Running headline: Eco-evolutionary dynamics in ungulates

Fluctuating effects of genetic and plastic changes in body mass on population dynamics in a large herbivore

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Abstract

Recent studies suggest that evolutionary changes can occur on a contemporary time scale. Hence, evolution can influence ecology and vice-versa. To understand the importance of eco-evolutionary dynamics in population dynamics, we must quantify the relative contribution of ecological and evolutionary changes to population growth and other ecological processes. To date, however, most eco-evolutionary dynamics studies have not partitioned the relative contribution of plastic and evolutionary changes in traits on population, community and ecosystem processes. Here, we quantify the effects of heritable and non-heritable changes in body mass distribution on survival, recruitment and population growth in wild bighorn sheep (*Ovis canadensis*) and compare their importance to the effects of changes in age structure, population density and weather. We applied a combination of a pedigree-based quantitative genetics model, statistical analyses on demography and a new statistical decomposition technique, the Geber method, to a long-term dataset of bighorn sheep on Ram Mountain (Canada), monitored individually from 1975 to 2012. We show three main results: (1) The relative importance of heritable change in mass, non-heritable change in mass, age structure, density and climate on population growth rate changed substantially over time. (2) An increase in body mass was accompanied by an increase in population growth through higher survival and recruitment rate. (3) Over the entire study period, changes in the body mass distribution of ewes, mostly through non-heritable changes, affected population growth to a similar extent as changes in age structure or in density. The importance of evolutionary changes was small compared to that of other drivers of changes in population growth but increased with time as evolutionary changes accumulated. Evolutionary changes became increasingly important for population growth as the length of the study period considered increased.

Our results highlight the complex ways in which ecological and evolutionary changes can affect population dynamics and illustrate the large potential effect of trait changes on population processes.

Key words: Eco-evolutionary, Population Dynamics, Ungulates, Biological Evolution, Breeding values, Animal model

Introduction

It has recently become apparent that evolutionary changes can occur on an ecological timescale (Thompson 1998). Rates of phenotypic changes are on average 1/4 (and up to 2/3) the rates of change in population size, suggesting that both processes occur on similar time scales (DeLong et al. 2016). Evolution on contemporary timescales has been documented in a wide range of organisms including plants (Maron et al. 2004), fish (Hendry et al. 2000), birds (Grant and Grant 2006) and humans (Milot et al. 2011). Contemporary evolutionary changes may affect ecological processes including population, community and ecosystem dynamics (Post and Palkovacs 2009) which could, in turn, produce a new selective landscape. Those reciprocal interactions between evolution and ecology are termed eco-evolutionary dynamics (Pelletier et al. 2009), and their quantification is important for a holistic understanding of factors driving population dynamics. For example, in predator-prey systems of rotifers (*Brachionus calyciflorus*) and green algae (*Chlorella vulgaris*), populations cycles varied according to whether or not prey populations were allowed to evolve (Yoshida et al. 2003). In another rotifer system, phosphorus limitation led to evolution of reduced investment in sex, which impacted population dynamics (Declerck et al. 2015). Most studies of eco-evolutionary dynamics to date, however, have been on short-lived species or in experimental systems (Hendry 2016a). Given the increasing reports of human-driven trait changes in nature (Darimont et al. 2009, Alberti et al. 2017), it is critical to assess the potential consequences of those changes in traits on population processes in wild and exploited species. For example, recent data-based models of the northeast Arctic cod stock suggest that both evolutionary and plastic changes in traits must be considered to accurately explain the observed trends in life-history traits and population dynamics (Eikeset et al. 2016).

Phenotypes can shape an individual's ability to survive, grow and reproduce. Consequently, the distribution of phenotypes in a population can have a strong impact on its dynamics (Pelletier et al. 2007a). In five ungulate populations under long-term monitoring, the effect of a change in mean birth weight on population growth was of similar magnitude to that of climatic drivers (Ezard et al. 2009). This suggests that evolutionary changes of traits with a genetic basis can modify population dynamics. Although a change in mean trait value in a population can be due to evolution, it can also be due to other ecological factors including changes in age structure or plastic changes (Coulson and Tuljapurkar 2008). Most eco-evolutionary analyses to date, however, have not evaluated whether traits changes are due to heritable or plastic changes (Ezard et al. 2009, Hendry 2016a).

Phenotypic plasticity, the ability of a single genotype to produce a range of phenotypes in response to environmental variation (Forsman 2015), can have a major effect on population growth and persistence (Reed et al. 2010) because it allows individuals to adjust their traits to variable environments to maximize their survival and reproduction. For example, defense structures, such as the spine in *Daphnia pulex*, can be induced by high predation risk (Spitze 1992) and the breeding phenology of red deer (*Cervus elaphus*) can change to match ecological conditions (Moyes et al. 2011). In the context of eco-evolutionary dynamics, it is important to know whether an effect of trait changes on population processes is due to plasticity, genetic evolution, or both to identify whether the feedbacks between traits and population processes are due to an eco-to-eco interaction, caused by a plastic change in trait, or to an evo-to-eco interaction catalysed by genetic change. Eco-to-eco interactions are likely to occur more frequently due to the rapidity of plastic trait change and may be of greater magnitude (Hendry 2016b), but evo-to-eco effects may be more critical to the persistence of populations facing a changing environment such as in the case of evolutionary rescue (Carlson et al. 2014). Partitioning the relative contribution of plastic and evolutionary changes is also important because phenotypic plasticity may compensate for evolutionary change, leading to cryptic eco-evolutionary dynamics (Kinnison et al. 2015). From an applied perspective, evolutionary changes in traits due to selective harvest are expected to revert to their pre-selection state more slowly than plastic changes when harvesting stops (Swain et al. 2007, Allendorf and Hard 2009, Pigeon et al. 2016). Thus, evo-to-eco interactions may have long-term effects on population growth and productivity (Dunlop et al. 2015) and might be critical for conservation and management. Thus, it is important to partition the effects of traits changes into those due to heritable and non-heritable change to obtain realistic effect sizes of the relative importance of evolutionary and ecological processes. Empirical examples of such distinctions remain scarce (Hendry 2016a).

Several methods have been developed to decompose trait changes into their ecological and evolutionary components (overview in van Benthem et al. 2017). When sufficient data are available, the best approach is to use a pedigree-based quantitative genetics model (e.g., the animal model; Kruuk 2004) to evaluate the genetic basis of a trait, which can then be combined with the Geber approach developed by Ellner et al. (2011) to partition the effects of plastic and evolutionary trait change on population growth. This is an extension of the approach proposed by Hairston et al (2005), combining it with the Price equation (Price 1970, 1972), to partition trait changes into the effects of heritable change, non-heritable phenotypic change and environment. The Geber approach provides a general framework to partition the contribution of change in breeding values, in trait and in environmental factors on population-level parameter such as population growth rate. It does this by: 1) fitting models to quantify the effects of the trait and ecological factors on population growth rate, 2) distinguishing heritable trait change from non-heritable trait change (i.e. plastic change, also referred to as environmental deviation) by comparing temporal phenotypic changes to changes in breeding values, and 3) partitioning the variance in population growth rate by combining the observed changes in average population breeding values, environmental deviation and ecological factors with their estimated effects obtained from statistical modeling (Ellner et al. 2011).

Here we compare the relative importance of changes in phenotypic traits, climate, density and age structure on population dynamics. We use the Geber approach to decompose the effects of heritable and non-heritable change in mass, age structure, density and a large-scale climate index on survival and reproduction of bighorn sheep (*Ovis canadensis*). Finally, we combine age-specific changes in survival and recruitment with age structure to quantify the effects of a change in environment, focal trait or age structure on population growth (Coulson et al. 2008). We do this for different time periods, when the population growth rates increased and decreased. We expect that non-heritable changes in traits should be more important than heritable changes in explaining the association between traits and population growth on a short time scale. Further, we explore the impact of period length on our quantification of the magnitude of ecological and evolutionary effects. We expected that the importance of heritable trait changes on population processes would increase over longer time periods. We used detailed long-term individual monitoring of female bighorn sheep from a wild population in Canada with a pedigree 8 generations deep (Coltman et al. 2005). By combining pedigree-based quantitative genetics models, demographic statistical analyses and the extended Geber approach (Ellner et al. 2011), we bring novel insights into the relative importance of density, age structure, heritable and non-heritable changes in mass on changes in population size. Our results suggest that while the distribution of body mass can have as much impact on population dynamics as density or age structure, this effect is mostly due to plastic changes. Heritable changes in morphological traits of long-lived species tend to be slow and may become larger than the non-heritable effect of traits changes only over a long temporal scale.

Methods

Population and study area

We studied bighorn sheep on Ram Mountain, Alberta, Canada (52ºN, 115ºW, elevation 1080 to 2170 m). The study area covers about 38 km^2 of alpine and subalpine habitat approximately 30 km east of the Rocky Mountains. The population has been closely monitored each summer since 1975 (Jorgenson et al. 1993). Individuals are marked using ear tags or visual collars. Annual resighting probability for ewes is over 99% (Jorgenson et al. 1997), so they can be considered dead when not seen for a year. Since all females in the population are marked and an exact census is made yearly (Jorgenson et al. 1997), we can precisely determine their annual survival rate. Sheep were captured each year between late May and late September in a corral trap baited with salt (Jorgenson et al. 1997). Ewes were typically recaptured every 4 to 5 weeks (mean= 3.10 captures/year, SD= 1.41).

Phenotypic and environmental measurements

Individuals were weighed at each capture. We adjusted mass to September 15 using linear mixed models with restricted maximum likelihood where both the intercept and the slope were allowed to vary for each individual (Martin and Pelletier 2011). Density was the number of adult females alive in June each year, because females are the recruitment-limiting sex. Climate was represented by the Pacific Decadal Oscillation (PDO) index, obtained from the Joint Institute for the Study of the Atmosphere and Ocean website (http://jisao.washington.edu). We used winter PDO, the average of monthly values from December to April, to evaluate the effect of winter harshness. Winter PDO affects population growth (Ezard et al. 2009) and horn length (Douhard et al. 2016) in mountain sheep.

Quantifying age structure

Several age classes were needed to quantify age structure because survival and recruitment have different age-specific patterns in large mammals. To choose age classes that best represent how survival and recruitment differ through age, we compared the Akaike Information Criterion corrected for small sample size (AICc) of all possible age class groupings and selected the classification that minimized AICc for both survival and recruitment (Appendix: Fig S1). Animals were thus classified as lamb, yearling, 2-3, 4-5, 6-7, 8-12 and older than 13 years. These classes broadly represent the ontogenetic changes in mass, survival and recruitment identified previously using alternative techniques (Bérubé et al. 1999, Loison et al. 1999).

Model fitting

The first step to partition variation of female population growth rate into the effects of five factors of interest (non-heritable and heritable change in mass, density, PDO and age structure) was to build models of individual annual survival and recruitment as a function of these factors. Population growth rate, in a closed population like Ram Mountain, can be approximated by the combination of survival and recruitment. Body mass was centered and scaled within each of the 7 previously determined age class to facilitate model convergence and remove multicollinearity with age class. This procedure also removed any effect of age from the change in mass, making it easier to partition the effect of age structure from the effect of change in mass. Density was also centered and scaled to one standard deviation to facilitate convergence (Bolker et al. 2013). We modeled survival from one year to the next and recruitment (the probability of weaning a lamb the following year) using binomial generalized mixed models, which controlled for non-independence due to repeated measurements by including individual identity and year as random effects. We used model selection based on AICc to identify parsimonious models with good predictive power. Candidate models included age class, mass, density, winter PDO and years of high cougar (*Puma concolor*) predation (Festa-Bianchet et al. 2006) as explanatory variables. Previous work detected positive density-dependence in a bighorn sheep population at very low densities (Bourbeau-Lemieux et al. 2011). We therefore tested quadratic effects of density to account for potential non-linear effects. We also tested the quadratic effects of mass and PDO as well as the interactions between mass, density, PDO and age. Given that multiple candidate models had similar support (difference in AICc < 4; Burnham and Anderson 2002), we used model averaging (Mazerolle 2016) to obtain predicted responses and unconditional standard errors weighted according to each model's AICc weight.

Distinguishing heritable from non-heritable changes in mass

To estimate breeding values, we constructed a pedigree of the population. The pedigree included 1066 marked sheep with 836 maternities and 508 paternities. Maternities are established from field observations. From 1988 (except 1994 to 1996), tissue samples were collected for genetic analysis (Poissant et al. 2012). Paternities were assigned using CERVUS (Marshall et al. 1998) at a confidence level of >95% following Coltman et al. (2005).

Estimated breeding values (EBV) of mass, which represent an individuals' genetic value for this trait, were obtained with a bivariate animal model with female and male mass as response variables using a Bayesian framework with the “MCMCglmm” R library V2.21 (Hadfield 2010, Hadfield et al. 2010, Wilson et al. 2010). More details on this animal model are reported in Pigeon et al. (2016). In dimorphic species with imperfect genetic correlation between male and female traits, a bivariate model maximizes information while accounting for genetic correlations (Wolak et al. 2015). Estimation of genetic parameters must account for the high genetic correlation between female and male mass (posterior mean= 0.74, CI= 0.39 – 0.99) in order to obtain less biased estimates. We centered and standardized mass in each age/sex (females aged 13 years and older were pooled due to low sample size (N= 91) above that age) to have a mean of 0 and a variance 1 before analysis, because phenotypic variances differed between sexes and increased with age. Centering and standardizing keeps EBV on the same scale for further analysis. The initial model partitioned the phenotypic variance in male and female body mass into its additive genetic (Va), permanent environmental (Vpe), maternal (Vm), cohort (Vce) and yearly environmental (Ve) components and residual variance (Vr) (see Pigeon et al (2016) for details on model parameterization). To obtain a comprehensive EBV accounting for the above variance partitions, models with different random effects were compared using the deviance information criterion (DIC), which balances model fit and complexity simultaneously (Wilson et al. 2010). The maternal variance component was dropped from the final model since it did not reduce DIC. The model was first fitted with a multivariate inverse-Wishart prior (Wilson et al. 2010) and run for 9000000 iterations with a burn-in period of 1500000 and a thinning of 7500. Sensitivity to the prior was tested by re-running the model with more informative priors, leading to similar results (Pigeon et al. 2016). We extracted the posterior distribution of breeding values from this final model, to reduce bias in error estimation (Hadfield et al. 2010).

Finally, we distinguished the effect of heritable from non-heritable changes in population average body mass. To do so, we fitted two linear regressions for each age-class, one of annual average population mass as a function of time and a second of annual average EBV as a function of time. The difference between the fitted values of these two regressions each year is the environmental deviation for that year. The environmental deviation is, therefore, the change in trait mean expected if genotype frequencies were constant. Any deviation from this constant expectation is a non-heritable change in the trait and considered to be a plastic change in trait. This smoothing using regression has been suggested to reduce noise due to yearly environmental stochasticity (Ellner et al. 2011).

Variance partitioning

During our study, population size varied substantially through periods of increase and decline (Fig. 1b). To ensure parsimony while allowing time for heritable change in mass to occur, we separated the study into periods characterized by changes in population growth rate. To define these periods, we fitted a generalized additive model of mean annual growth rate as a function of year. We then compared this model to broken stick regressions using version 0.5-1.1 of the "segmented" R library (Muggeo 2003) with an increasing number of breakpoints. The most parsimonious model included three periods: period 1 (1975-1989), period 2 (1989-1997) and period 3 (1997-2012) (Appendix: Fig S2). We partitioned the variance in survival and recruitment independently for each period using an extension of the Geber method (Ellner et al. 2011). The method partitions the changes in each focal variable between the first and the last years of the period. To test the importance of period length, we also applied the variance partitioning approach (without error estimation, using posterior mode of EBV) on a range of periods from 37 one-year periods to a single 37-year period. We therefore produced an additional 115 periods lasting 1 to 37 years (mean = 6), which started in different years to cover systematically the entire study. We then tested for linear and quadratic effects of period length on the absolute effect size of heritable change in mass, non-heritable change in mass, change in density, age structure and climate on population growth rate using linear regressions.

Partitioning the variance in survival and recruitment was done in several steps. First, assuming a constant reaction norm, we added the mean annual EBV predicted by the linear regression with time to the environmental deviation to obtain a prediction of the expected trait for a given breeding value and environmental deviation. Second, we used the previously parameterized models (see model fitting section) to predict the expected value of survival or recruitment for each age class, given all combinations of annual mean EBV, annual environmental deviation, density and PDO. Cougar predation was fixed as absent, as it only occurred in 5 of 38 years. Age-specific predicted survival and recruitment were obtained using model averaging (Mazerolle 2016). The age-specific predicted survival and recruitment rates were then combined to produce a weighted population average according to their respective proportions in the population at each given time (Coulson et al. 2008) to account explicitly for changes in age structure (Appendix: Fig S3). Finally, we estimated the average effect of the observed change in a given variable on population mean survival and recruitment when all other factors were kept constant. For example, the following equation was used to estimate the effect of heritable change on survival and recruitment (Ellner et al. 2011).

$$EVO = \frac{\sum_{e=1}^{2} \sum_{d=1}^{2} \sum_{a=1}^{2} \sum_{w=1}^{2} (X_{2edaw} - X_{1edaw})}{16}$$

Where X_{2edaw} is the predicted survival or recruitment of a population with mean breeding value at the end of the period, the environmental deviation e, density d, age structure a and PDO w. X_{1edaw} is the same but with the mean breeding value at the beginning of the period. Values of 1 or 2 for e, d, a and w

refer to their given value at beginning and end of the period respectively. The resulting value of EVO is the expected change in survival or recruitment due to the observed change in breeding value during the period. Equivalent formulas were used for all other factors of interest. The effects of the 5 partitioned factors (ECO, EVO, AGE.STR, DENS and PDO) sum to the change in survival and recruitment predicted by the models for a given period. To better understand the impact of these effects on population dynamics, we also repeated this last step with the predicted population growth rate, obtained by dividing the predicted recruitment by 2 (to account for the production of male lambs assuming an even birth sex-ratio) and adding the predicted survival.

Measuring uncertainty

We measured uncertainty at multiple levels. We used a Bayesian framework to estimate breeding values and properly quantify EBV errors (Hadfield et al. 2010). For each sample of the posterior distribution in breeding value, we re-calculated the temporal trend in breeding value and the yearly environmental deviation. We then used model averaging as previously described to estimate expected survival and recruitment for each age class and unconditional errors (eq. 6.12 of Burnham and Anderson (2002)) around these values. To account for errors in these estimates, we randomly drew values from a normal distribution centered on the expected value with standard deviation equal to the unconditional errors of the expected value. Hence, we obtained distributions of predicted survival and recruitment for each age-class that reflected uncertainty in both the estimation of environmental deviance and in the estimation of the model parameters. We then applied the variance decomposition approach described above on each realization of the Markov chain. The effects were considered significant when the 95% highest posterior density interval did not overlap 0. All analyses were done in R (Version 3.3.3; R Core Team 2016).

Results

Model fitting

Model selection for survival revealed that age class, density, their interaction and body mass best explained female survival, as these variables were present in all models with difference in AICc < 4 (Appendix: Table S1 and Fig S4). Density had a strong negative effect on lamb survival but no effect on survival for prime age classes (Fig S4). Body mass had a positive effect on survival of all age classes. Predation decreased survival, while PDO had a very small quadratic effect. Predictions of mean survival by year fitted observed values with a correlation of 0.36 ($P < 0.001$). Model selection for recruitment revealed that age class, body mass, their interaction, density and predation best explained female recruitment, as these variables were present in all models within <4 AICc units of the best model (Appendix : Table S2 and Fig S5). Density had quadratic effects on recruitment, with maximum recruitment at intermediate densities, suggesting an Allee effect. Mass increased the probability of recruitment for females of all ages, although it was least important in prime-aged females, which had a high probability of reproducing even when very light. PDO (associated with warm and dry winters) had negligible effects on recruitment. Predation decreased recruitment. Predictions of average recruitment by year fitted observed values with a correlation of 0.71 ($P < 0.001$).

Variance partitioning

Female mass varied substantially over time (Fig 1a) with periods of increase and decrease (Appendix: Table S3). A significant portion of this variation in phenotype could be explained by additive genetic variance; female mass was heritable ($h^2 = 0.22$, Appendix: Table S4). Temporal variation in EBV of female mass, however, was much smaller than the observed variation in mass (Appendix: Table S5 and Fig S6).

Partitioning the variance in survival into the effects of heritable change in mass, non-heritable change in mass, change in density, age structure and climate revealed substantial variation in their relative contribution over time (Fig 2a), except for PDO whose contribution was negligible over the entire study. During the first period, a change in age structure associated with aging of the population had the strongest effect (posterior mean=0.031, 95% CI = 0.022 – 0.040). Changes in heritable and non-heritable mass made smaller and non-significant contributions (posterior means of 0.002; CI=--0.013 – 0.015 and -0.008; CI=-0.008 – 0.019, respectively) resulting in an overall increase in survival of 0.044. Changes in both density and PDO made negligible contributions to change in survival during this period. During the second period, the observed non-heritable decline in mass and the observed increase in density contributed most to the decline in survival (posterior means = -0.042; CI=-0.054 – -0.031 and -0.020; CI=-0.030 – -0.011 respectively), resulting in an overall decrease in survival of 0.071. A non-significant negative effect (posterior mean of -0.002; CI=-0.013 – 0.010) of the heritable change in mass was also detected. The third period was characterized by a strong positive effect of non-heritable change in mass (posterior mean of 0.059; CI=0.039 – 0.077), which was opposed by the effect of the change in density (posterior mean of -0.031; CI=-0.044 – -0.016) to yield a very small increase in survival (0.011). Overall, non-heritable change in mass had the greatest effect on survival, followed by density, age structure and heritable changes in mass (average absolute effect size of 0.036, 0.018, 0.013 and 0.006 respectively). Winter PDO had a negligible effect (average absolute effect size of 0.001) on changes in survival observed over 4 decades.

The effects of heritable change in mass, non-heritable change in mass, change in density, age structure and climate on recruitment also varied considerably over the study periods (Fig. 2b). The first period was dominated by a positive effect of the change in age structure associated with aging of the population (posterior mean=0.174, 95% CI = 0.161 – 0.188). Ageing reduced the proportion of young females, especially lambs and yearlings, whose survival and recruitment are low (Appendix: Figure S7). Changes in density, heritable and non-heritable mass made smaller contributions (posterior means of 0.010 [CI=-0.004 – 0.022], -0.005 [CI=-0.030 – 0.017] and -0.002 [CI=0.027 – 0.024] respectively) resulting in an overall increase in recruitment of 0.177. During the second period, the non-heritable decline in mass and the strong change in density explained most of the 0.176 decline in probability to wean a lamb (posterior means of -0.059 [CI=-0.085 – -0.031] and -0.159 [CI=-0.180 – -0.140] respectively). Heritable change in mass had no effect (posterior mean of -0.002; CI=-0.0288 –0.024). These effects were counteracted in part by the positive effect on recruitment of the change in age structure, with more females in the more productive age classes (posterior mean of 0.043; CI=0.023 – 0.061). The third period was characterized by a strong positive effect of non-heritable change in mass (posterior mean of 0.097; CI=0.063 – 0.134). This was opposed by the combined negative effect of the change in density and an increasingly younger age structure (posterior mean of -0.079 [CI=-0.104 – -0.053] and -0.078[CI=-0.102 – -0.051] respectively) resulting in a net decrease in recruitment of 0.024. Overall, change in age structure had the greatest effect on recruitment, followed by density, plastic change in mass and heritable changes in mass (mean absolute effect size of 0.098, 0.083, 0.052 and 0.011 respectively). Winter PDO had a negligible effect (mean absolute effect size of 0.003) on changes in recruitment observed in the 4 decades monitored.

When survival and recruitment where combined into population growth rate, the relative importance of heritable change in mass, non-heritable change in mass, change in density, age structure and climate were similar to those presented above (Fig. 3). The first period was dominated by a positive effect (posterior mean=0.118, 95% CI = 0.108 – 0.131) of the change in age structure associated with aging of the population. Changes in density, heritable and non-heritable mass made smaller contributions (posterior means of 0.007 [CI=-0.004 – 0.018], 0.004 [CI=-0.017 – 0.028] and -0.0003 [CI=0.023 – 0.020] respectively). During the second period, the non-heritable decline in mass and the strong change in density explained most of the decline in population growth (posterior means of -0.071 [CI=-0.091 – -0.050] and -0.099 [CI=-0.113 – -0.085] respectively). No effect (posterior mean of -0.004; CI=-0.023 – 0.017) of the heritable change in mass was detected. The change in age structure had a slight positive effect on population growth (posterior mean of 0.014; CI=0.0004 – 0.026). The third period was characterized by a strong positive effect of non-heritable change in mass (posterior mean of 0.107; CI=0.075 – 0.136). This was opposed by the combined negative effects of the change in density and a younger age structure (posterior mean of -0.071 [CI=-0.089 – -0.050] and -0.042 [CI=-0.059 – -0.023] respectively). Heritable change in mass had a small non-significant effect (0.026 [CI=-0.005– 0.056]). In this population, non-heritable change in mass had the greatest effect on population growth, followed by density, age structure and heritable changes in mass (mean absolute effect size of 0.061, 0.059, 0.058 and 0.010 respectively). Winter PDO had a negligible effect (mean absolute effect size of 0.002) on changes in population growth observed in the 4 decades monitored.

By partitioned the relative importance of heritable and non-heritable changes in mass, change in density, age structure and climate on not only population growth rate, but also on survival and recruitment, we obtained a more mechanistic approach to population dynamics. To determine whether the effects on population growth manifested themselves mostly through effects on survival or on recruitment, we compared the absolute effect size of survival to the absolute effect size of half the recruitment, because population growth rate is equal to the mean survival added to half the recruitment (Coulson et al. 2008). Generally, effects through survival and recruitment did not differ significantly, but the relative importance of survival and recruitment upon how the variables we examined affected population growth varied among periods (Appendix: Table S6). Changes in age structure more strongly affected population growth in all 3 periods via their effects on recruitment rather than on survival ($P = 0, 0.004$ and 0.001 respectively). Changes in density had greater effects on population growth rate by affecting recruitment rather than survival, but this difference was only significant ($P < 0.001$) during the second period. In all other period-variable combinations, recruitment and survival did not differ significantly in their contribution to change in population growth rate.

The importance of heritable and non-heritable changes in mass, as well as changes in density, age structure and climate on population growth rate varied according to the temporal scale at which these processes were measured (Fig. 4). At smaller temporal scale, effects of change in age-structure and non-heritable change in mass were most important. However, the direction and magnitude of those effects were highly variable, ranging from -0.164 to 0.111 and -0.061 to 0.070 respectively. The importance of heritable change was minimal over short periods but increased with period length, producing a trend best fitted by a quadratic function (B= 6.89e-4, P<0.001; *B.quad*= -1.5e-5, P=0.050). The absolute effects of both density (B= 0.006, P<0.001; *B.quad*= -0.0002, P<0.001) and non-heritable change in mass (B= 0.004, P<0.001; *B.quad*= -0.0001, P<0.001) had strong quadratic trends, being highest at intermediate lengths. We did not detect any significant trend between period length and the importance of age structure. While a significant quadratic trend was found for PDO, its effect on population growth rate remained very weak regardless of the length of the period considered.

Discussion

By combining a pedigree-based quantitative genetics model, demographic statistical analyses and the recently developed Geber approach (Ellner et al. 2011) to exceptionally detailed data from a wild ungulate population, we found that although ecological variables such as age structure and density are major drivers of population dynamics, ecological and evolutionary changes in trait distribution also have a significant effect that varies between periods of different population trends. When decomposed by period, the most important cause of change in population dynamics was the non-heritable change in mass, closely followed by density and age structure, although the magnitude of these effects varied depending on the period considered. The effect of heritable changes in mass on survival, recruitment and population growth on a yearly basis was not significant, but it increased with the length of the period considered. We found only a weak signal of evolutionary change in bighorn ewe mass (Appendix: Table S5). This result is not surprising given that breeding values for female mass did not show major changes over the study period. Therefore, our retrospective analysis shows that female plastic changes in mass play a dominant role over short time scales. Altogether, our study serves as an example of how ecological and evolutionary variables can interact in rather complex ways within populations, varying temporally and affecting different fitness components (survival or recruitment) to ultimately drive population growth (Figs. 2, 3).

It has been suggested that intense selective hunting of males could have undesirable consequences on population dynamics through indirect evolutionary impact on other segments of the population (Conover and Munch 2002, Allendorf and Hard 2009). In bighorn sheep, intense selection for smaller horns is exerted on males by trophy hunting. This anthropogenic selection led to a significant decline in the EBV of male horn length (Pigeon et al. 2016), a trait genetically correlated to female mass (genetic correlation = 0.43, (Poissant et al. 2012)). It was therefore suggested that anthropogenic pressures, such as selective hunting, could lead indirectly to maladaptive changes in female mass and potentially negatively affect population dynamics (Kuparinen and Festa-Bianchet

2017). Our study shows, however, that heritable change in mass played no significant role in the change in population growth rate of this population, likely because evolutionary changes in mass were minimal despite the evolutionary response of horn length to selective harvest (Pigeon et al. 2016). While female mass has a strong genetic correlation with male horn length, it is also under strong natural selection, which would have opposed any detrimental evolutionary change. In a stable environment, traits with a high impact on fitness are likely to be near evolutionary optimum and are therefore less likely to vary, reducing their influence on population growth. In a changing environment, however, species may find themselves with sub-optimal phenotypes, and evolutionary change could be of crucial importance.

The importance of phenotypic trait distribution for population growth has been recognized (Pelletier et al. 2007a), leading to increased interest in eco-evolutionary dynamics (Pelletier et al. 2009). In line with previous studies, we found important effects of changes in mass, a trait often used as an integrator of condition, for both survival (Festa-Bianchet et al. 1997, Côté and Festa-Bianchet 2001) and recruitment (Jorgenson et al. 1993, Martin and Festa-Bianchet 2011). We also show that this result translates into an important effect of mass on population growth, as previously suggested by a simpler analysis of five ungulate populations (Ezard et al. 2009). The impact of change in body mass on population dynamics, however, was mostly due to non-heritable changes, suggesting that our system is mostly driven by an eco-to-eco interaction. Mass is a highly plastic trait in bighorn sheep (Pelletier et al. 2007b). Temporal trends in the mean age-adjusted mass (Fig 1a) of the population are likely to reflect changes in body condition due to changes in resource availability or environmental conditions. High population density likely played an important role in reducing mass (Festa-Bianchet et al. 1998), through competition for resources. However, on a yearly basis, change in density explained less than

1% of the effects of plastic change in mass on population growth rate (Table S7). This may be an underestimate, however, since density may have delayed effect on mass through, for example, maternal effects (Monteith et al. 2009). While maternal effects are present in bighorn sheep, they decline with age and mostly disappear by age 2 (Wilson et al. 2005). Hence, on the temporal scale of the 3 observed periods, the effect of density on mass through maternal effect is unlikely to be the main driver of population growth. Further, the effects of density and environmental changes are not always positively correlated: plastic changes in mass and density had opposite effects during the third period of the study, suggesting that drivers of mass change other than density are also present.

Important effects of age structure on population dynamics have been reported for many ungulates including bighorn sheep (Festa-Bianchet et al. 2003), Soay sheep (Coulson et al. 2001) and red deer (Clutton-Brock et al. 1997, Clutton-Brock and Coulson 2002). Survival and recruitment vary substantially according to age (Gaillard et al. 2000). Hence, population age structure can drastically affect population growth. Lambs have much lower survival than adults and do not reproduce, so an increase in the proportion of lambs can reduce population growth rate. The impact of age structure may be reduced over longer time periods if it was to stabilize, which has yet to happen in this population. While density had a strong negative effect on population growth during the second period, it had no significant effect during the first period. The negative effect of change in density during the third period was unexpected. A decrease in density is usually associated with increased population growth. The opposite effect we detect is due to the quadratic relationship between density and both survival and recruitment, which appeared in all but one of the top recruitment models. Although a quadratic relationship may oversimplify how density affects this population (Sugeno and Munch 2013), the shape of this curve suggests positive density-dependence at low density (Courchamp et al. 1999). This might reflect Allee effects which have also been observed in another population of bighorn sheep, where probability to wean a lamb increased with density up to a threshold of around 90 sheep (Bourbeau-Lemieux et al. 2011).

Ecological and evolutionary variables may affect population growth by acting through survival and/or recruitment. Our analyses show that while both pathways were significant, the effects through recruitment tended to be larger, especially for age structure and density. This result is novel but not surprising given that adult female survival is high and varies little due to environmental canalization (Gaillard and Yoccoz 2003). It must be noted, however, that the correlation between fitted and observed values was only 0.36 for the survival model compared to 0.71 for the recruitment model, which may account for the lower importance of survival compared to recruitment. The direction of the effects of change in age structure, density, climate and mass on survival was similar to how these variables affected mean population growth. In large herbivores, density dependence usually first affects juvenile mortality, then age at first reproduction, followed by reproduction of adult females, and finally adult mortality (Bonenfant et al. 2009). There are two likely reasons why density affected population growth less through survival than recruitment. First, density usually affects survival of juveniles to a much greater extent that survival of adults (Eberhardt 2002). Lambs represent a small proportion of the population (average = 18%, SD= 0.07), therefore changes in juvenile survival cannot have strong immediate impacts on population growth if survival of other age classes remains unchanged (Gaillard et al. 2000). Second, we measured recruitment as weaning success. Hence, changes in pre-weaning lamb survival will drive changes in recruitment while only survival from weaning to 1 year will be included in survival. High variability in recruitment for this species (Gaillard et al. 2000) is consistent with the large effect sizes of the observed variables on population growth rate through recruitment.

Changes in non-heritable and heritable components of mass, density, age structure and PDO varied substantially over 40 years, making the selection of periods used for analysis challenging. With long periods, the choice of start and end-points can influence the results. Choosing the period to maximize change in one of the factors influencing mean population growth will maximize its relative effects on population growth, biasing the analysis. By defining periods based on changes in population growth (the response variable), we sought to minimize these biases while still maximising the change in population growth rate available to partition. However, given the retrospective nature of this analysis, the choice of study period will always have a consequence, as shown by the variance in effect sizes (Figure 4). Analyses using an annual approach, however, over-emphasize factors with the potential for quick change (Gingerich 1983, Gingerich 2001). While evolutionary changes can occur over an ecological time scale (Thompson 1998, DeLong et al. 2016), significant genetic change requires a turnover of individuals and cannot occur over a single year in a ed species like bighorn sheep with a generation time of 6.6 years. At Ram Mountain, the yearly average turnover rate was only 20.1%. Thus, on a very short time-scale, at least for long-lived species, demography and other ecological factors will always prevail, while in this system the relative importance of evolutionary variables increased as longer time periods were considered. For species with higher turnover rate, however, evolutionary variables might drive ecological processes on shorter time scale. This suggests that there may be a partial mismatch between ecological time scales and evolutionary timescales as suggested by DeLong et al. (2016). This mismatch may be larger in species with slow life-history such as bighorn. To compare the relative importance of evolution and ecology, one must consider a time span when both processes are possible but also the life history speed of the organism under study. Interspecific comparisons of the relative importance of evolutionary changes should standardize the time span of observations relative to the potential change in genotypes, which will vary with generation time (Haldane 1949). For example, evolutionary changes over a year are likely to be much more important for species with a short generation time such as *Daphnia* than for bighorn sheep, where accurate knowledge of population age structure is much more important to predict near-term population dynamics. Standardizing time span over generation time would allow for comparison of the relative importance of evolution not only between systems of the same species, but also across taxa.

In conclusion, distinguishing plastic and genetic changes in traits is crucial to quantify the importance of eco-evolutionary dynamics. Ignoring this distinction would have largely inflated the importance of evolutionary changes in driving population dynamics in bighorn sheep. Instead, we concluded that changes in female mass, although a very important driver of the population dynamics in our study, were not driven by genetic changes. Therefore, at least for body mass, the effect of trait changes on population dynamics are driven by eco-to-eco feedbacks and less by an evo-to-eco one. Yet, it is important to note that plasticity has been shown to be heritable too (Pelletier et al. 2007b) and therefore our classification of all plasticity as an ecological process is very conservative. We may underestimate the contribution of evolution by using such a narrow definition. Indeed, evolution of plasticity can play an important role in variation in population growth (Stoks et al. 2015). Only three generations exposed to indirect selection through trophy hunting were included in this study, which may be insufficient to detect a strong signal of eco-evolutionary dynamics. More empirical studies, with different traits and species, are necessary to disentangle the effects of plastic and genetic trait changes before broad conclusions can be made about the importance of evolutionary changes in the wild and furthermore about the temporal scale at which these changes substantially affect population dynamics. Our study highlights both the potential of evolutionary changes to modify population growth rate and the dangers of considering all trait changes as signs of evolution. The distinction between plastic and genetic trait change must be an integral part of empirical studies investigating the importance of eco-evolutionary dynamics.

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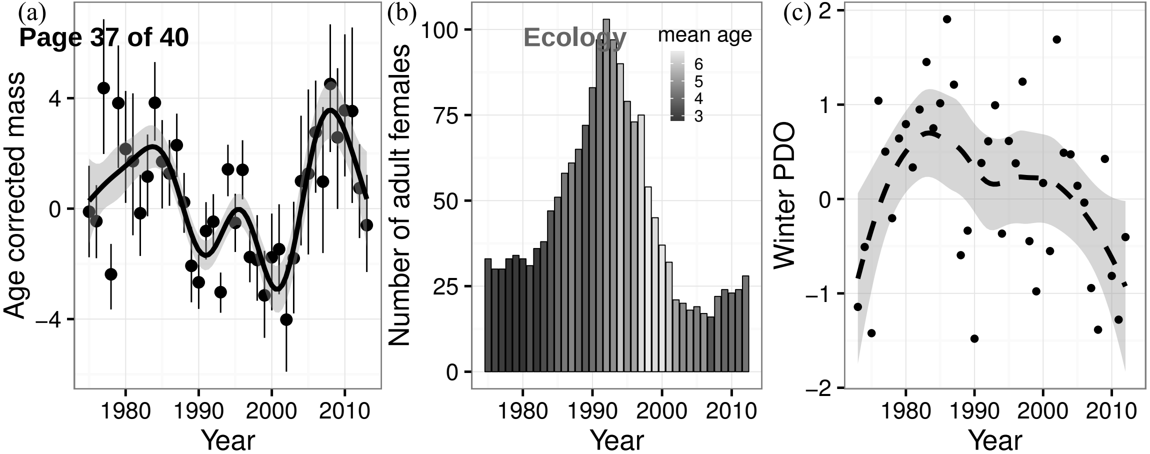
Figure Captions

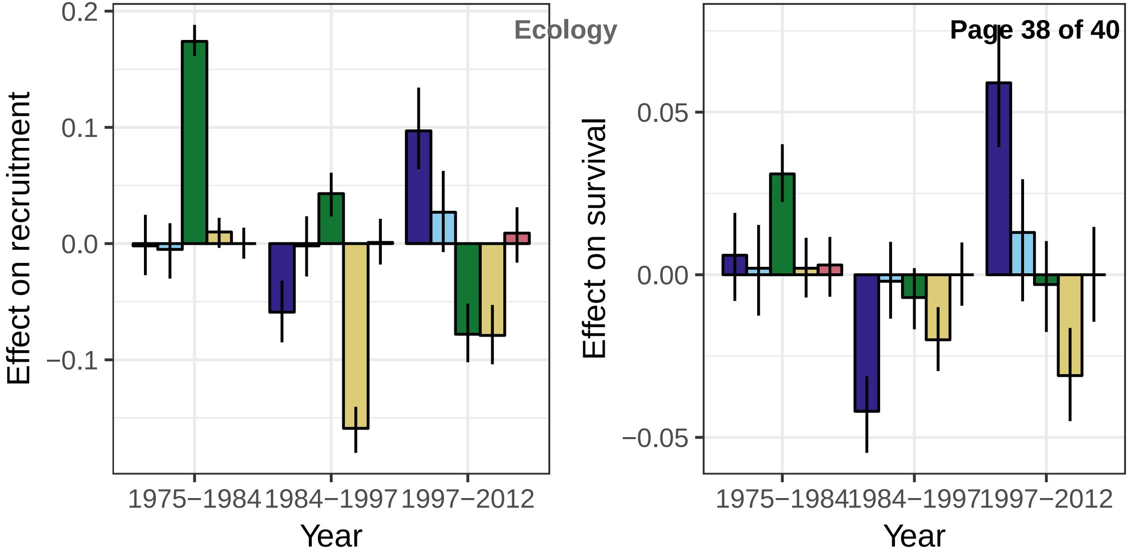
Figure 1: Temporal change in a) mean age-adjusted female mass in mid-September (error bars represent SD); b) number of adult females and mean age of all females; c) PDO from 1975 to 2012 for bighorn sheep at Ram Mountain, Alberta, Canada. Splines were fitted using locally weighted scatterplot smoothing (loess).

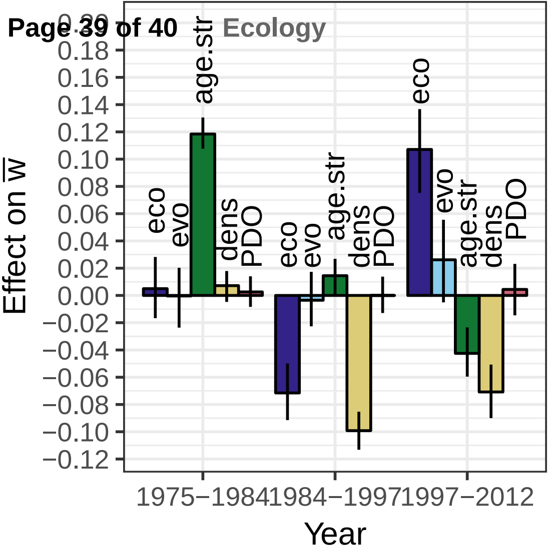
Figure 2: Partitioning the change in a) probability to survive and b) to wean a lamb into five components: non-heritable change in mass (dark blue; “eco”), heritable change in mass (light blue; “evo”), change in age structure (green; “age.str”), change in population density (beige; “dens”) and change in PDO (pink; “PDO”). Analyses of a long-term study of bighorn sheep in Canada were conducted separately for 3 periods: 1975-1984, 1984-1997 and 1997-2012. Bars show the effect on survival and recruitment of the observed change in a given variable. The values of the bar and the associated errors represent the mean and 95% CI (see Measuring uncertainty section).

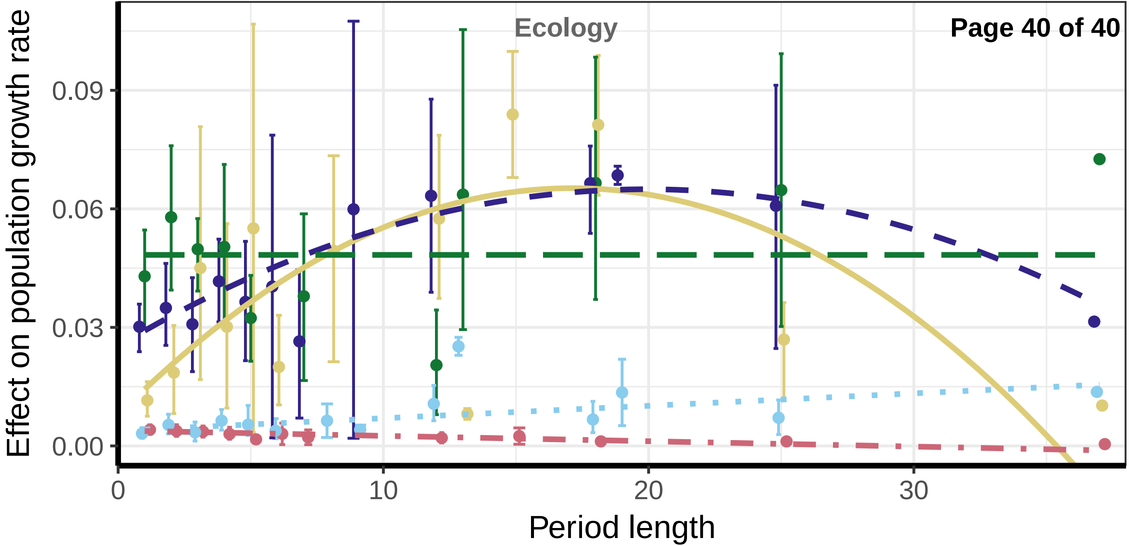
Figure 3: Partitioning the change in population growth into five components: non-heritable change in mass (dark blue; “eco”), heritable change in mass (light blue; “evo”), change in age structure (green; “age.str”), change in population density (beige; “dens”) and change in PDO (pink; “PDO”). Analyses of a long-term study of bighorn sheep in Canada were conducted separately for 3 periods: 1975-1984, 1984-1997 and 1997-2012. Bars show the effect on population growth of the observed change in a given variable. The values of the bar and the associated errors represent the mean and 95% CI (see Measuring uncertainty section).

Figure 4: Absolute effect of non-heritable change in mass (dark blue, short dash), heritable change in mass (light blue, dotted), change in age structure (green, long dash), change in population density (beige, solid) and change in PDO (pink, dot-dash) on population growth rate according to the length of the observation period (in years). Points represent the average absolute effect size (along with 95% confidence limits) for each estimated period length. Lines represent linear or quadratic (depending on which had lowest AICc) relationship between absolute effects size and the length of the period.


(a)
Age corrected mass
4
0
−4
1980
1990
2000
2010
Year
(b)
Number of adult females
100
75
50
25
0
mean age
6
5
4
3
1980
1990
2000
2010
Year
(c)
Winter PDO
2
1
0
−1
−2
1980
1990
2000
2010
Year


0.2
0.1
0.0
−0.1
Effect on recruitment
1975−1984
1984−1997
1997−2012
Year
0.05
0.00
−0.05
Effect on survival
1975−1984
1984−1997
1997−2012
Year


0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
−0.02
−0.04
−0.06
−0.08
−0.10
−0.12
Effect on $\overline{w}$
eco
evo
age.str
dens
PDO
eco
evo
age.str
dens
PDO
eco
evo
age.str
dens
PDO
1975−1984
1984−1997
1997−2012
Year


Ecology
Effect on population growth rate
0.00
0.03
0.06
0.09
0
10
20
30
Period length