

# Life history strategy varies with the strength of competition in a food-limited ungulate population

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## Abstract

Fluctuating population density in stochastic environments can contribute to maintain life-history variation within populations via density-dependent selection. We used individual-based data from a population of Soay sheep to examine variation in life history strategies at high and low population density. We incorporated life-history trade-offs among survival, reproduction, and body mass growth into structured population models and found support for the prediction that different life history strategies are optimal at low and high population densities. Shorter generation times and lower asymptotic body mass were selected for in high-density environments even though heavier individuals had higher probabilities to survive and reproduce. In contrast, greater asymptotic body mass and longer generation times were optimal at low population density. If populations fluctuate between high density when resources are scarce, and low densities when they are abundant, the variation in density will generate fluctuating selection for different life history strategies, that could act to maintain life history variation.

## Introduction

The idea that selection on life-history traits could vary with population density can be traced to the 1950s (Dobzhansky 1950) with  $r$ - $K$  selection theory formulated by 1967 (MacArthur 1962; Wilson & MacArthur 1967). According to this within-population  $r$ - $K$  selection theory, selection should favour strategies that can rapidly turn abundant resources into offspring at low population density, while at densities close to carrying capacity, strategies allowing the efficient acquisition of limiting resources should be optimal. Pianka (1970) attempted to generalize within-population theory to explain life history variation observed across distantly related species by proposing the  $r$ - $K$  selection continuum. By contrasting sets of life history

traits associated with  $r$ - and  $K$  selection he proposed an axis of life history strategy variation spanning species with fast rates of turn-over such as mice to those with a slow turn-over such as elephants.

$r$ - and  $K$ -selection theory and the  $r$ - $K$  continuum became dominant paradigms in evolutionary biology before their fall from grace in the late 1970s (Stearns 1977, 1992; Reznick *et al.* 2002). Two reasons for their demise were (i) the theory could not be extended to entire life histories, and (ii) a lack of evidence for the existence of the  $r$ - $K$  continuum from within populations (Stearns 1977; Mueller 1997; Reznick *et al.* 2002) despite support for its existence from comparative cross-species analyses (Stearns 1983; Boyce 1984; Gaillard *et al.* 1989). The emphasis of life-history evolution research primarily shifted from density-dependent selection to age-specific mortality (Stearns 1992; Reznick *et al.* 2002) and to the closely related ‘pace-of-life’ concept (Saether 1987; Ricklefs & Wikelski 2012).

Nowadays, there is increasing evidence of selection for traits associated with  $r$  and  $K$  life histories both across and within species. Within species, great tits (*Parus major*) that have small clutch sizes have a higher fitness at high densities than those with large clutch sizes and tend to be more  $K$ -selected than those at lower densities (Both *et al.* 2000; Saether *et al.* 2016). Furthermore, Trinidadian guppies (*Poecilia reticulata*) living in the absence of predators at high population densities exhibit larger adult size, mature later, and exhibit lower reproductive effort than those living with predators at lower densities (Reznick *et al.* 1990). Because guppies living without predators compete more strongly for food than those living with them, the guppies provide evidence of  $r$ - $K$  selection theory (Reznick *et al.* 2002; Bassar *et al.* 2013).

Examples such as the Trinidadian guppies have contributed to a revival in the popularity of  $r$ - $K$  selection within populations. Work typically focuses on characterising  $r$ - $K$  selection theory in micro-organisms in the laboratory (e.g. Mueller 2009) or in the

development of models (e.g. Engen *et al.* 2013; Oizumi *et al.* 2016; Lande *et al.* 2017). In addition, there is recent empirical evidence for density-dependent selection on clutch size within a population of wild great tits (*Parus major*) (Saether *et al.* 2016). However, the question remains of how to extend the theory to entire life histories while identifying life-history trade-offs that can be masked within populations in the field by variation in individual quality (van Noordwijk & de Jong 1986), and to test for the maintenance of different life history strategies. Until this is achieved, our understanding of the role of density-dependent selection in moulding life histories in nature will remain rudimentary.

In natural populations, stochastic environmental factors lead population sizes to fluctuate. These fluctuations are often caused by an interaction between density dependence and stochastic environmental factors. For example, in Soay sheep (*Ovis aries*) – the focus of this paper – population declines of up to 60% occurred when population size was large and winter weather was harsh (Coulson *et al.* 2001). Such periodic changes in population size have the potential to generate fluctuating selection on life history traits. In particular, according to *r-K* selection theory, at low densities, a fast turn-over of highly productive individuals should be selected for, whereas a slow turn-over of individuals with high competitive ability to acquire resources should be favoured at high density. In turn, these periodic changes could either contribute to the maintenance of variation in life history strategies within a population, or lead to stabilizing selection around an intermediate phenotype as found by Seather *et al.* (2016).

Here we studied how fluctuating population densities of Soay sheep affects within-population variation in life history strategies using Integral Projection Models (IPMs). IPMs are structured population models which describe the expected phenotypic trait trajectories based on functions of trait-dependent demography, and consequently the entire expected life history of the group of individuals over which they are parameterized (Easterling *et al.* 2000;

Ellner *et al.* 2016). These trait-dependent functions are typically identified using linear or linearized regressions. The trait we use, body mass, is known to affect both survival and reproduction in Soay sheep, and is affected by population density (Pelletier *et al.* 2007; Coulson 2012). First, we estimated covariances across all parameters by removing each individual from the dataset in turn i.e. ‘de-lifing’ the dataset (Coulson *et al.* 2006). The covariance structure is then used to generate random IPMs where each IPM is defined as a set of four functions with its own unique parameterisation and represents a life history strategy. These strategies span the range of possible life history strategies we expect sheep to follow given the phenotypic life history trade-offs within and between demographic functions (see Methods). Then, we investigated the evolutionary dynamics of life histories by competing each of the randomly generated strategies against one other at a range of densities, and ranked each strategy according to fitness. Next, we identified the fittest strategies (i.e. strategies with the highest equilibrium population growth rate) at low and high density. Finally, we repeated this exercise in a stochastic environment. Our work provides a way to extend research beyond laboratory experiments to observational field studies to examine selection on life history strategies, and provides an example where density-dependent selection has the potential to be an important driver of life history evolution.

## Methods

### Structured Population Model including body mass – IPM

Our model is of a long-term, individual-based study of Soay sheep living on a predator free island in the St. Kilda archipelago, Scotland (Clutton-Brock & Pemberton 2004). We used a previously published IPM parametrised for this population and analysed by Coulson (2012). The model was parameterised using data of female sheep as the growth rate of the population is female-dominant (Coulson *et al.* 2001). None of the statistical models used to construct the

128 IPM we use from Coulson (2012) include age (see discussion). The IPM consists of four  
 129 functions describing how body size  $z$  influences survival, reproduction, growth and offspring  
 130 size. The survival and reproduction functions are described by generalized linear functions:

$$S(z, t) = \frac{1}{1 + \exp(-(s_0 + s_1 z + s_2 N_t))} \quad (1)$$

$$R(z, t) = \frac{1}{1 + \exp(-(r_0 + r_1 z + r_2 N_t))} \quad (2)$$

131  
 132 with  $z$  representing body mass and  $N_t$  population size at time  $t$ . The growth  $G(z'|z, t)$  and  
 133 parent-offspring functions  $D(z'|z, t)$  are described by Gaussian probability density functions,  
 134 i.e. the probability that an individual with body mass  $z$  at time  $t$  will have a body mass, or  
 135 produce offspring, with body mass  $z'$  at time  $t + 1$ :

$$G(z'|z, t) = \frac{1}{\sqrt{2\pi\sigma_g^2(z')}} e^{-\frac{(z - E_g(z'))^2}{2\sigma_g^2(z')}} \quad (3)$$

$$D(z'|z, t) = \frac{1}{\sqrt{2\pi\sigma_d^2(z')}} e^{-\frac{(z - E_d(z'))^2}{2\sigma_d^2(z')}} \quad (4)$$

136  
 137 with the function  $E_g(z')$  predicting expected body mass and  $E_d(z')$  predicting offspring's  
 138 expected body mass at  $t + 1$  being linear and of the form

$$E_g(z') = \gamma_0 + \gamma_1 z + \gamma_2 N_t \quad (5)$$

139

$$E_d(z') = \delta_0 + \delta_1 z + \delta_2 N_t \quad (6)$$

140 The functions  $\sigma_g^2(z')$  and  $\sigma_d^2(z')$ , to describe the variance around the expectation, are also  
 141 linear but do not contain terms for population density

$$\sigma_g^2(z') = \gamma_3 + \gamma_4 z \quad (7)$$

142

$$\sigma_d^2(z') = \delta_3 + \delta_4 z \quad (8)$$

143 Model selection is described in Coulson (2012) and the resulting parameter values and  
 144 descriptions of the parameters can be found in Table 1.

145 The IPM then iterates the distribution of  $z$  at  $t$ ,  $n(z, t)$  to  $n(z', t + 1)$ :

$$n(z', t + 1) = \int [D(z'|z, t)R(z, t) + G(z'|z, t)S(z, t)]n(z, t)dz \quad (9)$$

146 where population size is  $N(t) = \int n(z, t)dz$ . The IPM can be written as a matrix  
 147 approximation as

$$\mathbf{n}(t + 1) = [\mathbf{D}(t)\mathbf{R}(t) + \mathbf{G}(t)\mathbf{S}(t)]\mathbf{n}(t) \quad (10)$$

148 We checked if the prediction did not produce negative values for body mass and variances,  
 149 which would indicate that the model is not properly parameterised.

150

### 151 **Estimating the correlation and variance-covariance between parameters**

152 The correlation and variance-covariance matrix across all parameters of the IPM capture  
 153 trade-offs between life-history characteristics. To estimate the correlation and variance-  
 154 covariance matrix, we needed to know how much each individual deviated from each of the



functions describing the population (functions 1 – 8), and correlate these deviations. We used a technique called ‘de-lifing’ (Coulson *et al.* 2006), which is analogous to the take-one out jack-knife. If individual  $l$  is taken out of the individual-based dataset, and the models re-parameterized, a new set of parameters  $\theta^{-l}$  is generated. This describes the life history of the population with individual  $l$  removed. Then, if this new set of parameters is subtracted from the original set,  $\delta^l = \theta - \theta^{-l}$ , it will result in a vector which describes the contribution of individual  $l$  to each of the parameters. If the data set across  $n$  individuals consists of  $m$  rows where  $m > n$ , which is the case for the Soay sheep dataset, each of the  $m$  rows was removed sequentially and  $\delta^m = \theta - \theta^{-m}$  calculated. Then  $\delta^l = \frac{1}{Q} \sum \delta^m$  was calculated, where  $Q$  is the number of rows associated with individual  $l$ .

Sometimes removing an individual from the data set does not impact the statistical estimation of a function or its parameters: in such cases element  $x$  of  $\theta$  will result in  $\theta_x = \theta_x^{-l}$ . For example, if an individual dies at time  $t$ , it will not contribute to the development function at time  $t$  because development is conditional on surviving. For those cases  $\delta_x^t$  is undefined, and these rows were removed. For the Soay sheep dataset, of 858 unique females we retained 852 females of a total of 2529 events for the survival parameters, 858 females of a total of 2601 events for the recruitment parameters, 644 females of a total of 1367 events for the development parameters and 223 females of a total of 377 records for the mother-offspring transmission parameters. We then calculated the pairwise correlation and covariances between each pair of parameters across the  $\delta^l$  sets and constructed their correlation matrix.

Prior to using the de-lifing approach we attempted to estimate the covariances between parameters using hierarchical Bayesian mixed models. In principle, parameter covariances could be estimated across posterior distributions. However, the different number of individuals available to parameterize each function made this approach problematic, as

missing values meant that trait values required imputation for growth and mother-offspring transmission for individuals that did not survive or reproduce. We consequently adopted the de-lifing approach. In Appendix S1 in the Supporting Information we demonstrate the conditions under which the de-lifing approach will give equivalent results to a mixed modelling approach when data do not need to be imputed. We are able to show that in our case, the de-lifing approach is expected to give similar estimates to the use of mixed models.

### **Ranking life history strategies in density-dependent deterministic environments**

We used the variance-covariance matrix to generate 10,000 random parameter sets. Each parameter set  $i$  was used to construct an IPM describing life history strategy  $i$ . When density-dependent processes do not operate, equilibrium growth rate  $r$  is mean fitness in deterministic environments (Fisher 1930). In initial simulations, we held the population size constant at 200 individuals, close to the lowest observed population size, and calculated equilibrium growth rate  $r$  of each IPM. We then ranked the strategies such that the fittest strategy has the highest growth rate. For each strategy  $i$  we calculated carrying capacity,  $K_i$ . For each IPM at high and low density we also calculated the equilibrium size structure  $\mathbf{u}_i$ , generation time (Steiner *et al.* 2014), and asymptotic body mass defined at the point where the function  $E_g(z)$  (eq. [5]) crossed the  $z = z'$  line where expected body mass growth from time  $t$  to time  $t+1$  is zero.

When population sizes are close to carrying capacity,  $r$  does not represent mean fitness (Benton & Grant 2000; Sæther & Engen 2015). Instead, at high population densities, we initially identified strategy rankings using pairwise evolutionary invasion methods (Maynard-Smith 1993; see Appendix S2). We found that at high population density, carrying capacity is fitness in our linearized density-dependent deterministic model, which extends a

204 result from previous models of  $r$  and  $K$  selection in linear, deterministic, density-dependent  
 205 models (Roughgarden 1971; Lande *et al.* 2009).

206 We ranked the 10,000 random life histories based on their  $r$  and  $K$ , and we plotted the  
 207 functions defining the five fittest life history strategies at low and high density. To  
 208 characterize these life history strategies, we calculated the mean survival rate, the mean  
 209 reproductive rate, the mean and variance in offspring and adult body mass, the equilibrium  
 210 population growth rate, and a metric of reproductive investment for each population size  
 211 between 100 and 600 individuals. We calculated reproductive investment as the potential  
 212 survival cost of reproduction by first calculating the elasticities (partial derivatives) of the  
 213 population growth rate of strategy  $i$  at density  $N$ ,  $\lambda_i(N)$  to each element  $pq$  of the survival and  
 214 reproduction matrices,  $S_{pq}$  and  $R_{pq}$  respectively, before summing across all  $pqs$ :  $\sum_{pq} \frac{\partial \lambda_i(N)}{\partial S_{pq}}$   
 215 and  $\sum_{pq} \frac{\partial \lambda_i(N)}{\partial R_{pq}}$ . We then define reproductive investment as the ratio  $\frac{\sum_{pq} \frac{\partial \lambda_i(N)}{\partial R_{pq}}}{\sum_{pq} \frac{\partial \lambda_i(N)}{\partial S_{pq}}}$  (Jones &  
 216 Tuljapurkar 2015).

## 217 **Stochastic IPMs**

218 We extended our models for each strategy to stochastic environments by including random  
 219 year effects in the survival, reproduction, development and mother-offspring functions  
 220 (Ellner & Rees 2006). We used the random effect models fitted by Coulson (2012), see Table  
 221 1 for parameter estimates. First, we constructed a correlation and variance-covariance matrix  
 222 in the same way as for the deterministic case. Then, for 100 randomly selected life history  
 223 strategies (i.e. parameter sets), we ran simulations for 1200-time steps and recorded the  
 224 population size at each  $t$ . At each time step we draw random perturbations to the intercepts of  
 225 each of the four functions. For each strategy  $i$  we consequently generated a time series of  
 226 population sizes  $\mathbf{N}_i = N_i(1), N_i(2), \dots, N_i(1200)$ . To determine whether strategy  $j$  could

invade strategy  $i$  we ran a simulation of the dynamics of strategy  $j$  using the population sizes  $N_i$ , recording  $N_{j,i}$ . For time steps 201 to 1200 we calculated the long-run stochastic growth rate,  $a_j$ . If  $a_j > 0$   $j$  invaded strategy  $i$ . This approach took prohibitively long to run for all 10,000 strategies competing against each other. To identify the optimal strategy at smaller population sizes we took time series of  $N_{iS}$  for each strategy at carrying capacity, calculated the mean, and then reduced each population size by subtracting a value  $x$  from each value such that the time series of  $N$  for each strategy had the same mean value (these mean values were 100, 200, ..., 600). We then calculated the long-run stochastic growth rate for each of these values. No population size in any simulated time series dropped to 0. Strategies were ranked by their fitness at each mean population size, with fitness measured as mean asymptotic population size. In a similar manner to the deterministic case, fitness at low density is the long-run stochastic growth rate (Tuljapurkar & Orzack 1980); at high density we used mean asymptotic population size as the fitness measure.

## Results

Examining covariances between parameters revealed negative relationships between the intercepts and the slopes within the survival and reproduction functions and a mixture of weaker negative and positive relationships of parameters across functions (Fig. S3.1a, b in Appendix S3). Covariances between intercepts and slopes are likely statistical artefacts that occur when the mean of  $x$  and  $y$  in regression analyses are greater than 0. In contrast, non-zero covariances across functions are consistent with life history trade-offs. However, extracting biological insight from high-dimensional correlation/(co)variance matrices such as these is difficult. Instead, we investigated the functions of the five best-ranked strategies in low and high-density environments.

As expected, at low density, the five fittest life history strategies in a low-density environment had higher survival and recruitment rates than the five strategies that are fittest in a density-dependent environment (Fig. 1ab). At high density close to  $K$  where density-dependence is strong, this pattern was reversed. Average body mass (Fig. 1c) and offspring body mass (Fig. 1d) both declined with increasing population density, but the functions for the fittest strategies in both low- and high-density environments overlap. The variance of adult body mass (Fig. 1e) and offspring mass (Fig. 1f) did not show a consistent pattern with population density, or with strategy. The fittest strategies at low population densities had the lowest reproductive investment relative to investment in survival in density-dependent environments, and *vice versa* (Fig. 1g). Population growth rate showed a similar pattern (Fig. 1h).

Why do these patterns occur? They arise because of a trade-off between demographic functions across changing densities. Survival and recruitment rate for a given body mass at low density does not translate to similar rates at high density. Individuals that are consequently fit at low density are unfit at high density and *vice versa*. Strategies arise that are best fitted to either high or low density, but not at both. In particular, heavier individuals always had highest survival and recruitment probabilities, but the slopes differed between population density and life history strategy (Fig. 2ab). At low population density, the life history strategy that is fittest in low-density environments includes highest survival rates for all body masses (Fig. 2a). This pattern is reversed at high population density. For recruitment the pattern is different: at low population size, lighter individuals of the fittest life history strategy in low-density environments produced more offspring than those of the fittest life history strategy in density-dependent environments (Fig. 2b), while heavier individuals of fittest life history strategies at both low and high density had a similar probability to produce recruits. At high population sizes, fittest life history strategies in both low- and high-density

environments recruited at a similar rate when individuals were light, while heavy individuals with an optimal life history strategy at high density produced more offspring. There was little variation in expected body mass development between strategies (Fig. 2c). At high population sizes expected offspring mass was lower compared to low population sizes for all adult masses, and there was little difference between optimal strategies at low and high density (Fig. 2d). Variance around the expected development and offspring body mass also did not differ between the two strategies (Fig. 2ef).

How do these differences translate into life history characteristics? Correlations of fitness (measured as equilibrium growth rate at low density and carrying capacity at high density) with generation time (Fig. 3ac) and asymptotic body mass (Fig. 3bd) at low (Fig. 3ab) and high (Fig. 3cd) density reveal that in low density there is selection for increased asymptotic body mass and longer generation times, while at high density there is competition for smaller asymptotic body mass and shorter generation times. There is substantial scatter around these associations, and in particular, selection for large body mass at low density is relatively weak.

The x-axes of fig. 3b and 3d show there is little overlap in asymptotic body mass between high and low population density suggesting that fluctuations in density generate a substantial amount of body mass plasticity. In Fig. 4 we plotted the distribution of the asymptotic body mass at low and high population density, and marked the body mass of the fittest strategy at high density in both distributions, as well as the body mass of the fittest strategy at low density in the low population density distribution. The difference in body mass between low and high population density of the fittest strategy at low density, and between low and high population density of the fittest strategy at high density, suggest that changes in average population body mass observed in the Soay sheep population are likely

almost entirely due to phenotypic plasticity rather than a change in strategy frequency (Ozgul *et al.* 2009).

If we included environmental stochasticity to allow populations to fluctuate around a mean (Fig. 5), optimal strategies at high density could only manifest themselves if the mean population size is higher than ~400 individuals (Fig. 5). In that case, the strategy at low density does not perform well, i.e. strategy rank is close to the 80<sup>th</sup> percentile. When density-independent mortality is high, leading to low population sizes, the strategy at low density wins all competitions. This model reveals that at a wide range of density-dependent environments, depending on mean population density, a single (i.e. low or high density) life history dominates.

## Discussion

We used a de-lifing approach (Coulson *et al.* 2006) to estimate life-history trade-offs which we included in structured population modelling followed by evolutionary invasion analyses to demonstrate evidence of density-dependent selection on life histories in Soay sheep. Our outcomes support the occurrence of  $r$ - $K$  selection within populations in the wild. We found that individuals with a particular life history could not simultaneously maximise fitness for both high- and low-density environments: survival and fertility rates were higher for the fittest life history strategies in low-density environments compared to the same strategies in high-density environments. Conversely, survival and fertility rates of the fittest life history strategies in high-density environments were higher compared to the same strategies at low density. Moreover, the fittest life history strategies in low-density environments involved more investment in reproduction than survival in low density environments compared to the strategies fittest in high-density environments. As population size increases, both strategies involve increased investment in survival relative to reproduction. As expected from current

evolutionary theories on life history evolution (Stearns 1992), trade-offs between survival and reproduction do exist across environments, which prevent individuals to be masters of all trades.

Environments where low density strategies thrive, i.e. environments where resources are not limited, are unlikely to last for long in the island population of Soay sheep examined here because they exist in a predator-free environment and as such, the population can rapidly increase towards carrying capacity where high-density strategies have higher fitness. However, in populations where predation plays a key role in limiting population size, the population could be kept well below carrying capacity thereby favouring low density life histories (Reznick *et al.* 2002; Bassar *et al.* 2013). In such an environment, it is possible that a set of phenotypic traits that reduce susceptibility to predation will be selected (Yoshida *et al.* 2003), which may alter trade-offs and thereby influence life history traits such as life cycle speed (Yoshida *et al.* 2003) or body size (Tollrian 1995; van Leeuwen *et al.* 2008).

The inferences from our deterministic modelling framework holds for stochastic approaches. We found that the same processes favour either low- or high-density strategies in both types of models such that, for a given stochastic environment with population densities fluctuating around the mean, a single strategy dominated. When density-independent processes substantially reduce survival or fertility rates, the population never reaches a sufficiently large size for density-dependence to exert a brake on population growth, and low-density strategies that fare badly at high densities, dominate. In contrast, when density-independent processes have little effect on survival or fertility, the population attains an average size where high-density strategies are evolutionary stable. This provides support for theoretical modelling approaches (Engen & Saether 2017; Lande *et al.* 2017). Furthermore it extends the relevance of our findings to natural situations as most animals experience fluctuating environments in the wild, caused for instance by severe weather and diseases, that



impose density-independent mortality reducing population size (Boyce 1984). To maintain different life history strategies within a population in a stochastic environment, density-independent processes that influence mean population size need to alternate over multiple time steps passing a population size threshold that results in a switch between evolutionarily stable life history strategies (Fig. 5).

Long-term changes of mean population size within a stochastic environment can be caused by habitat and climate change (Simmonds & Coulson 2015; Kentie *et al.* 2018; Paniw *et al.* 2019), outbreak of diseases (Altizer *et al.* 2006), or arrival or disappearance of a new competitor or predator species (Fritts & Rodda 1998; Courchamp *et al.* 2003; Duyck *et al.* 2007). For example, the North Atlantic Oscillation influences the Soay sheep population on St. Kilda (Coulson *et al.* 2001; Pelletier *et al.* 2007) – a large-scale driver of local climate that exhibits multi-decadal oscillations and has recently experienced a multi-decadal trend towards large mean values. Mortality is increased with a positive NAO, leading to a lower mean population size (Simmonds & Coulson 2015), thereby generating fluctuations in the relative contributions of density-dependent and density-independent processes to variation in demographic rates.

Trade-offs in other life history parameters were also evident, with favoured life histories at low population densities exhibiting longer generation time and larger asymptotic body mass, whereas the opposite was true for life histories favoured at high-density environments. This finding aligns with previous work on Soay sheep demonstrating longer generation time at lower population densities (Coulson & Crawley 2004). However, generation time does not always show this pattern with population density in ungulates (Gaillard *et al.* 2005; Bjørkvoll *et al.* 2012). For instance, in contrast to Soay sheep, roe deer populations show an increase in generation time with increasing population size (Nilsen *et al.* 2009). This contrasting pattern might be explained by the between-species differences in the

interplay between density-dependent responses of survival and reproduction and potential demographic impact of these parameters. When density-dependent responses exactly match demographic elasticity patterns, generation time remains unchanged. Generation time increases if density-dependent change relative to demographic elasticity is higher in reproduction than in survival and decreases if the reversed pattern occurs.

Our model shows that the difference in body mass between optimal life histories at low and high densities can be generated from density-mediated phenotypic plasticity rather than evolution. Asymptotic body mass within a life history strategy differed more between low- and high-density environments than the difference of asymptotic body masses of the best low- and high-density strategy within an environment. Soay sheep have shrunk in size over the course of the long-term study (Ozgul *et al.* 2009), which was predominantly thought to be due to a plastic response to altered winter conditions mediated through slower growth rates of lambs. Increased population density increases competition for food and, as sheep are scramble competitors (Pérez-Barbería & Gordon 1999), reduces the energetic gain per individual thereby lowering body growth rates. Less severe winter conditions extended the grass growing season, giving lighter individuals a better chance to survive the winter, resulting in reduced average growth rates and increased population density (Ozgul *et al.* 2009).

Although our approach revealed evidence for directional selection of longer generation times at low population densities, the predicted generation times exceeded maximum life expectancy in Soay sheep. The reason for this is that we did not include age-dependence of demographic parameters, and in particular senescence, in our model (Caswell 2001; Jones *et al.* 2008). Stage- and age-structured integral projection models have been developed (Coulson *et al.* 2010; Ellner *et al.* 2016) but they include more parameters than the simple IPM we used here. The inclusion of a senescent age-class would reduce estimates of

generation time at low density, but would have increased model complexity. It is not clear in what way the inclusion of a senescent age-class would have altered our results, but this should not alter our key finding that, contrary to the standard  $r$ - $K$  selection theory, generation time was longer at low than at high density. Indeed, from a life table approach including the full schedule of age-specific survival and reproduction, Coulson & Crawley (2004) did report longer generation times at low density (cohort generation time of 4.92 years vs. 2.95 at high density).

Our modelling approach provides a framework to study density-dependent selection within a natural population allowing for life-history trade-offs. Our model only considered a single trait, body mass. However, other traits influence survival and reproduction and hence carrying capacity, generation time and asymptotic body mass. If we were to extend our size-structured life history models to include other traits such as metabolic rate (Wortel *et al.* 2018) and energy budgets (Smallegange *et al.* 2017), we may expect the variance in the scatter around Fig. 3 to decline as we search for multi-trait structured life history-strategies. However, this would be challenging as model complexity would further increase while interpretation of the results becomes more challenging.

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## Table

**Table 1.** Parameter values used from deterministic and stochastic IPMs parameterized by Coulson (2012). Stochastic IPMs makes use of yearly random effects in each function. We report the standard deviation of the distribution of the random effect of year.

Parameter	Deterministic model	Stochastic model	Description
$s_0$	-0.2392	0.5807	Survival: intercept
$s_1$	0.1775	0.2128	Survival: slope body mass
$s_2$	-0.0043	-0.0074	Survival: slope population size
$\varphi_s(0, \sigma_s)$		0.9372	Survival: yearly random effect
$r_0$	-1.7839	-1.9421	Recruitment: intercept
$r_1$	0.1090	0.1112	Recruitment: slope body mass
$r_2$	-0.0032	-0.0030	Recruitment: slope population density
$\varphi_r(0, \sigma_r)$		0.2824	Recruitment: yearly random effect
$\gamma_0$	10.6032	11.0853	Development, mean: intercept
$\gamma_1$	0.6049	0.6032	Development, mean: slope body mass
$\gamma_2$	-0.0026	-0.0037	Development, mean: slope population size
$\varphi_\gamma(0, \sigma_\gamma)$		0.4245	Development, mean: yearly random effect
$\gamma_3$	3.7114	3.6716	Development, variance: intercept
$\gamma_4$	-0.0161	-0.0214	Development, variance: slope body mass
$\varphi_{\gamma v}(0, \sigma_{\gamma v})$		1.574	Development, variance: yearly random effect
$\delta_0$	9.8065	11.0003	Inheritance, mean: intercept
$\delta_1$	0.2544	0.2277	Inheritance, mean: slope body mass
$\delta_2$	-0.0069	-0.0081	Inheritance, mean: slope population size
$\varphi_\delta(0, \sigma_\delta)$		0.7428	Inheritance, mean: yearly random effect
$\delta_3$	8.7540	7.3228	Inheritance, variance: intercept
$\delta_4$	-0.1219	-0.0823	Inheritance, variance: slope body mass
$\varphi_{\delta v}(0, \sigma_{\delta v})$		0.0001	Inheritance, variance: yearly random effect

## 571 **Figure legends**

572 **Figure 1.** How survival (a), fertility (b), expected development (c,e), expected mother-  
573 offspring relationship (d,f), reproductive investment (g) and log population growth (h) vary  
574 with population density in the fittest low density (blue) and high density (red) life histories  
575 (solid lines) and the next four fittest life histories at low and high density (dotted lines). Each  
576 association is evaluated at the mean body mass of each strategy. The vertical dotted line at  
577 the population size of 400 individuals is approximate population size of the Soay sheep  
578 population over the period the model was parameterised (see Coulson 2012).

579 **Figure 2.** Relationship between body mass and survival (a), fertility (b), expected growth (c),  
580 expected mother-offspring relationship (d) at low population size of 200 individuals (orange  
581 lines) and at high population size of 600 individuals (light blue lines). Each of the 10,000  
582 orange and blue lines represent one strategy. The blue thick lines represent the best low-  
583 density life history strategy, the red thick lines represent the best high-density life history;  
584 solid at low population density, dashed at high population density. The variance around the  
585 expected growth (e), and variance around the expected mother-offspring relationship (f) are  
586 not density dependent and are therefore coloured grey.

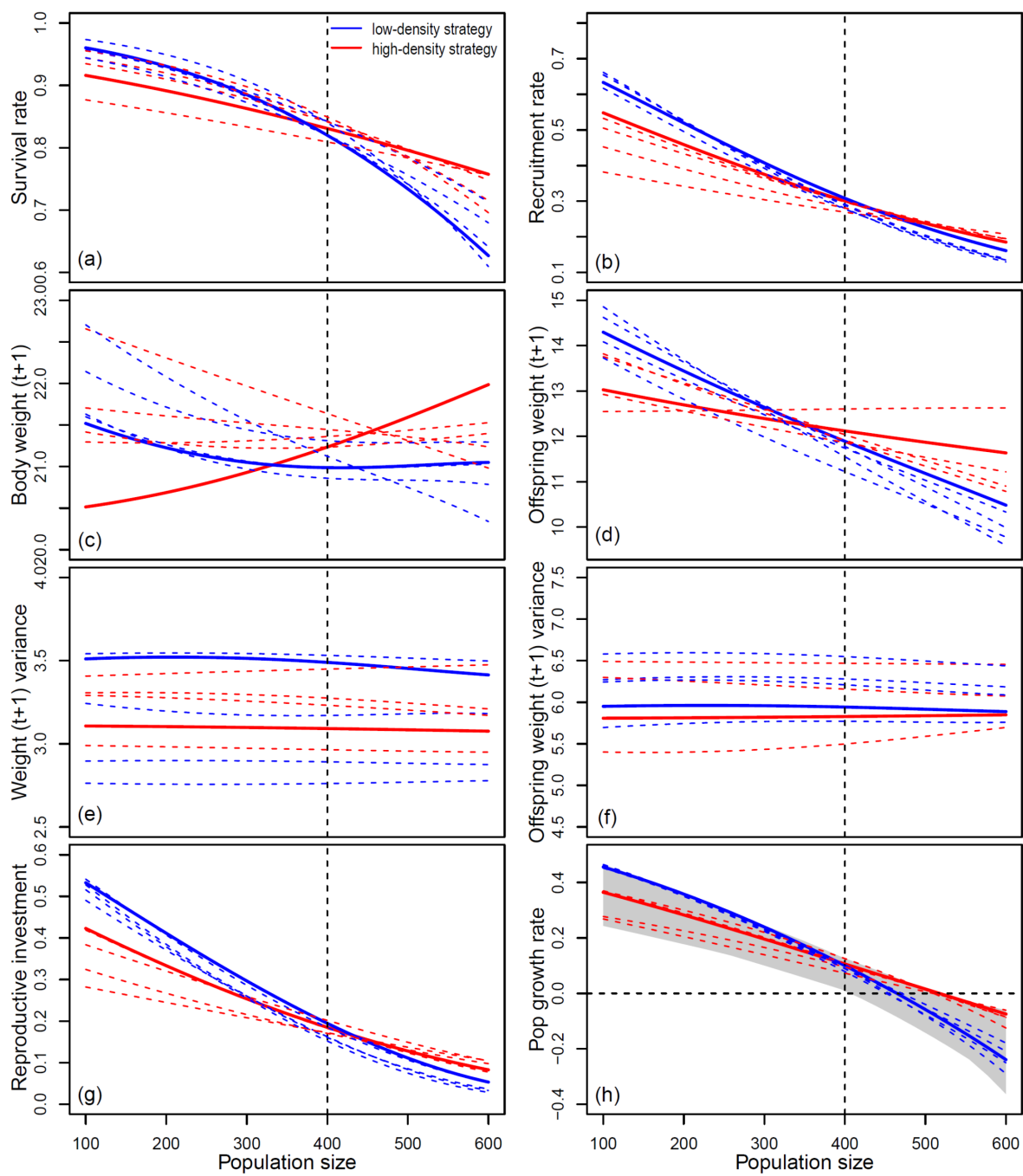
587 **Figure 3.** Correlation between generation time with carrying capacity (a) and population  
588 growth rate  $\lambda$  (c) and asymptotic body mass (b, d) at low (a, b) and high (c,d) density.  
589 Each point represents a strategy; green lines represent smooth loess curves. At low density  
590 the slopes of the regression lines are positive (a, b), indicating selection for a longer  
591 generation time and a large body size. The converse is true at high density (c,d).

**Figure 4.** Density plots of the distribution of asymptotic body mass at low (blue) and high (orange) population density. The blue and red vertical lines represent the location in the distribution of the fittest low- and high-density strategies, respectively. The red dashed vertical line represents the asymptotic body mass of the fittest high-density strategy in a low-density environment. Note that to reduce clutter, the location of the fittest low-density strategy is not marked in the distribution of asymptotic body masses at high population density. The horizontal black line represents the difference in asymptotic body mass between the fittest high-density strategy at low and high population density. The grey line represents the difference in asymptotic body mass between the fittest low- and high-density strategies at low population density. Because the black line is longer than the grey line this suggests that observed changes in body mass in the Soay sheep population are likely due to density-mediated phenotypic plasticity rather than evolution.

**Figure 5.** Population dynamics of low-density strategies and high-density strategies in stochastic environments. The figure on the left shows the population dynamic of the best low-density strategy (red line; mean population size was kept below carrying capacity mimicking density-independent mortality) and the best high-density strategy (red line).

610 Figure 1:

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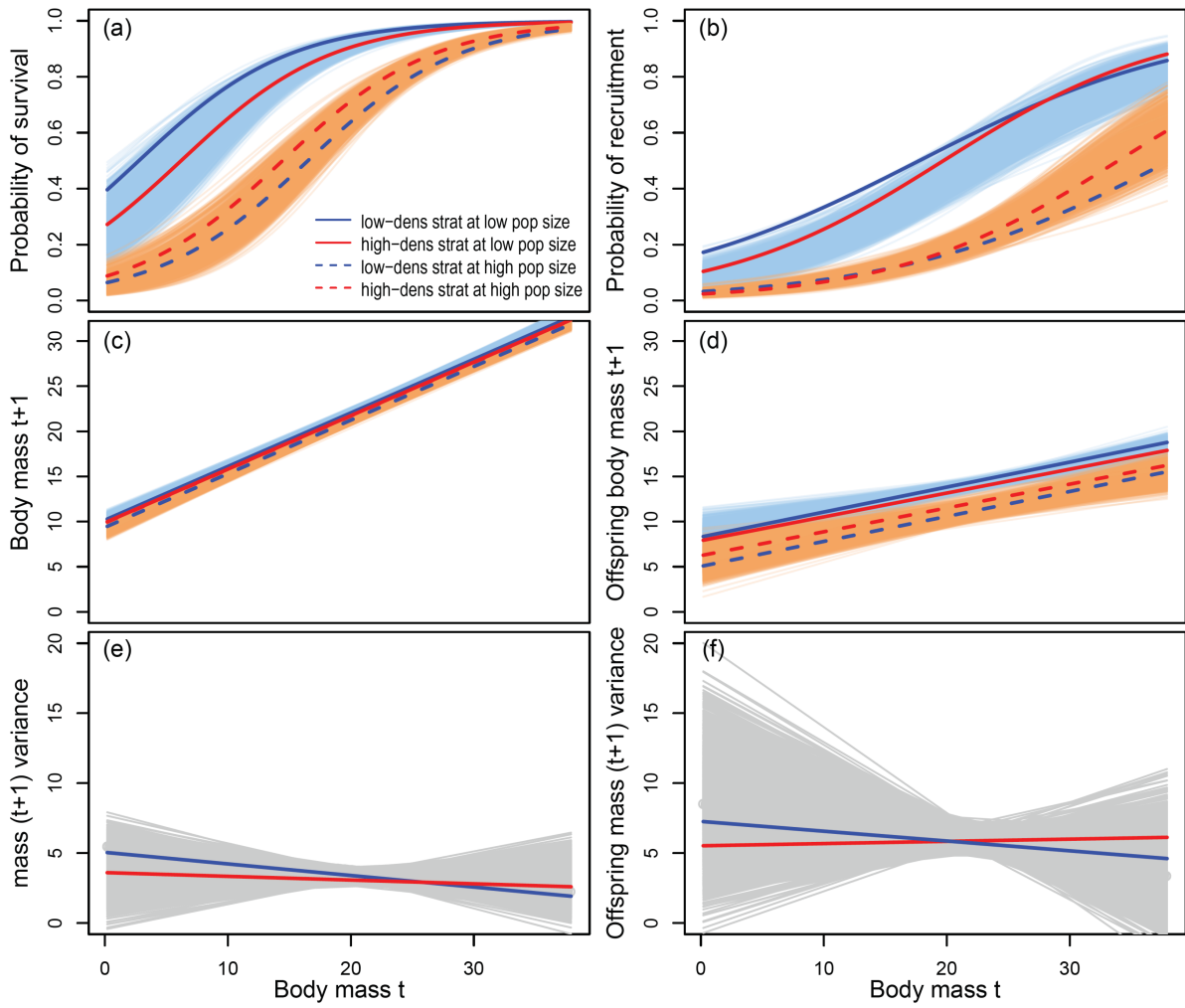


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614 Figure 2:

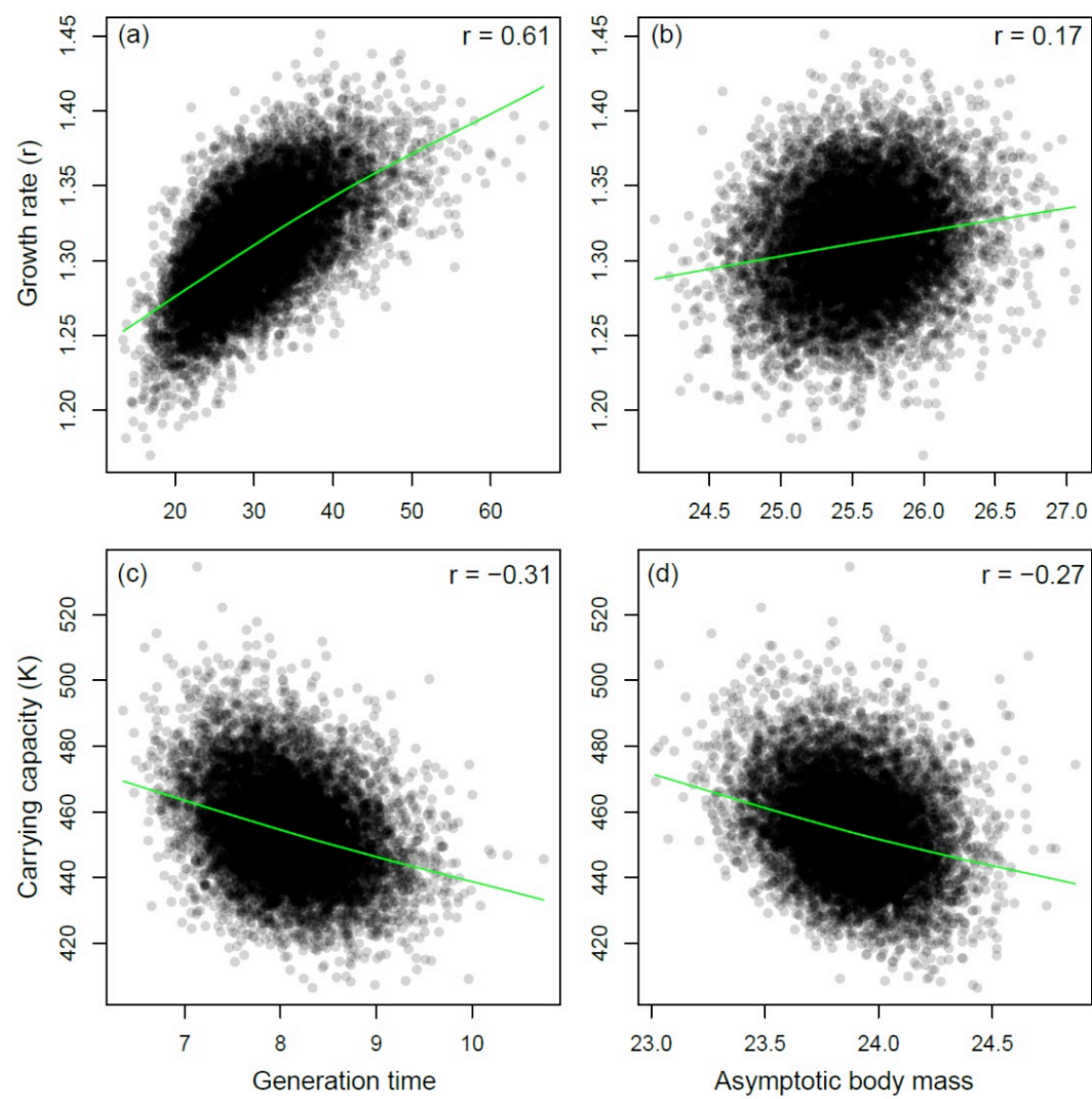
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617 Figure 3.

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Figure 4.

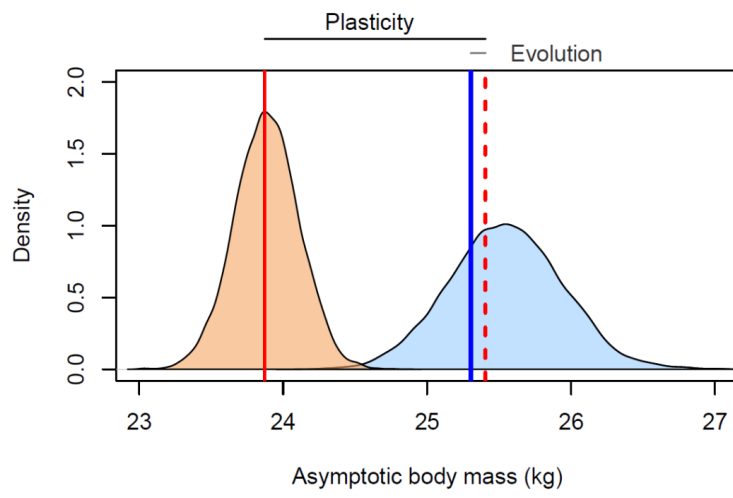




Figure 5:

