Density dependence shapes life-history trade-offs in a food-limited population

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Abstract

Quantifying trade-offs within populations is important in life-history theory. However, most studies focusing on life-history trade-offs focus on two traits and assume trade-offs to be static. Our work provides a framework for understanding covariation among multiple traits and how population density influences the traits. Using detailed individual-based data for Soay sheep, we find density strongly shapes life-history trade-offs and distribution of lifetime reproductive success (LRS). At low density, a trade-off between juvenile survival and growth structures life-history variation whereas at equilibrium density (K), trade-off between reproduction and juvenile survival is the major structuring axes. Contrary to Lomnicki's prediction, we find the distribution of LRS is highly constrained at K, with mothers of adult sizes contributing the most to reproduction. Our results offer insights into how high density limits diversity of individual life-histories, advance an understanding of dynamic nature of trade-offs and have implications for evolution via density-dependent selection.

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¹³ HJ performed analyses and writing, WZ, RK, JMG, TC, ST contributed ideas, analyses and writing, RK,

¹⁴ TC, contributed data.

15 Data accessibility statement

¹⁶ The data and code that support the findings of this study are publically available on Zenodo at the link. The

¹⁷ zenodo url is https://zenodo.org/records/10839977.

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Abstract

Quantifying trade-offs within populations is important in life-history theory. However, most stud-25 ies focusing on life-history trade-offs focus on two traits and assume trade-offs to be static. Our work 26 provides a framework for understanding covariation among multiple traits and how population den-27 sity influences the traits. Using detailed individual-based data for Soay sheep, we find density strongly 28 shapes life-history trade-offs and distribution of lifetime reproductive success (LRS). At low density, a 29 trade-off between juvenile survival and growth structures life-history variation whereas at equilibrium 30 density (K), trade-off between reproduction and juvenile survival is the major structuring axes. Con-31 trary to Lomnicki's prediction, we find the distribution of LRS is highly constrained at K, with mothers 32 of adult sizes contributing the most to reproduction. Our results offer insights into how high density 33 limits diversity of individual life-histories, advance an understanding of dynamic nature of trade-offs 34 and have implications for evolution via density-dependent selection. 35

36 1 Introduction

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There is tremendous variation in life-history strategies (Roff 1992; Stearns 1992). The evolution of these 37 strategies is known to be constrained by physiological limitations and in food-limited populations by trade-38 offs in resource allocation (Stearns 1989; Descamps et al. 2016). Evolutionary theory posits that organisms 39 must allocate limited resources towards different suite of traits to optimize their fitness thereby resulting in 40 trade-offs. Despite evidence for trade-offs, e.g., offspring-size/number (Smith and Fretwell 1974; Venable 41 1992), immunocompetence and life-history traits in birds (Norris and Evans 2000), trade-offs observed in 42 natural systems are less ubiquitous than those hypothesized by life-history theory (Metcalf 2016). Trade-43 offs may be difficult to detect because individual variation in resource acquisition is often larger than varia-44 tion in resource allocation (Van Noordwijk and De Jong 1986), thereby masking life-history constraints in 45 empirical studies. Although life-history theory predicts costs of reproduction and therefore negative corre-46 lations among certain traits, individuals can show positive, negative or zero correlations (due to individual 47 heterogeneity or environmental stochasticity) while simultaneously being involved in a classical physio-48 logical trade-off (Bell and Koufopanou 1991; Horvitz et al. 1997; Zera and Harshman 2001; Hodgson and 49 Townley 2004; Descamps et al. 2016). 50 Whether trade-offs within a population are static or change with environmental or demographic condi-51 tions is an important question. For instance, as population density varies, individual fitness (i.e. the ability 52 to survive and reproduce) may also vary thereby impacting life-history outcomes. This could result from 53

chance encounters with potential mates or competitive individuals. Thus, variation in population density

⁵⁵ can generate time-varying selection for different life-history strategies, via density-dependent selection.

⁵⁶ The concept that selection on life-history traits could vary with population density has been discussed both

⁵⁷ empirically and in theory by Dobzhansky (1950), MacArthur (1962), and Roughgarden (1971). Pianka

(1970) proposed the r - K selection continuum, where r (that refers to intrinsic population growth rate)

⁵⁹ corresponds to strategies that maximize productivity (i.e. putting all energy into reproduction and pro-

ducing more offspring) at low density and K (that refers to equilibrium carrying capacity) corresponds to

strategies that maximize efficiency (i.e. putting most energy into maintenance and producing only a few fit

62 offspring).

⁶³ This brings us to our central question:- how do we understand life-history variation at different densities

⁶⁴ while identifying life-history trade-offs (often masked due to individual variation in resource acquisition)?

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- ⁶⁵ Although we often tend to think of trade-offs and density dependence separately, we show here that they
- are intimately linked. Previous studies (Czesak and Fox 2003; Agrawal et al. 2010) have mostly focused
- on covariation between two traits but in our research we examine trade-offs among multiple traits by con-
- ⁶⁸ sidering the exceptionally detailed long-term observational data collected on Soay sheep (*Ovis aries*) in
- ⁶⁹ the St. Kilda archipelago, Scotland. The sheep system is of special interest because this population has
- ⁷⁰ been shown to fluctuate dramatically thereby exhibiting potential for density-dependent selection. Coulson
- ⁷¹ et al. (2001) noted population declines of up to 60% occurred when population size was large and winter
- ⁷² weather was harsh. This is due to nonlinear interactions between winter weather, population's response
- ⁷³ to changes in density, and food availability (Grenfell et al. 1992; Clutton-Brock et al. 1996; Coulson et al.
- ⁷⁴ 1999). The life-history and physiological mechanisms operating at low density may differ from those oper-
- ⁷⁵ ating at high-density (under intense resource limitation), altering the nature and direction of trade-offs.
- ⁷⁶ Our first result is that density dependence shapes life-history trade-offs in a food-limited population of
- ⁷⁷ large herbivore. At low densities, we find negative correlations between survival and growth during the
- ⁷⁸ juvenile stage (defined in the methods section). However, the intensity and strength of the negative associ-
- ⁷⁹ ation between juvenile survival and growth is density-dependent and increases with increasing population
- 80 density. Interestingly, at equilibrium capacity (K), new trade-offs appear and strong negative association
- ⁸¹ between reproduction and juvenile survival structures life-history variation within the population. Mul-
- ⁸² tiple trade-offs are revealed by performing a Principal Component Analysis (PCA) on average vital rate
- ⁸³ functions (survival, recruitment, growth). We find changes in population density affect the relationships
- ⁸⁴ among vital rates such as, survival, growth and fecundity. The strength of density-dependent responses of
- vital rates varies a lot, thereby resulting in trade-offs. Our findings are consistent with life-history theory
- ⁸⁶ (Stearns 1992) which predicts trade-offs prevent individuals from being proficient at both surviving and
- growing to large sizes. In addition, Kentie et al. (2020) found Soav sheep individuals with an optimal life
- history strategy at high density were different to those having an optimal strategy at low density and thus
- ⁸⁹ individuals could not maximise fitness in both high- and low-density environments.
- ⁹⁰ Next, we examined the effects of density on variation in demographic measures. The demographic mea-
- sures of interest are variation in average vital rate functions, net reproductive rate R_0 , and stable age-stage
- ⁹² distribution (SSD). We also calculated the distribution of lifetime reproductive success (LRS) using Tul-
- ⁹³ japurkar et al. (2020) to tease apart trade-offs between allocation in survival and future reproduction. Many
- ⁹⁴ empirical studies have consistently revealed that distribution of LRS are often non-normal, zero-inflated
- ⁹⁵ and highly skewed (Cabana and Kramer 1991; Tatarenkov et al. 2008). This begs the question: does the
- ⁹⁶ distribution of LRS and the skew remain consistent across all population density regimes?
- ⁹⁷ We find the distribution of LRS to be highly constrained at high densities. LRS is an important compo-
- ⁹⁸ nent of individual fitness and our research predicts density dependence strongly affects the distribution of
- ⁹⁹ LRS. In particular, it is the females at prime adult size (~ 25 kg) that contribute the most at high densities,
- whereas at low densities contributions come from a wider range of body size ($\sim 14-25$ kg). We find a sim-
- ¹⁰¹ ilar pattern for average vital rate functions and stable stage distribution. We base our model and results on
- ¹⁰² previously published Integral Projection Model (IPM) and delifing method presented in Coulson (2012)
- and Coulson et al. (2006), respectively. Using empirical data and life-history trade-offs between IPM pa-
- ¹⁰⁴ rameters, Kentie et al. (2020) created a covariance matrix that allows us to generate strategies spanning the
- ¹⁰⁵ range of possible individual life-histories that Soay sheep are expected to follow.

¹⁰⁶ The work allows us to examine trade-offs, variation in LRS at low and high densities, and comment on

¹⁰⁷ how density can operate. Characterizing trade-offs as a function of population density can not only help

elucidate the various determinants of observed life-history variation but will also determine what strategies

¹⁰⁹ may be most important for population persistence. Our framework is especially relevant for plant or an-

imal species with individual-based life-history data such as *Hypericum cumulicola* (Quintana-Ascencio

and Morales-Hernández 1997), *Heliconia acuminata* (Brooks et al. 2019), *Poecilia reticulata* or com-

monly Trinidad guppies (Reznick et al. 2006; Bassar et al. 2016), and *Cervus elaphus* or commonly red

deer (Gaillard et al. 2003), among others.

114 2 Model and Methods

¹¹⁵ We begin with IPM for Soay sheep and then describe sampling life-histories to evaluate trade-offs and the

distribution of lifetime reproductive success. IPMs are structured population models that use linear (or

linearized) regressions to describe the expected phenotypic trait trajectories (Coulson 2012; Ellner et al.

2016). The IPM consists of four functions that describe how traits such as body size (z) influence survival,

reproduction, growth and offspring size. All analysis was carried in R version 4.1.3 (2022-03-10) and the

data and code are available here (zenodo link is: https://zenodo.org/records/10839977).

¹²¹ For Soay sheep survival, stage transitions and reproduction during a single time interval depend on age and

stage (Coulson 2012). Based on Coulson (2012) and Kentie et al. (2020), we model Soay sheep demogra-

phy in discrete time with population projection matrices (PPMs) structured effectively by stage and add an

maximum age of death. That is, we assume that at each age, the stage-structured matrices have same sur-

vival and fertility rates until the sheep eventually die off at a certain age. Based on empirical observations,

a maximum age of death is set to 16. This enables us to construct a block matrix with stage-structured ma-

127 trices for each age.

¹²⁸ Note that the models are parameterised using female sheep data since the growth rate of Soay sheep pop-

¹²⁹ ulation is known to be female-dominant (Coulson et al. 2001) and there is no limiting effect of the num-

¹³⁰ ber of males for female reproductive output. We use previously published data and IPM for Soay sheep

131 (Coulson 2012; Kentie et al. 2020). The generalized linear functions for survival and reproduction are as

132 follows:

$$S(z,t) = \frac{1}{1 + e^{-(s_0 + s_1 z + s_2 N_t)}}$$
$$R(z,t) = \frac{1}{1 + e^{-(r_0 + r_1 z + r_2 N_t)}}$$

Here, N_t is the population size at time *t*. s_0, s_1, s_2 are the intercept, slope and coefficient for body size and

density dependence and are our parameters of interest for varying survival. The same holds with r_0, r_1, r_2

and recruitment function. For the parameter values, both survival and reproduction increase with body size

¹³⁶ *z* until it eventually saturates.

The growth G'(z' | z, t) and parent-offspring (also called inheritance) D(z' | z, t) functions are described by Gaussian probability density functions. The growth function G'(z' | z, t) is the probability that an individual with body mass z at time t will have a body mass z' at time t + 1. The parent-offspring function D(z' | z, t) is the probability that an individual with body mass z at time t will produce an offspring with body mass z' at time t + 1.

$$G'(z' | z, t) = \frac{1}{\sqrt{2\pi\sigma_g^2[z']}} e^{-\frac{(z-E_g[z'])^2}{2\sigma_g^2(z')}}$$
$$D(z' | z, t) = \frac{1}{\sqrt{2\pi\sigma_d^2[z']}} e^{-\frac{(z-E_d[z'])^2}{2\sigma_d^2(z')}}$$

Here, $E_g[z']$ is a linear function that predicts expected body mass and similarly $E_d[z']$ predicts offspring's expected body mass at t + 1 and are given by $E_g[z'] = \gamma_0 + \gamma_1 z + \gamma_2 N_t$ and $E_d[z'] = \delta_0 + \delta_1 z + \delta_2 N_t$. The function describing variance around the expectation $\sigma_g^2(z')$ and $\sigma_d^2(z')$ are also linear and are independent of population density. $\sigma_g^2(z') = \gamma_3 + \gamma_4 z$ and $\sigma_d^2(z') = \delta_3 + \delta_4 z$. The table below summarizes the descriptions of our parameters of interest.

We define Growth Increment as average size in the next time minus size today divided by the size today: 142 Growth Increment, $G = (E_g[z'] - z)/z = (\gamma_0 + (\gamma_1 - 1)z + \gamma_2 N_t)/z$. The intuition is that individuals reach 143 an asymptotic size based on the stage (say y) at which growth increment (G) becomes 0. We can then par-144 tition growth increment until stage y for which individuals reach their asymptotic size. The individuals yet 145 to reach their asymptotic size will have a positive growth increment and is denoted by G. We refer to these 146 individuals as juveniles in this manuscript. This is important to note because we then partition survival 147 based on individuals who have not yet reached their asymptotic size and describe it as juvenile survival (as 148 is described in the next section). Soay sheep are determinate growers, meaning that they grow from con-149 ception to some time on their trajectory when they reach an asymptotic size. Effectively, from this time 150 onwards, the sheep should not vary much in size on average during the adult stage and hence we do not 151 consider growth beyond reaching asymptotic size. 152

We use body mass distributed along 50 size classes as the trait since it is known to affect both survival and reproduction in Soay sheep, and is affected by population density. The IPM functions describe how body size z influences survival, reproduction, growth and offspring size by iterating the distribution of z at t, n(z,t) to n(z',t+1):

$$n(z',t+1) = \int \left[D(z' \mid z,t) R(z,t) + G'(z' \mid z,t) S(z,t) \right] n(z,t) dz$$

where population size is $N(t) = \int n(z,t) dz$. In matrix terms, the IPM can be written as:

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

Using the IPM functions described above, we construct 50×50 stage-based matrices corresponding the each age for fertility and survival given by F(z',z) = D(z',z)R(z) and P(z',z) = G'(z',z)S(z) (Steiner et al. 2014). We can construct a matrix \mathbf{P}_a which describes probability that an individual in stage z at age t is alive in stage z' at t + 1 which is then used to calculate survivorship denoted by \mathbf{L}_a . Similarly, we get \mathbf{F}_a matrix which describes the number of stage z' recruits produced by a female of size z at age a. The net reproductive rate R_0 is calculated as the dominant eigenvalue of the matrix $\sum_a \mathbf{F}_a \mathbf{L}_a$. Note that the summation for ages a is until the maximum age of death (set to 16). In addition, we keep the matrices constant

Parameter	Description
<i>s</i> ₀	Survival: intercept
<i>s</i> ₁	Survival: slope body mass
<i>s</i> ₂	Survival: slope population size
<i>r</i> ₀	Recruitment intercept
r_1	Recruitment: slope body mass
r_2	Recruitment: slope population density
γ	Development, mean: intercept
γ_1	Development, mean: slope body mass
γ_2	Development, mean: slope population size
γ3	Development, variance: intercept
γ4	Development, variance: slope body mass
δ_0	Inheritance, mean: intercept
δ_1	Inheritance, mean; slope body mass
δ_2	Inheritance, mean: slope population size
δ_3	Inheritance, variance: intercept
δ_4	Inheritance, variance: slope body mass

Table 1: The table provides a list of 16 parameters we use for the four IPM functions (Coulson 2012).

¹⁶⁰ for all ages below the age of death which greatly simplifies our analysis. We can do this for different life-

histories to understand the pattern of variation within the population. Below we describe how we generate

many life-histories based on Coulson et al. (2006) and Kentie et al. (2020).

2.1 Average vital rate functions at SSD to evaluate trade-offs

Coulson et al. (2006) introduced an approach called delifing or leave one out to estimate the contribution 164 of an individual to realized changes in population size and stage-age distribution during a time interval. 165 Using delifing, Kentie et al. (2020) estimated covariance across Soay sheep life-history parameters (such 166 as s_0, s_1, \dots and so on) and examined how fluctuating population densities affect within-population varia-167 tion in life-history strategies. The covariance structure for Soay sheep life history parameters is then used 168 to span the range of possible strategies we expect sheep to follow given the phenotypic life-history trade-169 offs within and between demographic functions. We sample parameter sets of vital rates from a space of 170 10,000 life-history strategies (description of delifing in Coulson et al. (2006) and in Methods section of 171

¹⁷² Kentie et al. (2020)).

A parameter set comprises of the 16 parameters: $(s_0, s_1, s_2, r_0, r_1, ...)$, and are described in Table 1. For

specific distribution (and values) for each of the parameters we refer to Kentie et al. (2020). We sample

¹⁷⁵ 200 such sets from the covariance matrix (using the delifing method). We calculate population growth rate

 $_{176}$ given by λ as the dominant eigenvalue of the age-stage block matrix. The individuals are classified into 50

- equal sized stage classes from 1 kg to 38 kg (based on their body size). Thus the dimension of the block
- matrix is 800×800 because we have 50 size classes and 16 ages. For each parameter set, carrying capacity *K* is evaluated by finding the population size that results in λ converging to 1. Carrying capacity ratios
- ity *K* is evaluated by finding the population size that results in λ converging to 1. Carrying capacity ratios (0,0.5,1) correspond to population size N = 0, N = K/2 and N = K, respectively. The results are robust
- with respect to the sampling procedure and sample size. Figure A1 in the Appendix shows the range of

equilibrium capacity for the 100 parameter sets.

¹⁸³ To explore trade-offs, we calculated vital rate functions such as, juvenile survival (Ss), adult survival (Sb),

Recruitment (R), and Growth (G). As discussed before, we partition individuals before they reach asymp-

totic size based on the stage (say y) at which growth increment becomes 0 and take the average for growth increment until stage y (denoted by G). Similarly, survival for those individuals (Ss) is evaluated by aver-

increment until stage y (denoted by G). Similarly, survival for those individuals (Ss) is evaluated by averaging up to the stage (v) and is called invenile survival. Sheep are considered at their asymptotic size and

should not vary much in size on average during the adult stage. Hence we do not consider growth beyond

reaching asymptotic size. This way we generate a dataframe/matrix of average vital rates weighted by sta-

¹⁹⁰ ble stage distribution (SSD) for 200 parameter sets. Note that the function describing variance around the

- expectation $\sigma_{\rho}^{2}(z')$ is independent of population density so we don't consider it (we verified using calcula-
- ¹⁹² tions and the variance is small).

¹⁹³ To understand trade-offs, we perform a PCA on average vital rate functions discussed above and the corre-

lation plot at three densities. We evaluate the carrying capacity K for each parameter set described above

¹⁹⁵ and then calculate the average vital rate functions at the carrying capacity. This gives us a dataframe with

¹⁹⁶ 200 values for the 4 vital rate functions of interest (Ss, Sb, R, G). We can then repeat the exercise by calcu-

¹⁹⁷ lating the average vital rate function at any ratio of carrying capacity. We predict the effects of density by

focusing on population N = 0, N = K/2, N = K. We also explore the results from increasing the equilib-

¹⁹⁹ rium capacity beyond N = K.

²⁰⁰ Since we are interested in examining the influence of population density on vital rate covariations, we note

the derivative of S(z,t) and R(z,t) with respect to N is of the form:

$$\frac{\partial S(z,t)}{\partial N} = s_2 S(z,t)(1 - S(z,t))$$
$$\frac{\partial R(z,t)}{\partial N} = r_2 R(z,t)(1 - R(z,t))$$

Since S(z,t) and R(z,t) are both logistic functions, they are always between 0 and 1. The values of s_2 and r_2 are negative and thus the derivative of S(z,t) and R(z,t) with respect to N will always be negative. We plot S(z,t) and R(z,t) for different values of N in the Appendix (Figure A2).

205 2.2 Lifetime Reproductive Success (LRS)

LRS measures the number of offspring an individual produces over its lifespan and individuals may produce 0, 1, 2... offspring, until they eventually die. The number of offspring produced during a time interval depends on the age and stage at the beginning of the time interval and is specified by probability distributions of producing $0, 1, 2, \cdots$ offspring. The distribution is assumed to be Bernoulli since Soay sheep produce either 0 or 1 offspring in a time interval and we ignore twinning (less than 1.9% of the offspring recruited are twins Simmonds and Coulson (2015)). Thus, following Tuljapurkar et al. (2020), we can compute the exact distribution of LRS for the age-stage-structured vital rates.

Tuljapurkar et al. (2020, 2021) developed an exact analysis to calculate the probability distribution of LRS for species described by age + stage models. The method assumes the empirical vital rates are known for a large cohort of individuals, for each st(age) of individuals life cycle. We use the method detailed in (Tuljapurkar et al. 2020) to compute LRS distribution of Soay sheep individuals and examine demographic

²¹⁷ heterogeneities in the distribution.

The mean of LRS distribution is the net reproductive rate R_0 . We decompose R_0 into probability of having

²¹⁹ no offspring and R_0 conditional on making non-zero offspring, denoted by γ and is easily calculated as one ²²⁰ minus the probability of reproductive failure (β_0).

 $R_0 = \sum_{k \ge 0} k eta_k = \sum_{k > 0} k eta_k$ $eta_0 = 1 - \sum_{k > 0} eta_k$

where β_k is the probability of having *k* offspring. We are interested in $\gamma = \sum_{k>0} \beta_k$, which is the mean LRS conditional on reproducing at least once.

223 **3 Results**

3.1 Trade-offs and Correlations at different densities

Using PCA, we examine trade-offs between average vital rate functions evaluated at SSD, juvenile survival (Ss), adult survival (Sb), recruitment (R), and growth increment for individuals before they reach asymp-

²²⁷ totic size (G) (Figure 1).

Most (between 68 and 80%) of the observed variation in vital rates is explained by the first two principal 228 components. The variance along the first principal component is explained by the trade-off between sur-229 vival and growth until individuals reach their asymptotic size at low densities. However, at high densities 230 the trade-off between survival and reproduction becomes most significant and structures life-history co-231 variation as shown in Figure 1 and Table A3 (sign for Reproduction and juvenile survival are opposite). 232 We validated our results using broken stick model and identified principal components whose eigenval-233 ues surpass those predicted by the broken stick model (Figure A5 in Appendix). The variation captured by 234 these components reflects significant underlying patterns in our data and is not a result of chance alone. 235 We find negative correlation between Growth Increment (G) and Survival (Ss) for individuals before they 236

reach asymptotic size is present at all densities and corresponds to the main structuring axis of life history

variation across individuals. As we increase the density to equilibrium capacity (K), the strength of the

negative correlation between growth increment and survival further increases (Figure A6 in Appendix).

²⁴⁰ Interestingly, the trade-off between reproduction and juvenile survival is the largest at high population den-

sities and reveals itself only in the density dependent case in the bottom panel of the figure A4. In addition,

juvenile survival negatively correlates with all other vital rates- recruitment (R), adult survival (Sb) and

243 growth (G).

²⁴⁴ The figure A4 in Appendix shows the intensity of the association between juvenile survival, growth and

reproduction at the three densities. This association has an increasing importance in shaping life history

variation with increasing density and that at high densities there is a three-way trade-off between survival,

247 growth increment, and recruitment.

²⁴⁸ What happens beyond equilibrium carrying capacity? We examine the demographic consequences when

- the population density increases beyond the equilibrium carrying capacity (Figure A7 in the Appendix).
- ²⁵⁰ We find that now the trade-off between survival and reproduction weakens as population density is in-
- creased beyond carrying capacity (K) but the growth-survival trade-off remains strong as shown in the
- ²⁵² correlation and PCA plot evaluated at population density N = (1.2)K and N = (1.4)K.



Figure 1: PCA results for average vital rate functions at SSD. Each panel corresponds to a density scenario. Top most panel is for N = 0 case, followed by N = K/2, and N = K. Here Ss and Sb correspond to average survival (over 200 life-histories) for individuals before and after they reach their asymptotic size, respectively. Similarly, GIs and GIb is the average growth increment from one time to next for individuals before and after they reach their asymptotic size, and R is the average reproductive output.

3.2 Variation in *R*₀ at different densities

Having identified the dynamic nature of trade-offs with population density, we wanted to examine density effects on demographic measures such as the net reproductive rate (R_0) (same as mean of LRS) and the stable stage distribution. The R_0 is calculated as the mean of the LRS distribution as well as through the age-stage block matrix (results are consistent). As discussed in the methods section, the model is age and stage-based in the sense that at age 16 we set survival to 0.

- Figure 2 depicts the decrease in variation in R_0 as a function of population size and we find both mean and
- variance of R_0 decreases with increasing N. Since both S(z,t) and R(z,t) are monotonically decreasing

in N, R_0 is also a monotonically decreasing function of *N*. The key point here is the extent of variation in R_0 for a density-independent (N = 0) and density-dependent case. The life-histories with large R_0 at low densities are highly impacted.



Figure 2: R_0 as a function of population size. Each black point represents the R_0 for a life-history evaluated at the particular population size. The red triangle denotes the mean of the 200 life-histories from the covariance matrix.

²⁶⁴ What factors contribute to decline in R_0 ? We explore the question by understanding the variation in SSD

- and mother's size distribution at three population sizes (N = 0, N = K/2 and N = K). Since we are interested in sizes (stages), we examine the SSD for stage-based matrix population model. For each sample
- of parameter set, we estimate the equilibrium size K and calculate the stable stage (size) distribution (Figure A8 in Appendix). We take the average of SSD over 200 of our samples. Then we repeat by setting the
- population size at 0 and at K/2.

As population size increases from 0 to equilibrium population size K, the distribution/proportion of adults 270 increases while the proportion of juveniles decreases, in contrast with density-independent case which has 271 a higher proportion of juveniles (as shown in Figure A8 in the Appendix). We observe the same when we 272 examine the distribution for mother's size (scaled by SSD) as shown in Figure 3. We find the range of 273 mother's size to be less at higher densities thus contributing to lower R_0 . Thus, as density increases there 274 is a concentration toward individuals of large prime sizes (about 25kg) and contribution from individuals 275 of sizes between 15-25kg is diminished. This is interesting because not only is there more competition and 276 resource scarcity at high density but there are also less individuals contributing to reproduction. Thus, the 277 focus is to produce few extremely fit offspring and this aligns with r-K selection theory. 278

Lastly, we examine the relationship between R_0 at density-independence (by setting N = 0 to evaluate the matrices) and the equilibrium size K for the parameter sets. Figure A9 (in the Appendix) shows K and R_0 are slightly negatively correlated as found in Kentie et al. (2020). Our results align with Pande et al. (2020, 2022) as they show mean population growth rate when rare (a measure of invasibility Chesson (2003)) is
 limited in its use as a metric for persistence.



Figure 3: Plot for the distribution of Mothers size: on the x-axis we have mother's size distribution scaled by SSD and on the y=axis we have offspring size. Each panel corresponds to a density scenario. Left most panel is for N = 0 case, followed by N = K/2, and N = K.

3.3 Variation in vital rates

This section examines the relationship between average vital rate functions at SSD and mean lifetime reproductive success conditional on making at least one offspring (given by γ). We evaluate average juvenile survival (weighted by SSD) for our parameter set and regress against γ evaluated at the three population sizes (Figure 4).

We find although increase in juvenile survival increases γ_0 at low densities, near equilibrium size, R_0 and γ_0 are indifferent to changes in juvenile survival. We repeat the above by considering the relationship between average recruitment and average growth (at SSD) with γ_0 and the results are similar to that for juvenile survival. Figure 4 show the constraints operating at high densities and equilibrium population sizes and perhaps how the mechanisms operating at different population sizes are different.

294 3.4 Variation in LRS trajectories at different densities

²⁹⁵ We calculate the distribution of LRS (Tuljapurkar et al. 2020) for the 200 life-histories sampled from the

²⁹⁶ covariance matrix. From Lomnicki (1978)'s work, we hypothesize a higher variation in LRS among fe-

²⁹⁷ males at high than at low density and our results are different from Lomnicki's prediction (Figure A10 in

- Appendix). The LRS trajectories show considerable variation at N = 0 which is not reflected at high den-
- ²⁹⁹ sities since the size distribution is skewed toward individuals of large body sizes. It is remarkable how the



Figure 4: Trends for average vital rates at different population densities. On the y-axis is γ , that is the mean lifetime reproductive success conditional on making at least one offspring. The first three panels (left to right at N = 0, N = K/2, and N = K) have average juvenile survival rates at SSD on the x-axis, the second panel has average recruitment at SSD, and the last three panels have average growth at SSD.

- shape of the LRS distribution varies for the three density scenarios. At N = K (right-most panel in Fig-
- ³⁰¹ ure 5), the probability of havin zero offspring is higher when compared to the case when N = 0. For ani-
- mals (as discussed in the Methods section), the probability of having zero offspring corresponds to juvenile
- ³⁰³ mortality. The results are consistent with empirical observations since field studies find high juvenile mor-
- tality at equilibrium population sizes than at low densities.
- ³⁰⁵ To further examine trade-offs from LRS distributions, we generated life-histories where survival parame-
- ters (s_0, s_1, s_2) are sampled from the covariance matrix and the rest of the 13 parameters are fixed to their
- mean values. Similarly, we fixed all parameters to their mean values but recruitment parameters (r_0, r_1, r_2) .
- The top panel of Figure 5 shows the average distribution of lifetime reproductive success and the confi-
- dence intervals for each offspring number. In the bottom panel of 5, we find at low population density and
- despite fixed survival, small variation in fertility by chance alone can lead to higher or lower probability of
- having zero offspring. In the Appendix (Figure A10), we also calculate the distribution when all parame-
- 312 ters are perturbed and our results remain consistent.
- Finally, we fixed all parameters but growth parameters. Our expectation was the additive effect of survival
- (only) and growth (only) would be greater than the effect of varying both survival and growth parameters
- together. We find slight evidence for such a trade-off for low offspring (0, 1 and 2) but further analysis is
- needed to uncover the trade-off (Figure A11 in Appendix).



Figure 5: Plot for distribution of LRS. The top-three panels correspond to LRS distribution when only survival parameters are sampled from the covariance matrix and the rest of the parameters are fixed to their mean values. The bottom-three panels correspond to LRS distribution when only recruitment parameters are sampled and the rest of the parameters are fixed to their mean values. Each panel corresponds to a density scenario. Left most panel is for N = 0 case, followed by N = K/2, and N = K.

317 **4 Discussion**

³¹⁸ We examine the interplay between life-history trade-offs and changes in density in Soay sheep. We use

data from Kentie et al. (2020) to generate life-histories and found strong evidence for a trade-off between

survival and growth during the juvenile stage at low density and between reproduction and juvenile sur-

vival at high density (Figure A4 and Figure 1 in Appendix). Thus, the nature of this trade-off is not static.

The negative correlation and its explanatory power increase as population density increases. In addition, at carrying capacity (K) new trade-off arise between adult survival and juvenile survival. Thus, not all vital

carrying capacity (K) new trade-off arise between adult survival and juvenile survival. Thus, not all vital rates are equally impacted by changes in density, which gives rise to trade-offs. At low density, the demo-

rates are equally impacted by changes in density, which gives rise to trade-offs. At low density, the demographic trade-off between growth and survival during the juvenile stage can be viewed as the main axis of

graphic trade-off between growth and survival during the juvenile stage can be viewed as the main axis of life-history variation among individuals within population and aligns individuals along a slow-fast contin-

³²⁷ uum similarly to what has been consistently reported across species (Stearns 1983; Oli 2004; Gaillard et al.

³²⁷ uum similarly to what has been consistently reported across species (Stearns 1983; Oli 2004; Gaillard et al ³²⁸ 2016; Jiang et al. 2022; Van de Walle et al. 2023; Salguero-Gómez et al. 2016). However at high density,

³²⁸ 2016; Jiang et al. 2022; Van de Walle et al. 2023; Salguero-Gomez et al. 2016). However a ³²⁹ juvenile survival and reproduction structure life-history variation within the population.

³³⁰ Our findings are consistent with theory of life-history evolution (Stearns 1992) in that we find the evidence

for trade-offs which prevent individuals from being proficient at both surviving and growing to large sizes.

However, this markedly differs from previous analyses of intraspecific variation in life histories of verte-

However, this markedly differs from previous analyses of intraspecific variation in life histories of vertebrates, which reported a lack of structuring axis of variation among individual life histories and no support

for a slow-fast continuum (Van de Walle et al. 2023). This discrepancy might come from the absence of

³³⁵ control for density dependence in previous studies. Alternatively, our simulated individual life histories

might have included vital rate combinations that might have not been possible to observe in real individu-

³³⁷ als. Future work comparing potential (as investigated here) and realized (as analysed by Van de Walle et al.

(2023)) variation in individual life history strategies should allow to explain this discrepancy.

Our results align with Kentie et al. (2020) as we find individuals with an average life history can not si-339 multaneously maximise fitness for both high- and low-density environments. This is because demographic 340 measures such as average survival, reproduction at SSD and distribution of lifetime reproductive success 341 are highly constrained at high population densities (Figure 5). The level of variation and diversity at low 342 population densities is not maintained at high population densities. Ozgul et al. (2009) found population 343 density and maternal body size explain significant amounts of variation in temporal trends of mean body 344 weight in Soay sheep. We find the contribution to reproduction at high population density comes from 345 females of prime adult size (~ 25 kg). However, at low densities reproductive contribution is from fe-346 males of both small and large sizes. There is a concentration of individuals of prime size at high densi-347 ties as shown in Figure A8 for stable stage distribution in Appendix. Increase in density may be a double 348 whammy for females of small sizes since there is more competition and less individuals contribute to re-349 production. However, individuals of large body size may allocate in producing few extremely fit offspring 350 at high population densitie. 351

³⁵² Our finding for probability of reproductive failure supports empirical evidence within Soay sheep popu-

³⁵³ lation in the wild. At low density, juvenile mortality in Soay sheep is lower than the juvenile mortality at

high density. Travis et al. (2023) provide a comprehensive review of density-dependent selection and how

it may promote contrasting patterns of trait means at different population densities. Our research finds ev-

³⁵⁶ idence for density-dependent effects on reproductive effort in natural populations, and aligns with r-K se-

³⁵⁷ lection theory (Bassar et al. 2013). Our research predicts how density dependent influences strongly shape

- the distribution of LRS and can lead to density-dependent selection since LRS is an important component
- of individual fitness. The decreasing complexity in life history variation at highest density does not support
- Lomnicki's prediction that individual differences should be more pronounced at high than at low density
- ³⁶¹ (Lomnicki 1978). On the contrary, our findings reveal that resource limitation constrains the size distri-
- ³⁶² bution of females in population, which thereby restrict individual variation in vital rates and demographic
- ³⁶³ outcomes such as lifetime reproductive success.
- ³⁶⁴ There is empirical evidence for links between life-history trade-offs and density dependent selection from
- ³⁶⁵ Drosophila cultures (Mueller and Ayala 1981; Mueller et al. 1991), insects (Gilbert and Manica 2010) and
- fisheries (Goodwin et al. 2006; Eikeset et al. 2016; Christie et al. 2018), among others. Mueller and Ay-
- ala (1981) studied populations of *Drosophila melanogaster* kept at low population densities (r-populations
- for about 200 generations) and then placed them in crowded cultures (K-populations). They found after 25
- ³⁶⁹ generations the K-populations showed higher growth rate and productivity at high densities (relative to the
- controls), but lower growth rate at low densities and experimentally confirmed fitness trade-offs can arise
- from density-dependent selection. A study (Sæther et al. 2016) on great tits *Parus major* showed females
- ³⁷² laying the largest clutch sizes at small population sizes experienced the greatest density-dependent reduc-
- tions in fitness at large population sizes, thus providing empirical support for r- and K-selection. At small
- population sizes, phenotypes with large growth rates are favored, whereas phenotypes with high competi-
- tive skills are favored when populations are close to the carrying capacity K.
- ³⁷⁶ Our framework is general and can be applied to plant or animal species with individual-based life-history
- data such as, Hypericum cumulicola (Quintana-Ascencio and Morales-Hernández 1997), Heliconia acumi-
- nata (Brooks et al. 2019), Poecilia reticulata (Reznick et al. 2006; Bassar et al. 2016), and Cervus elaphus
- and (Gaillard et al. 2003). Our results are based on life-histories generated from the covariance matrix and
- don't correspond to data from real individuals. We also do not account for stochastic dynamics Lande et al.
- (2017) or climatic variation that has been found to affect population structure in Soay sheep (Ozgul et al.
- ³⁸² 2009). Further exploration of density effects can account for timing of reproduction and age-dependence
- of demographic parameters, especially senescence for which there has been a compelling evidence for
- many ungulate populations (Loison et al. 1999; Gaillard and Lemaitre 2019).

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518 A Appendix A



Figure A1: Equilibrium Distribution: mean 454



Figure A2: Plot of Survival and Recruitment functions for different values of Population, N.

	PC1	PC2	PC3	PC4	Ν
Juv. Survival	-0.6879697	0.12862049	0.1212322	-0.7038872	0
Ad. Survival	-0.686233	-0.0630279	0.2061516	0.69470369	0
Reproduction	-0.2023425	-0.6648947	-0.7174507	-0.047297	0
Growth	0.1218173	-0.7330752	0.65426962	-0.1403301	0
Juv. Survival	0.68750662	-0.0194718	0.39635595	-0.6081591	K/2
Ad. Survival	0.68088722	0.20812351	-0.1056572	0.69420008	K/2
Reproduction	0.04627893	0.72806789	-0.585899	-0.3528424	K/2
Growth	-0.2481642	0.65285726	0.69889976	0.15404882	K/2
Juv. Survival	-0.6428758	0.01294431	-0.1599549	0.74897098	К
Ad. Survival	0.25436365	-0.7802743	-0.560259	0.11216476	к
Reproduction	0.61068116	-0.0551793	0.4797481	0.62758707	К
Growth	0.38610661	0.62286408	-0.6560229	0.18054366	К

Figure A3: Table 2: Table of PCA loadings for the Principal Components.



Figure A4: Correlation Matrices for the three population densities. The top most panel corresponds to N = 0, followed by N = K/2, and N = K. The colors red, blue, and white correspond to negative, positive and no correlation.



PCA Eigenvalues vs. Broken Stick

Figure A5: Eigenvalues from data and broken stick model. The top most panel corresponds to N = 0, followed by N = K/2, and N = K. Blue corresponds to observed eigenvalues from the data and red corresponds to eigenvalues from the broken stick model.



Figure A6: Plot for negative association between average growth increment for juveniles at SSD on the x-axis and average juvenile survival at SSD on the y-axis. The colors correspond to population density at N = 0, N = K/2, N = K, N = (1.2)K, and N = (1.4)K.



Figure A7: The top two panels show the correlation matrix and corresponding PCA at N = 1.2K. The bottom panels correspond to N = 1.4K. The colors red, blue, and white correspond to negative, positive and no correlation.



Figure A8: Stable Stage Distribution at different ratios of equilibrium population size. The legend N/K = 0, 0.5, and 1 correspond to N = 0, N = K/2, and N = K.



Figure A9: The plot shows negative correlation between carrying capacity, *K* on the x-axis and R_0 at N = 0 on the y-axis.



Figure A10: Distribution of LRS when all parameters are sampled from the covariance matrix at different population densities.



Figure A11: Distribution of LRS when survival and growth parameters are sampled from the covariance matrix at different population densities. The first and second panel correspond to varying survival and growth parameters. The third panel corresponds to varying both survival and growth parameters simultaneously.