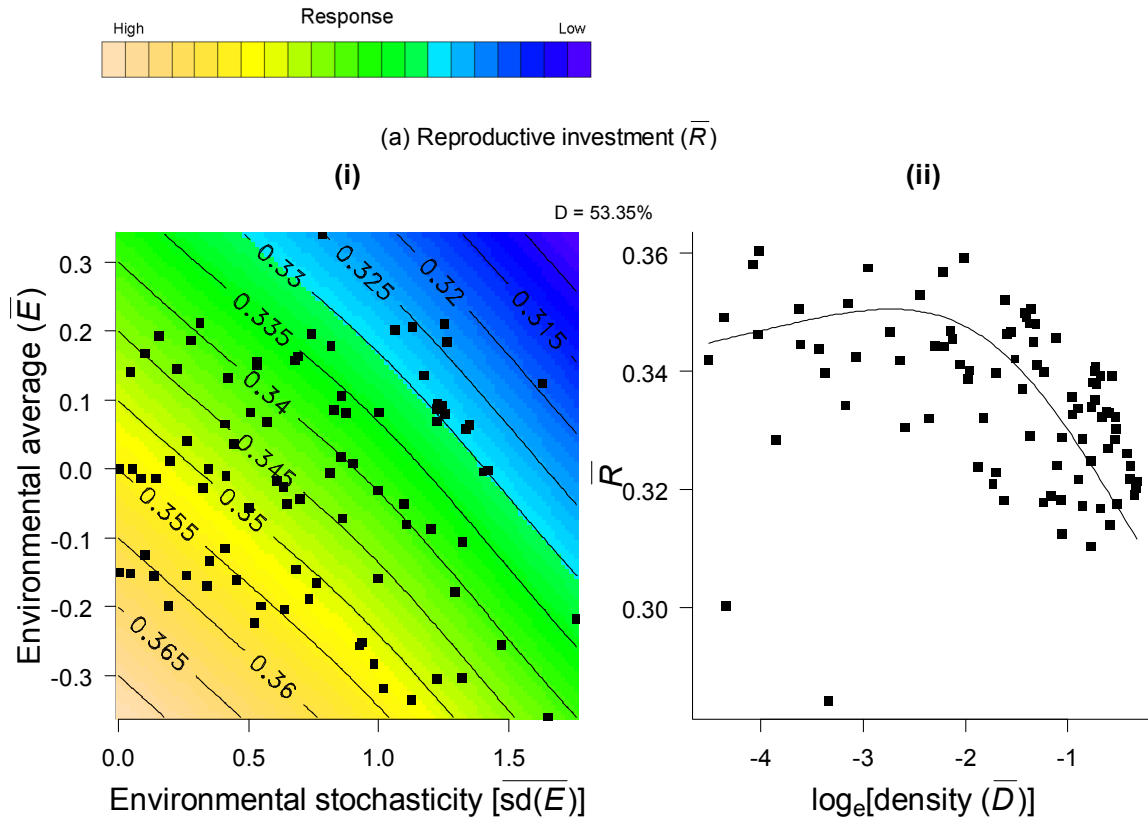


Figure 4.

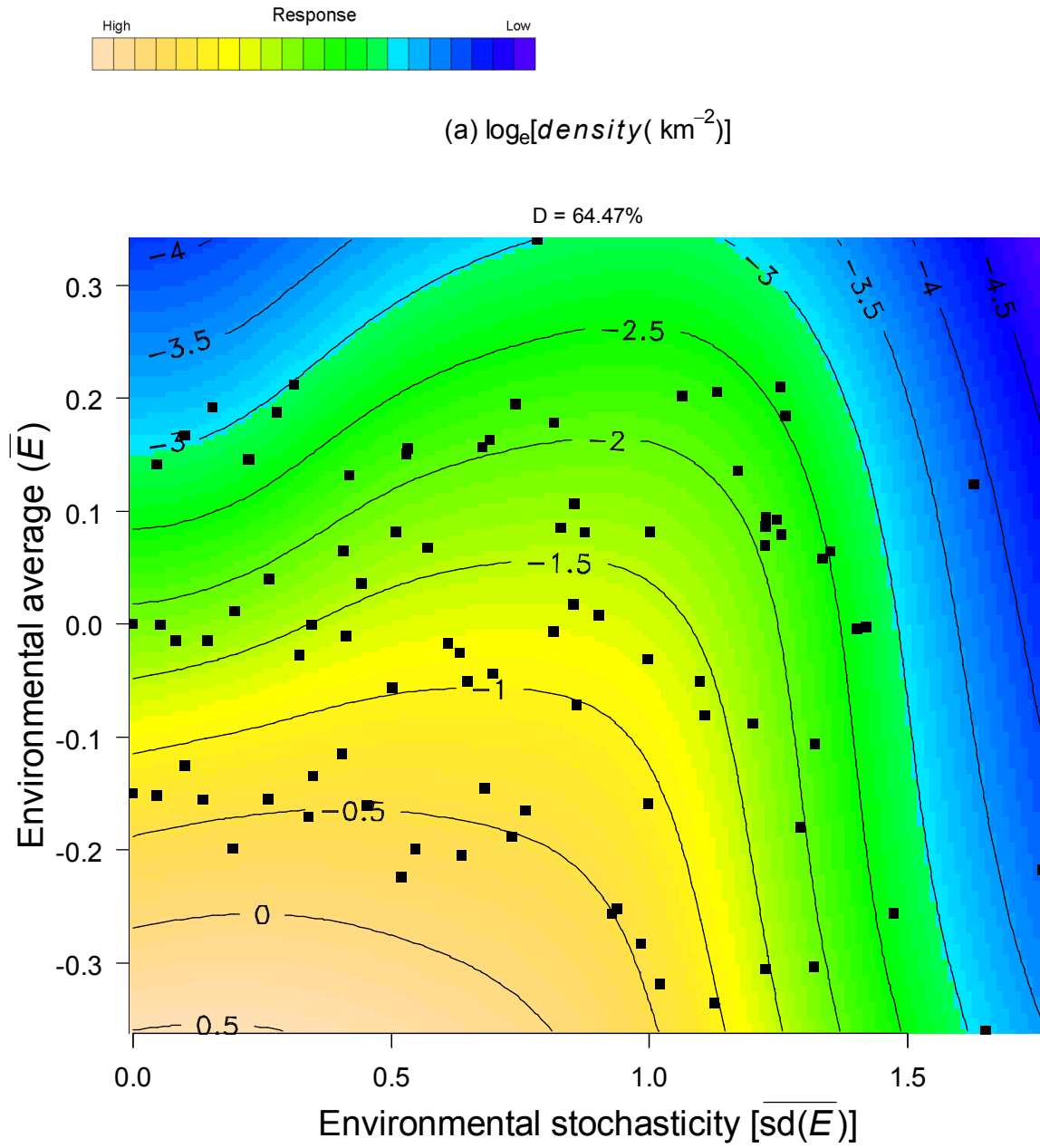


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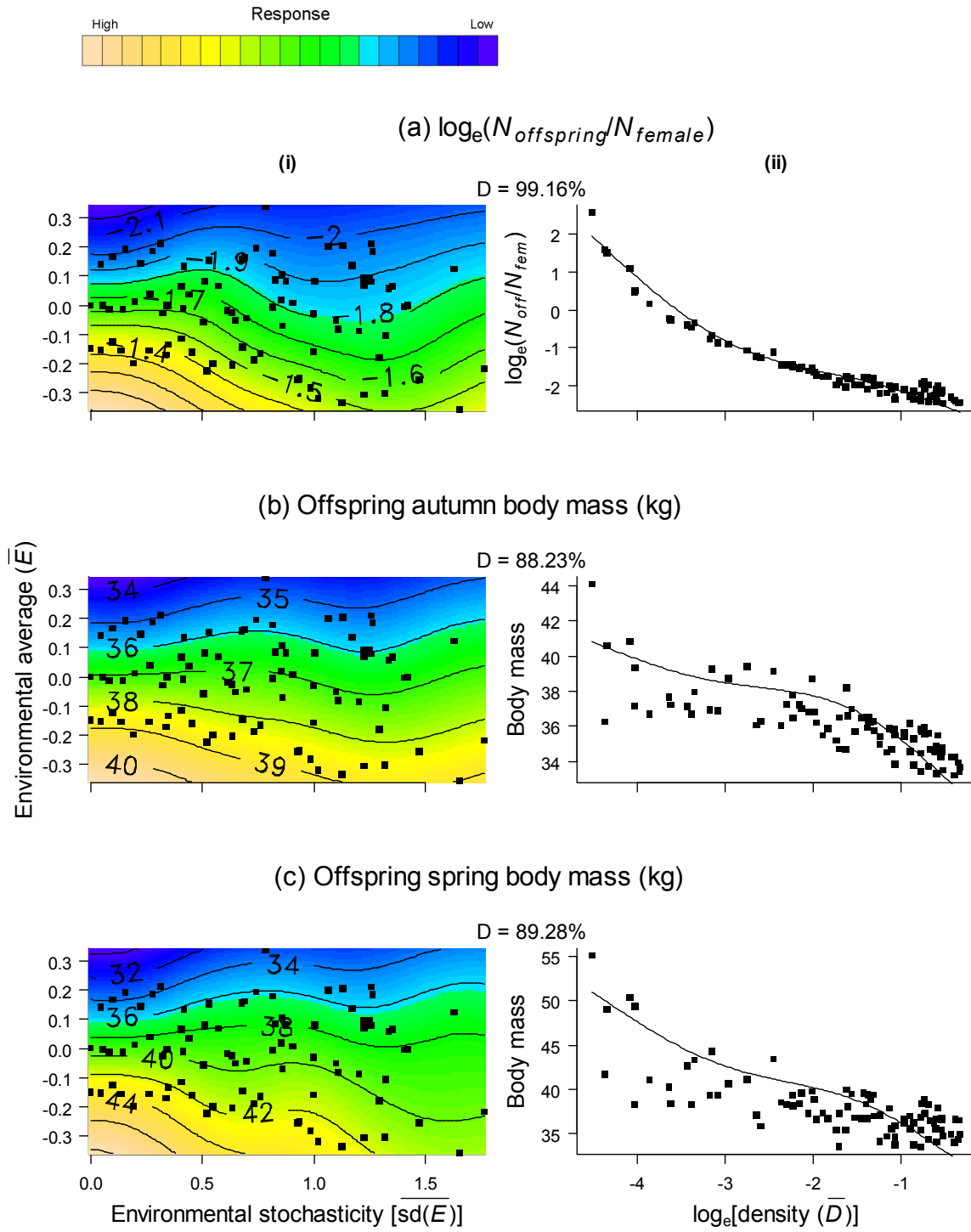


Figure 6.

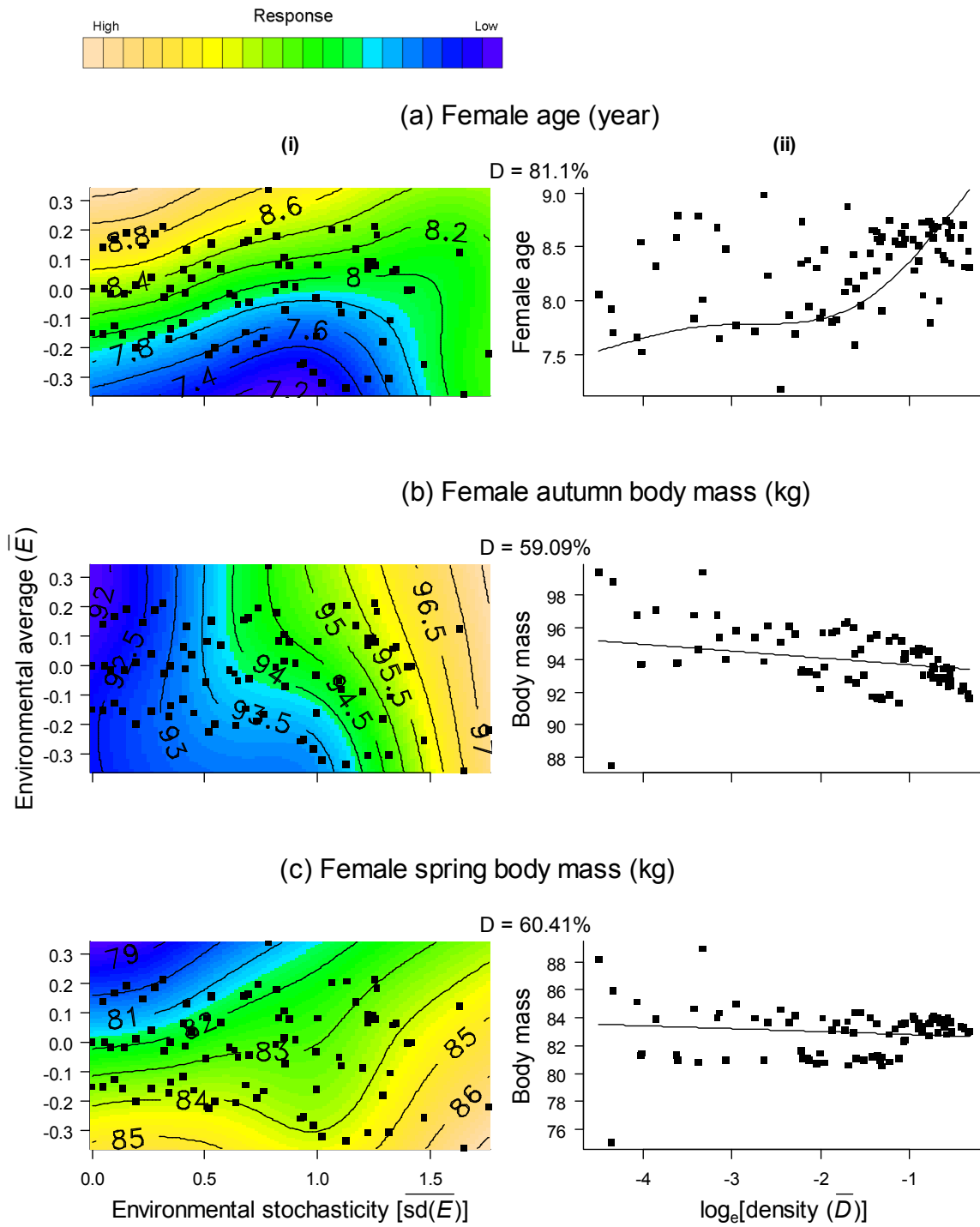


Figure 7.

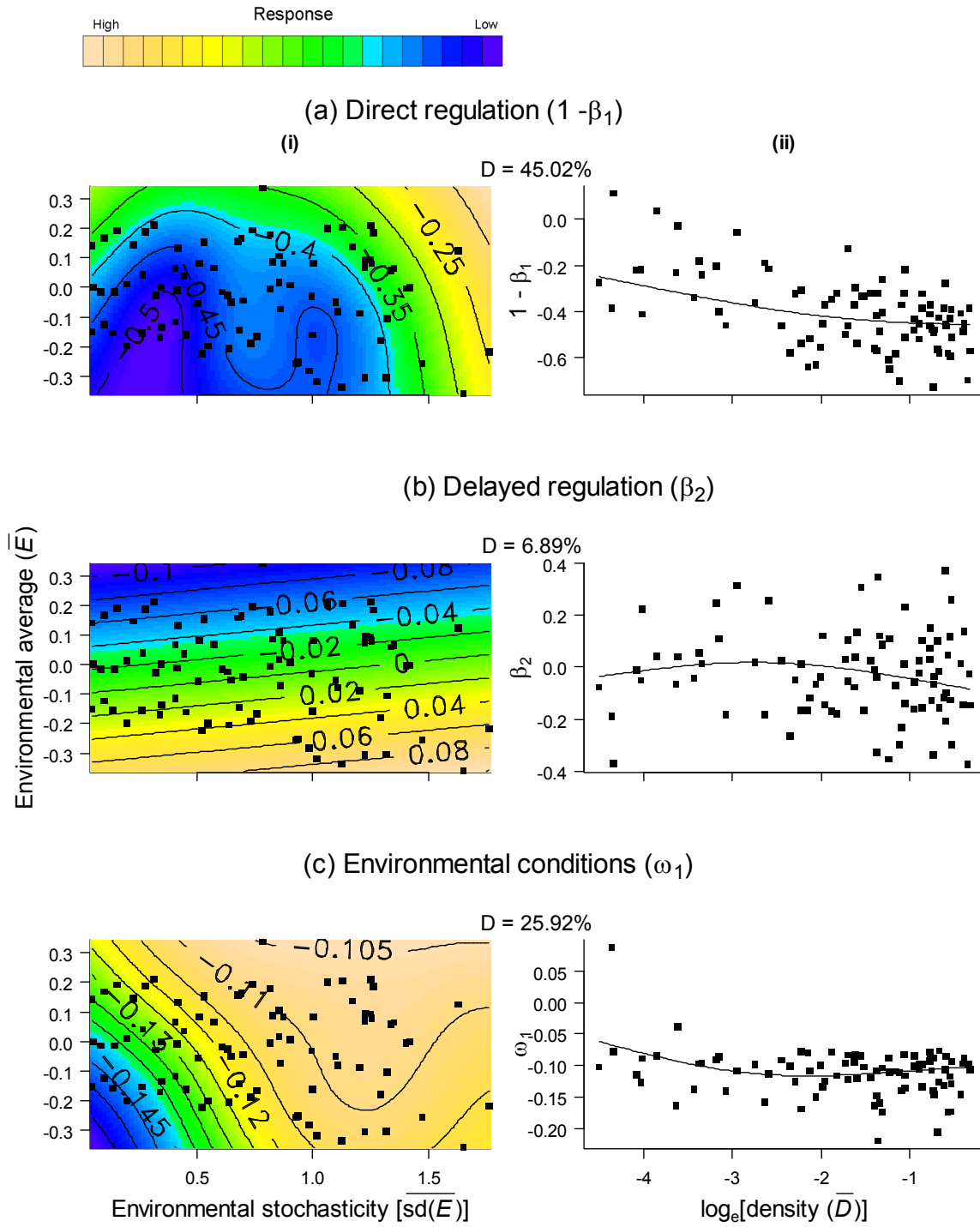


Figure 8.