Adding sexes to life history theory

Validating a pedigree based estimate of reproductive value in populations with sexes

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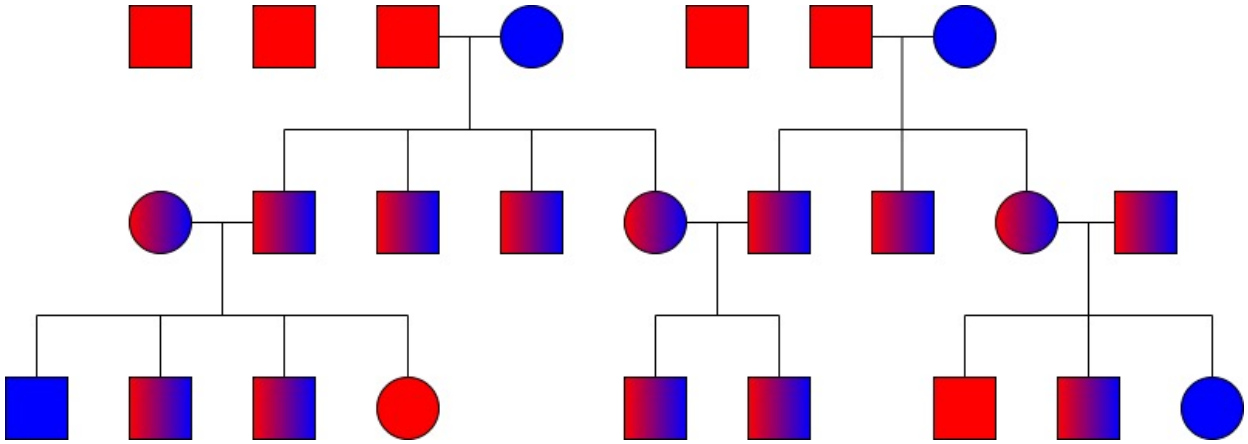


Abstract

Reproductive values are a useful measurement of fitness and can lead to insights in evolutionary biology and population dynamics by comparing individuals or categories in a population. A new method, the pedigree-based method, of estimating this reproductive value (RV) is easier to perform, but has not yet been properly validated in populations with sexes. We performed computer simulations based on different life history scenarios to assess estimates of the pedigree-based reproductive value (pRV) and compare these values to the theoretical reproductive values. We found that for the same simple life histories, the different pRV estimates diverged significantly over time, while the median of the pRV estimates approached the theoretical RV. The median of the estimates was able to clearly show differences in the RV of different categories of individuals based on different ratios between the sexes and different life history parameters. The variation in the pRV estimates means a single pedigree-based estimate of the RV in the field is not reliable.

1 Introduction

Darwinian fitness has been used to describe how well an organism is adapted to its environment. There are many definitions of fitness. One commonly used definition is defined as how successful an organism is expected to be at passing on its genes (Kimbrough, 1980). There is even more debate about how you measure fitness. Different proxies for fitness have been used in studies, depending on the available data (Roff, 1993) Most of these proxies can approach fitness reasonably well under simple conditions, but they often miss out on essential aspects of fitness. Two commonly used proxies are expected lifetime reproductive success and reproductive value (RV) (Fisher, 1993). Expected lifetime reproductive success corresponds to the average number of offspring individuals of a group produce over their entire lifespan. This value is relatively easy to measure when it is possible to track an individual over its entire life, as it only requires counting the number of offspring of an individual. However, this value does not take age of first reproduction and type of offspring into consideration (Brommer, 2000). The reproductive value is the relative value of how much an individual class (age or stage) (Grafen, 2006) is expected to contribute to the genetic ancestry of future generations (Taylor et al., 1974). The RV can be useful to quantify advantages and disadvantages of trade-offs and decisions made by individuals. The RV can also give insight in population dynamics, as it is intrinsically linked with population growth (Sæther et al., 2021). The RV includes the life history of an organism. Thus, the traditional method of measuring RV requires extensive knowledge about this life history and its corresponding values of fecundities and death rates of different classes (Caswell, 1982).

A new method of estimating RV uses pedigrees by making use of modern genotyping techniques that allow for cheaper and more precise pedigrees (Huisman, 2017; Sardell et al., 2010). This method was first described by MacCluer et al., 1986 and there has been an increase in its use since then (Barton et al., 2011; Chen et al., 2019; Reid et al., 2019). The pedigree-based reproductive value (pRV) measures the actual genetic contribution to future generations of individuals. This intuitively approaches the theoretical definition of RV by Fisher, 1993, which is the value of the expected genetic contribution to future generations. This method requires an extensive pedigree but is more intuitive and requires less mathematics, especially in more complex life histories. Therefore, the introduction of this method was welcomed by many biologists that were looking for a more straightforward way of estimating the RV However, until recently, this method has never been validated. Comparing a pRV from field data with a RV based on life history parameters that are also estimated from field data cannot give a definitive answer, as there is uncertainty in both these values. Therefore, simulations can be used to make pedigrees. These simulations will have life history parameters that are known as they are set before the simulation starts.

Borger et al., 2022 used this method to validate the pRV. The research suggests that the estimated pRV is either imprecise or systematically biased. The genetic contribution of a class of individuals is a consequence of stochastic processes and therefore often differs substantially from the "real" theoretical value calculated with the traditional method. The pRV was estimated from individual-based simulated populations. Different simple life histories were used using only a few age stages or behavioural classes. Some parameters that were included in the simple models are sexual reproduction and fluctuating environments. It was also tested how robust the RV was to uncertainties in life history parameters when using the traditional method of calculating the RV. At the start of the simulation, a zigzagging pattern in the pRV was present. After some generations, the median of these simulations usually approached the true RV, but the outcomes of individual simulations had increasingly diverging outcomes when generations were increased. When sampling a real population, you only have one estimate of the pRV and you cannot rely on a median. This single estimate can be way off-target and is unreliable according to this research.

The simple life histories make the calculation of the RV and the model straightforward. However, an oversimplification of real populations could also cause unrealistic population dynamics. A logical step in improving the model is adding different sexes. Different sexes can have different RVs when the ratio between the sexes is not $1:1$, as the total RV of males and females is always equal. For example, if there are more males than females, the average RV of females is higher than the average RV of males according to Fisher's principle (Fisher, 1993). Different sexes can also have different fecundities and death rates due to genetic, morphological or behavioural differences (Clobert et al., 1988; Maklakov et al., 2009). There can also be differences in the social structure of sexual behavior. For example, you can have a dominant male that mates multiple times and subordinate males that do not mate at all, while there is not such an extreme difference between dominant and subordinate females. These sex

ratios and differences between sexes are often excluded from models and data and often only females and female offspring are considered for simplicity. Different sexes have not yet been implemented in the model with respect to a pRV by Borger et al., 2022. Adding sexes to the life history could lead to different dynamics and to a more precise estimation of the RV.

This study will test the pedigree-based estimate of the RV in individual-based simulations that include different sexes. The precision, the accuracy, and the median of the pRVs over multiple simulations. These simulations will allow us to answer the question: to what extent is the pedigree approach able to quantify RVs for males and females? We will tackle this question by answering the following sub-questions: What is the effect of different sex ratios in a population on the pRV estimates? What is the effect of different life history parameters between the sexes on the pRV estimates? How do differences in life history strategies concerning dominant and subordinate behavior by males affect the pRV estimates?

These questions will be answered using individual-based simulations in C++. Simulations used by Borger will be extended or adapted. We will simulate individuals of different sexes that reproduce sexually. We will track the individuals and their offspring to make a pedigree. This pedigree will be used to calculate the pRV. This pRV will be compared to a theoretical "true" RV, which can be calculated using either Fisher's principle or a mathematical approach using a life history matrix. It is possible to calculate the true RV since the parameters as death rate and fecundity are set by us in the model and are not estimated from field data. We will then compare these pedigree-based and theoretical values for the different scenarios and investigate how accurate and precise a pRV is.

2 Methods

All simulations are individual based and based on specific life history scenarios, as described in figure 1. Scenario 1 exists of males and females. Scenario 2 has males and females of different age classes. Scenario 1 and 2 will be further explained in section 2.1 and 2.2 respectively.

Time proceeds in discrete time steps, where every time step matches one reproductive season. In our models we usually used 20 time steps, unless stated otherwise. In a reproductive season, an individual can reproduce and after that either survive and stay in their age class, survive and change age class or die.

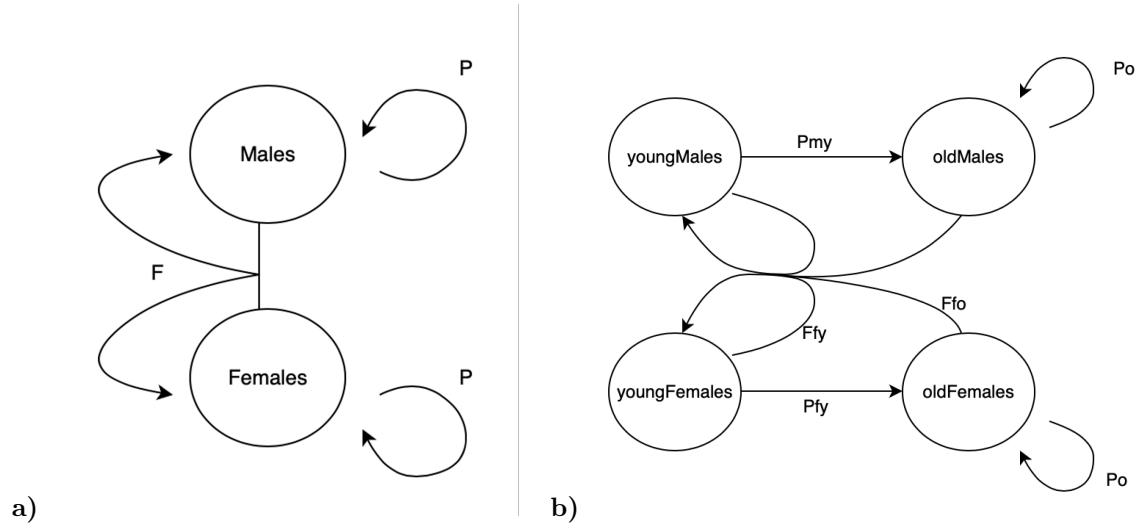


Figure 1: Life history diagrams. Each circle represents a type of individual in the population. The arrows represent the expected fecundity (F) or survival (P) of individuals. **(a)** Scenario 1: P is the density dependent survival probability and F is the average number of offspring produced per individual per reproduction event. **(b)** Scenario 2: Pmy and Pfy are the probabilities for young males and young females to survive to adulthood respectively. Ffy is the average fecundity of young females. Ffo is the average fecundity of old females. Po is the density dependent survival probability of old males and females. The fecundity of males depends on their mate.

Reproduction occurs first. We used a reproductive system where all females always mate once. A female is assigned to a male which is picked randomly from the population. This means that some males mate once, some mate multiple times and some do not mate at all. The number of offspring produced per mating is determined by a Poisson distribution around a predetermined fecundity (F). All offspring survive at least until the next reproductive season and enter the population at $t+1$. Each offspring inherits one gene of its mother and one gene of its father. Which gene is inherited from the parent is determined by chance and has equal probability. The sex of the offspring is determined by a discrete distribution, using the probability p of producing a son (and $1-p$ for the probability of producing a daughter).

After reproduction, survival occurs. The survival probabilities are determined so that the population remains stable in size. Which individuals survive is determined by a Bernoulli distribution with the survival probability as its mean. The survival probability can be density dependent, and it is then calculated by the following equation:

$$\frac{1}{1+\alpha \cdot N} \tag{1}$$

Here, N is population size and alpha is the intensity of the density dependence. We set the initial population size and then adjusted the parameter alpha depending on the model in such a way that the population remained stable around 1000 individuals.

Different types of density dependent population were also investigated. Density dependency in the young population, density dependency in only one sex, and density dependency in the fecundity were investigated.

The effect of the number of generations was also be tested to see what happens to the pRV when more time passes. Simulations will be run with 100 generations instead of 20 generations.

Every generation, the pRV is calculated using 'gene-dropping'. The initial population started in a stable stage distribution. Therefore, there was no need to wait with gene-dropping until the populations were stable. At initialization of the populations, every individual was given 2 genes. These genes are unique per life history stage, and individuals in these stages were homozygous for this gene. For example, in the most basic scenario, all males were homozygous for gene '1', and all females were homozygous for gene '2'. These genes spread throughout the population, through inheritance by the offspring. When a male and female mate, the offspring gets one of the genes of its mother and one of the genes of its father. The pRV is then calculated by counting how many of each of the genes of the original population are present in the current population. This count is then divided by 2 as every individual has 2 genes and the theoretical reproductive value is measured on the individual level. To further scale this countback to the individual level, the count is divided by the number of individuals of that age class at the start of the simulation, to calculate the number of offspring per original individual in each age life history stage. The reproductive value is always relative. The pRV of the youngest male population is always set to 1. The pRV of the other stages is then calculated by dividing the number of offspring per original individual of that stage by the number of offspring per original individual of (young) males.

Stochasticity in individual reproductive success is extensive. Estimating RV based on single individuals hence is highly unreliable (Borger et al., 2022; Chen et al., 2019). Therefore, we base our estimates of RV on classes of individuals. One simulation is comparable to field situations. The pRV will be calculated for 100 simulations per life history and parameter setting. To easily be able to see the variation between simulations we will make graphs that show the median, the 50% central values and the 90% central values of these 100 simulations.

2.1 Scenario 1

This scenario is the simplest scenario. There is a male population and a female population (see figure 1a). The density dependent survival rate is determined solely on the size of the adult population, not on the number of offspring that was just born. Each simulation was done for twenty generations and was repeated a hundred times. The RV of the males was set as one, and the female RV was calculated using Fisher's Principle. The offspring produced by one female can have different fathers.For simplicity we assumed that the initial population was homozygous for its marker gene.

We used Fisher's Principle to estimate the true reproductive values. This principle states that because offspring have one father and one mother, in a population the total RV of all males and females is the same. This means that when there are more males than females, the RV of a single female individual is on average higher than the RV of a single male individual. We used set ratios and proportional start population sizes so that the true RV was equal to the sex ratio. For example, when there are 3 times as many males as females, the RV of a female is 3 compared to the RV of a male which is set to 1.

2.2 Scenario 2

This scenario has four life history states (see 1b). Males and females can be young or old. Both young and old individuals reproduce, but can have different fecundities. Females of both age classes can mate with males of both age classes. The fecundity is solely determined by the age of the female. The survival probability of young individuals is fixed and can differ between the sexes, Pmy for males and Pfy for females. The survival probability of old individuals is density dependent and is the same for both males and females.

In scenario 2 it is not possible to use Fisher's principle to calculate the true RV. Therefore, recurrence relations were used (see appendix A). Equations including the life history parameters were made to calculate the stable stage distributions and the reproductive values and were solved in Excel. The life history parameters that were fixed, such as fecundity and death rate of young individuals were put in directly. The survival probability of adult individuals was calculated by solving the density dependent equation 1 for the alpha used in the model and N = 1000.

Technical note
Simulations were written in C++. Figures were made in R3.4.1, with the packages ggplot2 and cowplot.

3 Results

3.1 Scenario 1

When looking at multiple simulations of a population with the same life history and the same life history parameters, there is a significant variation in the pRV (see figure 2). The variation arises due to the stochastic effects in the population, which can outweigh the effects of the true reproductive value of an individual. This variation is partly dependent on the values of the life history parameters. For example, when the fecundity and the death rate are both higher, there is more variation in the pRV compared to a population with a low fecundity and death rate. Individual simulations usually

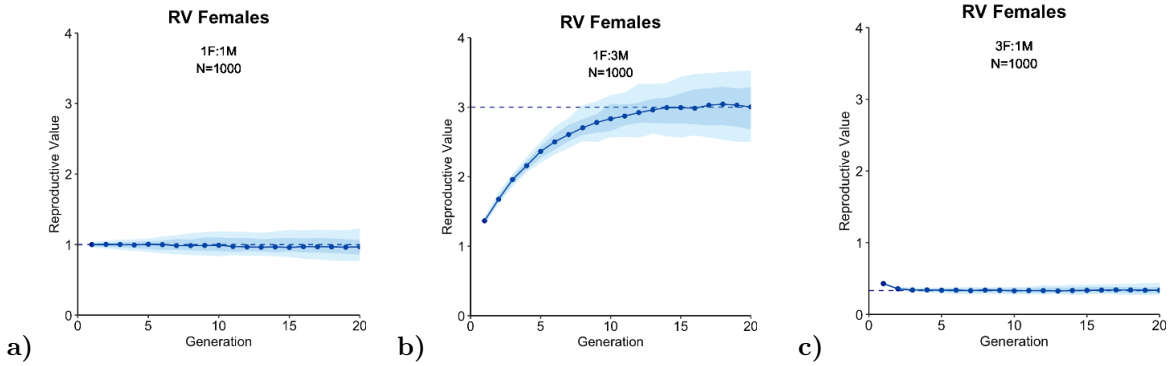
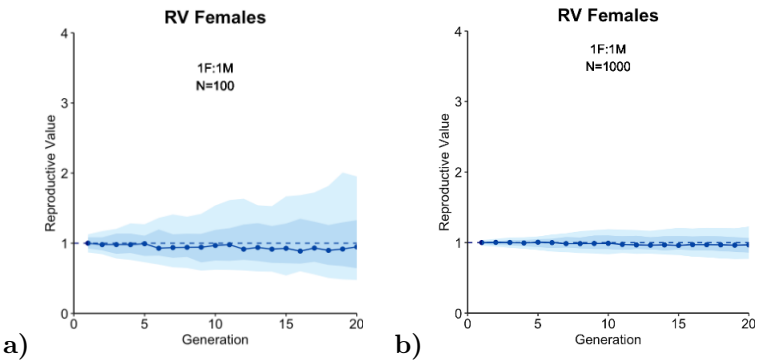
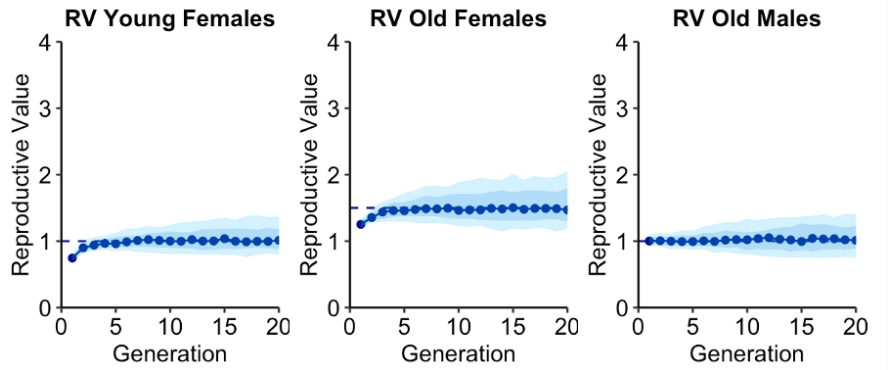


Figure 2: Example simulations of scenario 1, two-stage model. Dashed horizontal lines represent the true RV. Dotted lines indicate the medians of the 100 simulations per time step. The dark blue (light blue) bands represent the 50% (90%) confidence intervals of the simulations. Parameter values: $F = 1$ for all graphs, α is 0.001 for a), 0.00033 for b), 0.003 for c). **(a)**. Reproductive value of females in a population with a 1F:1M ratio. **(b)** Reproductive value of females in a population with a 1F:3M ratio. **(c)** Reproductive value of females in a population with a 3F:1M ratio..

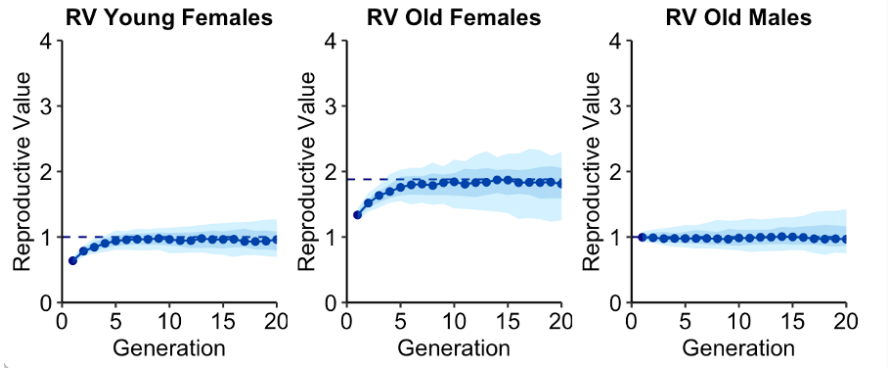


a) **b)**

Figure 3: Simulations of scenario 1, two-stage model. Dashed horizontal line represent the true RV. Dotted line indicate the medians of the 100 simulations per time step. The dark blue (light blue) band represents the 50% (90%) confidence intervals of the simulations. Parameter values: $F = 1.0$ for both graphs. **(a)** Reproductive value of females in a population with a 1F:1M ratio, a population size of 100 individuals, and an α of 0.01. **(b)** Reproductive value of females in a population with a 1F:1M ratio, a population size of 1000 individuals, and α of 0.001.



(a)



(b)

Figure 4: Simulations of scenario 2, the four-stage model. The population has 1000 individuals and the offspring sex ratio is 1F:1M. Dashed horizontal lines represent the true RV. Dotted lines indicate the medians of the 100 simulations per time step. The dark blue (light blue) bands represent the 50% (90%) confidence intervals of the simulations. **(a)** Equal survival probability for young males and young females. Parameter values: $Fy = 0.5$, $Fo = 1.5$, $Pmy = 0.5$, $Pfy = 0.5$, $\alpha = 0.001$. **(b)** Different survival probability for young males and young females. Parameter values: $Fy = 0.5$, $Fo = 1.5$, $Pmy = 0.6$, $Pfy = 0.4$, $\alpha = 0.000667$.

have a pRV that is either significantly lower or higher than the true RV. They also do not stabilize over time. The median of the pRV's does approach the theoretical value of the RV. The accuracy of the pRV estimates consequently seems fine. The average sometimes also reflects the theoretical RV, but in other cases is a multiple of the true RV because there are very large estimates of the pRV in the simulations. This implies that the precision of the pRV seems systematically incorrect.

The results of the one generation model clearly reflect Fisher's principle. When the population ratio is skewed, one sex gets a higher reproductive value (see figure 2b and 2c). At first glance it looks like there is more variation in the scenario with a 3 to 1 male to female ratio. However, as the RV is higher for this ratio compared to the other ratios, the variation is also higher. The relative variation is equal for the different ratios.

The variation becomes larger with a smaller population size. The graphs in figure 3a show population sizes that are more realistic for fieldwork. Here the variation is significantly larger than in the larger population sizes, even for this relatively simple life history, compared to figure 3b.

In the beginning of the simulations the variation is the smallest but in most cases it is not yet near the theoretical reproductive value. Over time, variation in the pRV increases and the median comes closer to the theoretical value. How fast this happens differs between life histories and parameter settings. Usually, the estimate is best after 5 to 10 generations. However, sometimes the best estimate is earlier, but it can even be as late as 12 generations. Increasing the time horizon from 20 to 100 generations did not change the results.

3.2 Scenario 2

The results from the life history with 2 age classes are similar to the results of 1 age class. Again, the median of the simulations corresponds well with the theoretical RV. Variation arises over time and appears similar to scenario 1 (see figure 4a).

None of the different types of density dependent population size control gave different results than the scenario with density dependency in the adult survival probability.

When the survival probability of males is higher than females, the median of the pRV's still coincides with the theoretical value. However, this came with an increase in the variation (figure 4b) compared to the equal survival probability simulations (figure 4a).

4 Discussion

The new method of estimating the RV, which uses the pedigree, might not be as reliable as previously thought. Our research confirms this: The pedigree-based method of estimating the reproductive value is not reliable to quantify the reproductive value in a population with males and females. Estimates of the reproductive value can be multiple times smaller or larger than the true reproductive value in realistic population sizes. In larger population sizes, the estimates come closer to the real value, but are still not reliable. The estimates also have not stabilized in a large proportion of the simulations. The variation in estimates increases over time. The median of the estimates does come close to the true RV. In the start of the simulations, there is less variation, but the estimates are not accurate. The estimates of the RV did not improve in populations with different sex ratios. However, the median of the estimates was able to nicely reflect Fisher's principle, which means that our model likely works well. However, this median of the estimates is not useful in real populatios as you only have one estimate. In populations with different age classes and different survival parameters between the sexes, the median was again able to closely reflect the true reproductive values but including different age classes did not cause a decrease in the variation of the individual estimates.

Our findings are in line with previous studies in real populations (Chen et al., 2019; Hunter et al., 2019) and with a previous computer study with simulations without sexes (Borger et al., 2022). Research in Soay sheep by Chen et al., 2019 show very diverse genetic contributions to future generations per individual and different estimates of the pRV for different cohorts in the same population. This research suggested that this was caused by stochastic effects and a high mortality in young individuals, which concentrates the reproductive value in only a few surviving individuals, which are subject to more stochasticity. Research by Hunter et al., 2019 show that there is a surprisingly large amount of variation in the pRV of sparrow populations which is also caused by stochastic effects. Borger's simulations agree with these findings and also suggest that the traditional method of calculating the

RV is more reliable than the pedigree-based method, even considering uncertainty in the life history parameters used to estimate the RV. When comparing our results with that of Borger, there is an equal amount of variation in the estimates of the RV. One aspect that is noticeably different is that in our simulations, the median of the estimates approached the true RV with a smooth curve, while in Borger's simulation, this happened through a zig-zagging pattern. In both models there the number of timesteps it took for the median to converge to the true RV differed between different life histories and was not predictable.

We conclude that pedigree-based estimates of the reproductive value are not reliable due to lack of precision and accuracy. As it is also expensive to sequence a large population over a long time span, we argue that this method should not be used. Due to stochasticity in number of offspring, survival rate, and population dynamics, estimates can diverge significantly from the true reproductive value over time. The systematic bias in the start of the measurements also make estimates that are taken after only a few generations unreliable. It is likely that the estimates are even more unreliable in real populations for several reasons. More complex life histories will lead to more stochastic effects. It is also unlikely that a complete pedigree will be obtained due to not sampling the same individuals by chance, or emigration and immigration.

It is possible that our life history assumptions influenced the outcome of simulations. Different life histories may lead to more stable estimates of the RV. For example, if there is a life history with a low stochasticity due to dampening effects, the estimates can be more reliable. However, we tested multiple life histories with different parameter settings and in all cases, there was enough stochasticity to make the estimates imprecise. Furthermore, field studies have tested pRV's for up to 30 years. What happens to the pRV after these 30 years in real populations is not known, although our model suggests that the estimates will only diverge further. We have not answered our research question that asks how the pRV is affected by a population where there is dominant and subordinate behavior in males. However, we expect that this will further increase the variation in the pRV as fewer individuals hold more of the reproductive value which causes the pRV to be more susceptible to stochasticity.

An interesting life history which we have not analyzed in detail is one that has a higher birth ratio and death rate for one sex. This is the case in humans for men. To check what would happen to the model in more complex life histories, one could also base a model on a real organism of which the life history is known and there is a traditional estimated of the RV.

Some biologists may be disappointed with our results that the pedigree-based method of estimating the reproductive value is not reliable. This intuitive method could have been applied to existing pedigrees and would have required less measurements of life history parameters for new RV estimates. However, our simulations did show that a population with sexes is easily simulated, and this method is promising for future research in life history theory including sexes.

References

Barton, N. H., & Etheridge, A. M. (2011). The relation between reproductive value and genetic contribution. *Genetics*, *188*: 953–973.

Borger, M. J., Komdeur, J., Richardson, D. S., & Weissing, F. J. (2022). Putting life history theory to the test - the estimation of reproductive values from field data. *The American Naturalist,* under review.

Brommer, J. E. (2000). The evolution of fitness in life-history theory. *Biological Reviews*, ***75***: 377–404.

Caswell, H. (1982). Stable population structure and reproductive value for populations with complex life cycles. *Ecology*, ***63***: 1223–1231.

Chen, N., Juric, I., Cosgrove, E. J., Bowman, R., Fitzpatrick, J. W., Schoech, S. J., Clark, A. G., & Coop, G. (2019). Allele frequency dynamics in a pedigreed natural population. *Proceedings of the National Academy of Sciences*, ***116***: 2158–2164.

Clobert, J., Perrins, C., McCleery, R., & Gosler, A. (1988). Survival rate in the great tit parus major in relation to sex, age, and immigration status. *The Journal of Animal Ecology*, ***57***: 287–306.

Fisher, R. (1993). The genetical theory of natural selection. The Clarendon press.

Grafen, A. (2006). A theory of fisher's reproductive value. *Journal of mathematical biology*, ***53***: 15–60.

Huisman, J. (2017). Pedigree reconstruction from snp data: Parentage assignment, sibship clustering and beyond. *Molecular ecology resources*, ***17***: 1009–1024.

Hunter, D. C., Pemberton, J. M., Pilkington, J. G., & Morrissey, M. B. (2019). Pedigree-based estimation of reproductive value. *Journal of Heredity*, ***110***: 433–444.

Kimbrough, S. O. (1980). The concepts of fitness and selection in evolutionary biology. *Journal of Social and Biological Structures*, ***3***: 149–170.

MacCluer, J. W., VandeBerg, J. L., Read, B., & Ryder, O. A. (1986). Pedigree analysis by computer simulation. *Zoo biology*, ***5***: 147–160.

Maklakov, A. A., Hall, M. D., Simpson, S. J., Dessmann, J., Clissold, F. J., Zajitschek, F., Lailvaux, S. P., Raubenheimer, D., Bonduriansky, R., & Brooks, R. C. (2009). Sex differences in nutrient-dependent reproductive ageing. *Aging cell*, ***8***: 324–330.

Reid, J. M., Nietlisbach, P., Wolak, M. E., Keller, L. F., & Arcese, P. (2019). Individuals' expected genetic contributions to future generations, reproductive value, and short-term metrics of fitness in free-living song sparrows (melospiza melodia). *Evolution letters*, ***3***: 271–285.

Roff, D. (1993). Evolution of life histories: Theory and analysis. Springer Science & Business Media.

Sæther, B., & Engen, S. (2021). Reproductive value and analyses of population dynamics of age-structured populations. *Demographic Methods Across the Tree of Life*, ***285***: 285.

Sardell, R. J., Keller, L. F., Arcese, P., Bucher, T., & Reid, J. M. (2010). Comprehensive paternity assignment: Genotype, spatial location and social status in song sparrows, melospiza melodia. *Molecular Ecology*, ***19***: 4352–4364.

Taylor, H. M., Gourley, R. S., Lawrence, C. E., & Kaplan, R. S. (1974). Natural selection of life history attributes: An analytical approach. *Theoretical Population Biology*, ***5***: 104–122.

Appendix

A Equations for calculating the theoretical RV in scenario 2

The following formulas were used to calculate the stable stage distributions and the theoretical reproductive value in scenario 2.

The input values were taken from the simulation parameters. When there was density dependency, equation 1 was used to calculate the survival probability where α was taken from the simulation and N was assumed to be 1000.

$$n_{f,o} = P_{f,y} \cdot n_{f,y} + P_{f,o} \cdot n_{f,o} \tag{2}$$

$$n_{m,o} = P_{m,y} \cdot n_{m,y} + P_{m,o} \cdot n_{m,o} \tag{3}$$

$$n_{f,y} = F_{f,y} \cdot n_{f,y} \cdot (1-s) + F_{f,o} \cdot n_{f,o} \cdot (1-s) \tag{4}$$

$$n_{m,y} = F_{f,y} \cdot n_{f,y} \cdot s + F_{f,o} \cdot n_{f,o} \cdot s \tag{5}$$

$$V_{f,y} = P_{f,y} \cdot V_{f,o} + \frac{1}{2} \cdot F_{f,y} \cdot s \cdot V_{m,y} + \frac{1}{2} \cdot F_{f,y} \cdot (1-s) \cdot V_{f,y} \tag{6}$$

$$V_{f,o} = P_{f,o} \cdot V_{f,o} + \frac{1}{2} \cdot F_{f,o} \cdot s \cdot V_{m,y} + \frac{1}{2} \cdot F_{f,o} \cdot (1-s) \cdot V_{f,y} \tag{7}$$

$$\begin{aligned} V_{m,y} = P_{m,y} \cdot V_{m,o} &+ \frac{1}{2} \cdot F_{f,y} \cdot s \cdot V_{m,y} \cdot \frac{n_{f,y}}{n_{m,y}+n_{m,o}} + \frac{1}{2} \cdot F_{f,y} \cdot (1-s) \cdot V_{f,y} \cdot \frac{n_{f,y}}{n_{m,y}+n_{m,o}} \\ &+ \frac{1}{2} \cdot F_{f,o} \cdot s \cdot V_{m,y} \cdot \frac{n_{f,o}}{n_{m,y}+n_{m,o}} + \frac{1}{2} \cdot F_{f,o} \cdot (1-s) \cdot V_{f,y} \cdot \frac{n_{f,o}}{n_{m,y}+n_{m,o}} \end{aligned} \tag{8}$$

$$\begin{aligned} V_{m,o} = P_{m,o} \cdot V_{m,o} &+ \frac{1}{2} \cdot F_{f,y} \cdot s \cdot V_{m,y} \cdot \frac{n_{f,y}}{n_{m,y}+n_{m,o}} + \frac{1}{2} \cdot F_{f,y} \cdot (1-s) \cdot V_{f,y} \cdot \frac{n_{f,y}}{n_{m,y}+n_{m,o}} \\ &+ \frac{1}{2} \cdot F_{f,o} \cdot s \cdot V_{m,y} \cdot \frac{n_{f,o}}{n_{m,y}+n_{m,o}} + \frac{1}{2} \cdot F_{f,o} \cdot (1-s) \cdot V_{f,y} \cdot \frac{n_{f,o}}{n_{m,y}+n_{m,o}} \end{aligned} \tag{9}$$

Where $n_{f,y}$ is the number of young females, $n_{m,y}$ is the number of young males, $n_{f,o}$ is the number of old females, $n_{m,o}$ is the number of old males, s is the sex ratio (proportion of males), $P_{f,y}$ is the probability the a young females survives and becomes old, $P_{f,o}$ is the probability that an old female survives, $P_{m,y}$ is the probability the a young males survives and becomes old, $P_{m,o}$ is the probability that an old male survives, $F_{f,y}$ is the average fecundity of a young female, and $F_{f,o}$ is the average fecundity of an old female.