What is the best fitness measure in wild populations? A case study on the power of short-term fitness proxies to predict reproductive value

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Abstract

Fitness is at the core of evolutionary theory, but it is difficult to measure accurately. One way to measure long-term fitness is by calculating the individual's reproductive value, which represents the expected number of allele copies an individual passes on to distant future generations. However, this metric of fitness is scarcely used because the estimation of individual's reproductive value requires long-term pedigree data, which is rarely available in wild populations where following individuals from birth to death is often impossible. Wild study systems therefore use short-term fitness metrics as proxies, such as the number of offspring produced. This study obtained three frequently used short-term proxies for fitness obtained at different offspring life stages (eggs, hatchlings, fledglings and recruits), and compared their ability to predict reproductive values derived from the genetic pedigree of a wild passerine bird population. We used twenty years of precise field observations and a near-complete genetic pedigree to calculate reproductive success, individual growth rate and de-lifed fitness as lifetime fitness measures, and as annual de-lifed fitness. We compared the power of these metrics to predict reproductive values and lineage survival to the end of the study period. The three short-term fitness proxies predict the reproductive values and lineage survival only when measured at the recruit stage. There were no significant differences between the different fitness proxies at the same offspring stages in predicting the reproductive values and lineage survival. Annual fitness at one year old predicted reproductive values equally well as lifetime de-lifed fitness. However, none of the short-term fitness proxies was strongly associated with the reproductive values. In summary, the commonly short-term fitness proxies capture long-term fitness with intermediate accuracy at best, if measured at recruitment stage. As lifetime fitness measured at recruit stage and annual fitness in the first year of life were the best proxies of long-term fitness, we encourage their future use.

Keywords: de-lifing, reproductive values, fitness, individual growth rate, lifetime reproductive success

Introduction

The concept of fitness is central to evolutionary theory (1). Natural selection maximises fitness, which is therefore a driving force of evolution as well as a measure of evolutionary success (2). One definition of fitness is how good an individual is at spreading its genes into future generations, relative to all other individuals in the population (2). A universal definition of fitness in mathematical terms that applies to all population structures and dynamics is however not agreed on (2–5).

Ecological studies measure fitness in diverse ways, often depending on the research question, the population dynamics, and the ecology of the study species (6,7). While some studies measure fitness across lifetimes, other studies measure individual annual fitness to examine variation in selection between years (8). Lifetime fitness is considered more accurate than annual measures, as the latter is influenced by environmental stochasticity (7,9). Alternative fitness measures have been developed that account for environmental stochasticity and population dynamics (5,10–12).

Some fitness metrics include both survival and fecundity components (8,13), while others focus on only one component as a proxy, such as lifespan (4), or on only a single life-history trait, such as the age at first reproduction (13,14). The two most commonly used individual fitness proxies are lifetime reproductive success (LRS) (15) and individual growth rate (IGR) (13). Both count the number of offspring produced in the individual's lifetime, but IGR gives more weight to offspring produced at a younger age (13), therefore results differ (16). As a consequence, different fitness proxies do not necessarily correlate well (7) and more research is needed to determine which is the most appropriate measures of fitness (6). Choosing the appropriate fitness proxy is therefore an important consideration when designing a study (7).

The age of an offspring at the time it is included in the fitness measurement of the parent must also be considered, particularly given that studies count offspring at varying ages or life-history stages. Offspring survival can be both a part of offspring fitness due to its unique genotype, or a part of parental fitness in cases where parental phenotype affects offspring mortality, for example through parental care (17). Counting offspring at higher stages of development assigns a part of offspring fitness into parental

fitness, thus potentially affecting the strength and direction of selection. Furthermore, Brommer et al. (6) show that the age of offspring census directly affects IGR values, while it does not affect LRS, making the two fitness proxies less comparable at different stages. It is therefore important to understand what census time best captures parental fitness.

Although fitness is considered to be a measure of an individual's gene copy frequency in future generations, most fitness proxies focus on an individual's direct descendants. Alternatively, the reproductive value from a single individual, defined as the expected number of copies of each of an individual's alleles in a future generation conditional on a realised pedigree of descendants, can be used to measure long-term fitness (18). The reproductive values can be estimated from a genetic pedigree, following rules of mendelian inheritance to calculate how many allele copies survive on average. The reproductive values stabilise after $\log_2 N$ generations, where N is the population size (4,18,19). While the ultimate genetic contribution of an individual will only emerge over long timescales (>100 generations), the reproductive values are determined in ~10 generations and are a good predictor of the ultimate genetic contribution (18).

The reproductive values closely predict allele survival probability, but not their frequencies (18). Due to recombination and segregation in meiosis, the actual genetic frequencies, conditional on allele survival, instead follow a random distribution (18–21). Consequently, not all genealogical ancestors are also genetic ancestors (22). Despite the difference between actual allele frequencies and the reproductive values, reproductive value is a practical and relevant measure for evolutionary studies as it is maximised by natural selection, thus closely corresponding to fitness (18,23).

This study examined the correlation between several short-term fitness proxies and reproductive values. We used data from an isolated house sparrow (*Passer domesticus*) population on Lundy Island (United Kingdom) with 20 years of life history data, unusually precise measures of survival and reproductive success, and nearly complete genetic pedigree information (24). We examined the two most commonly used individual fitness proxies based on fecundity (25): lifetime reproductive success (LRS) and individual growth rate (IGR) (13). We measured both at four different offspring stages (eggs, hatchlings, fledglings, and recruits) to investigate which are most accurate. We also used a short-term

95 fitness proxy that incorporates survival – de-lifed fitness (8). This is based on individual offspring
96 production and survival adjusted for population growth.

Methods

Study system

The house sparrow population on Lundy Island has been continuously monitored since 2000. Lundy is a small island 19 km off the south-west English coast (51°11N, 4°40W). In 2000, 50 individuals were brought to Lundy from the mainland for an experiment (26). Due to the distance of the island from the mainland and the sedentary nature of sparrows, there is minimal dispersal to and from the island (24). The sparrow population size has fluctuated between 166 and 1242 individuals (juveniles included) between 1999 and 2019 (Fig 1A).

During systematic annual monitoring, each sparrow is ringed with three colour rings and one metal ring from the British Trust for Ornithology. Since most sparrows are initially caught as nestlings and ringed as fledglings, we know the identities of the parents attending their nests, and the exact age of all individuals (27). Over 99% of the population has been ringed since 2000 (27). If an individual is not seen for two years or more, it is assumed dead, with this assumption based on previous mark–recapture success data (27,28). Blood samples are collected upon bird capture and genotyped at up to 23 microsatellite loci (24). This allows for the assignment of genetic parentage with 95% confidence (24). From the genetic pedigree and the social brood information, the reproductive success of individuals is calculated. Thanks to these data, the study system provides unusually accurate survival, reproduction, and pedigree data for the complete population (24).

Pedigree analysis

We calculated fitness proxies and the reproductive values for founders and half-founders that were born between 1999 and 2002, the starting years of the long-term study. Founders and half-founders were defined as individuals for which both parents, or one parent, respectively, were unknown. To calculate reproductive values, we used our genetic pedigree containing all reproducing individuals up to 2018. We removed any individuals from cohorts after 2002 that had at least one unknown parent; thus 8% of all individuals in the pedigree were removed.

Reproductive values were calculated using gene dropping (29). Gene dropping is a computer simulation in which each individual is assigned two alleles (one paternal and one maternal), and their Mendelian transmission down the pedigree is simulated. By repeating this simulation many times and calculating the mean values, robust estimates of reproductive values can be obtained by examining the frequency of an individual's alleles in subsequent generations. In addition, the allele survival probability can be calculated by examining in how many simulations the allele survives in present-day individuals. We ran the simulation 10,000 times using R package nadiv (30). Using the results, we derived lineage longevity, reproductive values, and allele survival probability. We define lineage longevity as the number of years before a lineage originating from one individual goes extinct, and allele survival probability is the proportion of gene dropping simulations in which a lineage survives. We explored whether lineages from the experimentally introduced sparrows differed from native lineages in their rate of survival to 2018 (last year with complete data) and in their reproductive values. We chose to work with years rather than generations as a measure of time because sparrows have overlapping generations.

Short-term fitness metrics

We calculated the short-term fitness proxies for the founders and half-founders from cohorts between 1999 and 2002 with complete life-history data. Founders with incomplete life-history data were removed because this could lead to an underestimation of their reproductive success. The individual lifetime production of eggs, broods, hatchlings, fledglings, and recruits was then calculated, as well as IGR at all four offspring stages, and de-lifed fitness. Hatchlings were defined as offspring counted in a nest two days after hatching, and fledglings were birds that survived until ringing, which is typically 12 days after hatching. Recruits were defined as offspring that successfully reproduced and produced at least one egg in any subsequent years.

The IGR is the dominant eigenvalue of an individual population transition matrix, as described in (13). In an individual population transition matrix, the sub-diagonal represents survival, and the first row is filled with the number of offspring produced at each parental age, divided by two to account for parent–offspring relatedness being ½. An example of an individual population transition matrix for an

149 individual that survived three years and had 1, 2 and 1 offspring at ages 1, 2, and 3 respectively, is given
150 below:

151 $$\begin{bmatrix} 0.5 & 1 & 0.5 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix}$$

152 We also calculated annual de-lifed fitness based on the formula (8):

153 $$p_{ti} = \frac{\xi_{t(i)} - w_{t(i)}}{N_t - 1}$$

154 Where:

155 • p_{ti} is individual fitness
156 • $\xi_{t(i)}$ is the number of individual's surviving offspring at the end of the time step plus one if the
157 individual survived
158 • $w_{t(i)}$ is the population size in year t+1 divided by population size in year t
159 • N_t is the population size of adults on 1st April each year

160 While LRS and IGR are both lifetime fitness measures, de-lifing was designed primarily as a per-
161 generation fitness proxy and is here calculated annually. However, lifetime de-lifed fitness can be
162 obtained by summing the annual fitness values for each individual (8,31). We therefore used de-lifed
163 fitness as both an annual fitness proxy and, after summing, as a lifetime fitness proxy.

164 We calculated Pearson's correlation between each fitness metric and the reproductive values for the
165 lineages that survived. We ran a binary logistic regression model in R version 4.0.3 (32), using
166 MCMCglmm (33) with lineage survival to 2018 as the response variable, and each fitness metric as the
167 explanatory variable. The fitness metrics were z-transformed so that the slopes were not affected by the
168 variable variances. We used priors with the residual variance fixed at 0.5 and ran the model for 100,000
169 iterations with the thinning interval set at 70 and the burn-in at 7,000. We examined which fitness metric
170 had the strongest association with reproductive values based on the slope of the regression.

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Ethics statement

As this was a theoretical study using previously selected data, no ethics approval was required.

Results

Reproductive values

There were in total 111 lineages arising between 1999 and 2002 used for the analyses. Of these 111 lineages, 18 lineages were founded by sparrows experimentally introduced in 2000 (26) and 93 lineages stem from native sparrows already present on the island in 2000. Forty-three lineages survived to 2018, of which 11 were introduced and 32 were native. Hence, at most, 39% of the founders passed genetic material to 2018, and there was no statistically significant association between a lineage's origin and survival ($p = 0.06$, Fisher's exact test). The mean lineage survival probability was 0.16 (95% CI 0.13–0.18), and the survival probability for lineages appearing in 2018 was 0.40 (95% CI 0.37–0.43, Fig 1A). There was variation in the absolute reproductive values (mean = 1.64, 95% CI 1.32–1.95 range: 0.41–18.89, Fig 1B). The introduced lineages had on average higher reproductive values than native lineages ($t = 2.70$, df = 17.90, $p = 0.015$). Contributions varied over time, but after 2007 fluctuations were more synchronous among lineages, and the ranking of lineages based on their reproductive values remained similar (Fig 1E). Population fluctuations closely follow fluctuations in the reproductive values in the previous year. The change in lineage behaviour after 2007 is visible in lineage longevity, as all lineages that survived the from 2000 to 2006 also survived until 2018 (Fig 1C). After 2007, the correlation between annual reproductive value and reproductive values in 2018 also increased, and stabilised around 2011 subsequent to which the correlation was above 0.95 (Fig 1D).

193 ***Fig 1: (A) Reproductive values and population size during the study period. Bars represent the population size***
194 ***and lines represent the reproductive values of each of the 43 lineages that survived to 2018. (B) Survival***
195 ***probability of 111 house sparrow lineages on Lundy Island from 1999 to 2018. (C) Reproductive values of the***
196 ***111 lineages. (D) Number of years to lineage extinction for the 111 lineages. Lineages that survived 18, 19, 20***
197 ***or 21 years are those that were still extant in 2018, corresponding to cohorts 1999, 2000, 2001 and 2002***
198 ***respectively. (E) Correlation between the reproductive values in each year and the final year.***

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Fitness proxies

Fitness proxies were calculated for 86 founders, 44 males and 42 females. We estimated the correlation with the reproductive values of 42 lineages that survived to 2018 and had no missing fitness data. In total, individuals included in the analysis produced 2,054 eggs of which 1,746 (85%) survived to hatching, 881 (43%) to fledging and 294 (14%) recruited into the breeding population.

The fitness proxies were all positively associated with the reproductive values (Fig. 2). De-lifed fitness, IGR and LRS for recruits were all statistically significantly correlated with the reproductive values. There were no statistically significant differences between the IGR, LRS and de-lifed fitness correlation coefficients. None of the other correlation estimates were statistically significant (Table 1). De-lifed fitness at ages 1 and 2 significantly correlated with reproductive value, but in older age classes the correlation estimate was not statistically significant (Figs 3A and 3B).

212

213 ***Fig 2: Correlation between each of the fitness proxies at different life stages with reproductive value. Error***
214 ***bars represent 95% confidence intervals. Black bars represent significant results, while light grey bars***
215 ***represent non-significant results.***

216

217 ***Fig 3: (A) Correlation between reproductive value and de-lifed fitness by age class (in years), with 95%***
218 ***confidence intervals. N represents the sample size. Older age classes have lower sample sizes because fewer***
219 ***individuals survive to that age. (B) Correlation between de-lifed fitness and reproductive value. The black cross***
220 ***represents mean de-lifed fitness for the respective age. Colours represent the same age class.***

221

222 ***Table 1: Mean and standard deviation for short-term fitness proxies at different offspring stages, and de-lifed***

223 ***fitness at different ages.***

	Mean	SD
LRS Eggs	23.78	18.02
LRS Broods	5.80	4.26
LRS Hatchlings	20.30	16.04
LRS Fledglings	10.24	7.85
LRS Recruits	3.42	3.36
De-lifing	0.01	0.03
IGR eggs	4.24	1.53
IGR hatchlings	3.71	1.37
IGR fledglings	2.43	0.99
IGR recruits	1.13	0.78
De-lifing – Age 1	0.0003	0.0198
De-lifing – Age 2	0.0056	0.0170
De-lifing – Age 3	0.0027	0.0115
De-lifing – Age 4	0.0023	0.0087
De-lifing – Age 5	0.0033	0.0048
De-lifing – Age 6	0.0005	0.0046

224

225 There was a significant positive relationship between lineage survival odds and de-lifed fitness, LRS at
226 recruitment and fledgling stages, and IGR at recruitment (Table 2). The estimated slopes for the de-
227 lifed fitness and LRS recruits were significantly higher than the slopes of IGR and LRS at fledgling
228 stage as their 95% confidence intervals are non-overlapping, indicating that fitness measured at the
229 recruitment stage for these two metrics is a better predictor of lineage survival. There were no
230 statistically significant differences between IGR, LRS and de-lifed fitness at the same offspring stage
231 (Table 2).

232

233 ***Table 2: Results of binary logistic regressions with lineage survival as a response variable. l-95% CI and u-***

234 ***95% CI are the lower and upper boundaries of the 95% confidence interval for the slope, respectively.***

Variable	Slope	l-95% CI	u-95% CI	p value
LRS eggs	0.42	-0.07	0.95	0.101
LRS hatchlings	0.45	-0.08	0.95	0.063
LRS fledglings	1.06	0.41	1.71	0.001*
LRS recruits	3.26	1.73	4.74	0.001*
LRS broods	0.47	-0.02	0.96	0.056
IGR eggs	0.24	-0.21	0.75	0.310
IGR hatchlings	0.35	-0.09	0.87	0.167
IGR fledglings	1.06	0.49	1.71	0.002
IGR recruits	2.65	1.67	3.70	0.001*
De-lifed fitness	3.01	1.74	4.32	0.001*

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Discussion

We showed that fitness proxies measured at recruit stage correlates best with long-term reproductive values and lineage survival, while fitness proxies measured at earlier stages are less useful.

Similar to a study by (4) lineage survival is low. While there was no difference in the rate of lineage survival between native and introduced lineages, the introduced lineages had significantly higher reproductive values. This indicates that the introduced lineages might have a fitness advantage over the native ones. For lineages that survived to 2018, there was wide variation in survival probability and reproductive value. The survival probability of a lineage is associated with its reproductive value in that year (4,18). While several lineages died out every year prior to 2007, all lineages that survived the bottleneck in 2008 also survived the next 10 years to 2018. Lineage extinctions are expected to become less likely over the generations, as all founders with non-zero reproductive values become genealogical ancestors of all individuals in the future population after only a few generations (19,22). After a founder becomes an ancestor of all individuals in the current population, its lineage can only go extinct if the entire population goes extinct. During the 2008 bottleneck, the population size decreased significantly, shortening the time it took for all founders of persisting lineages to become the common ancestors of the current population members.

There was variation in reproductive value, with most lineages ranging from 0 to 10 but some reaching contributions of over four times that much. There was also large variation over time as lineages fluctuated. Lineage stabilisation is also visible in the pattern of lineage fluctuation through time after 2007, as the ranking of lineages based on reproductive value remains similar. The rapidly increasing correlation between reproductive value in the final year and each of the previous years also shows a pattern of stabilisation, as found in other studies too (4,18,34). Stabilisation is reached after 12 years, with the correlation exceeding 0.95 afterwards. Despite stabilisation, reproductive values fluctuated through time. As we examined reproductive values that are absolute rather than relative to population size, any change in population size is also reflected in the sum of the reproductive values the year before. The change in reproductive value occurs one year previously, because the estimates are based on

reproducing offspring, which are only recognised in the next year and form the basis of next year's population.

The fitness proxies based on the number of recruits outperformed all other fitness proxies in predicting reproductive values and lineage survival. Recruits are likely to be the best measure because they are adult individuals that reproduced, while other proxies include the uncertainty of survival to adulthood before reproduction even occurs. Given that sparrow offspring experience high rates of mortality, with only 14% of laid eggs successfully surviving to recruitment, mortality will have a big impact on reproductive values from short-term metrics measured at early offspring stages. For species with lower offspring mortality the age at which offspring are counted towards fitness may have less influence on the predictive power of short-term fitness metrics. While recruits are clearly the best predictor of long-term fitness, they are the most difficult to measure in most study systems, as it is rarely possible to monitor all offspring until their first reproduction. This highlights the importance of long-term isolated island population studies (35), as only in such studies is it possible to accurately estimate the number of genetic recruits that an individual produced.

We found no differences in the performance of de-lifed fitness, IGR or LRS in predicting reproductive values or lineage survival. A previous study on Ural owls (*Strix uralensis*) and collared flycatchers (*Ficedula albicollis*) found that LRS performed significantly better than IGR at fledgling stage in predicting reproductive values, while they both performed similarly at recruitment (10). The correlation between reproductive value and different fitness proxies at recruit stage was of similar strength as discovered in previous studies (4,10).

In this study, annual de-lifed fitness at ages 1 and 2 were correlated with the reproductive values, but not at later ages. The correlation at age 1 with reproductive value was similar to that for lifetime de-lifed fitness, indicating that reproductive success in the first adult year may be sufficient to provide a good prediction of long-term fitness. Hence, individual reproductive performance in the first year may be an important proxy for an individual's fitness.

There is, however, considerable variation that is not explained by the fitness metrics. A strong correlation between a short-term fitness metric and the reproductive value measured two decades later, during which the population has been exposed to varying environmental conditions and population fluctuations, is unlikely. The strength of the correlation will also depend on the additive genetic variance and heritability of reproductive success (4). In particular, in our population annual fitness is somewhat heritable (36), and there has been significant demographic stochasticity in our population for which LRS and IGR metrics tested here were not designed (37).

The underlying theoretical results about reproductive value were derived under the assumption of diploid Wright-Fisher population and weak selection (18). The Lundy sparrow population might not meet these assumptions, as there could be undetected strong selection and non-random mating. The sparrow population can therefore be used to test theoretical predictions on real data but could lead to erroneous conclusions if assumptions are severely breached. Despite that, reproductive values can lead to new insights about natural selection and evolutionary outcomes, such as inbreeding, lineage introgression or cohort effects (2,4,34). Particularly in the presence of environmental, social, or demographic interactions, such as those occurring in any wild population, studying fitness across an entire lineage by examining reproductive values can potentially lead to better estimation of evolutionary outcomes for a certain allele (38).

In conclusion, by using reproductive values as a measure of long-term individual fitness we have shown that recruits, rather than earlier offspring stages, best predict reproductive values. Additionally, annual fitness measured in the first reproductive season is an equally good predictor of fitness as lifetime fitness measures. We therefore suggest that future studies should measure short-term fitness at higher offspring ages to better capture long-term fitness.

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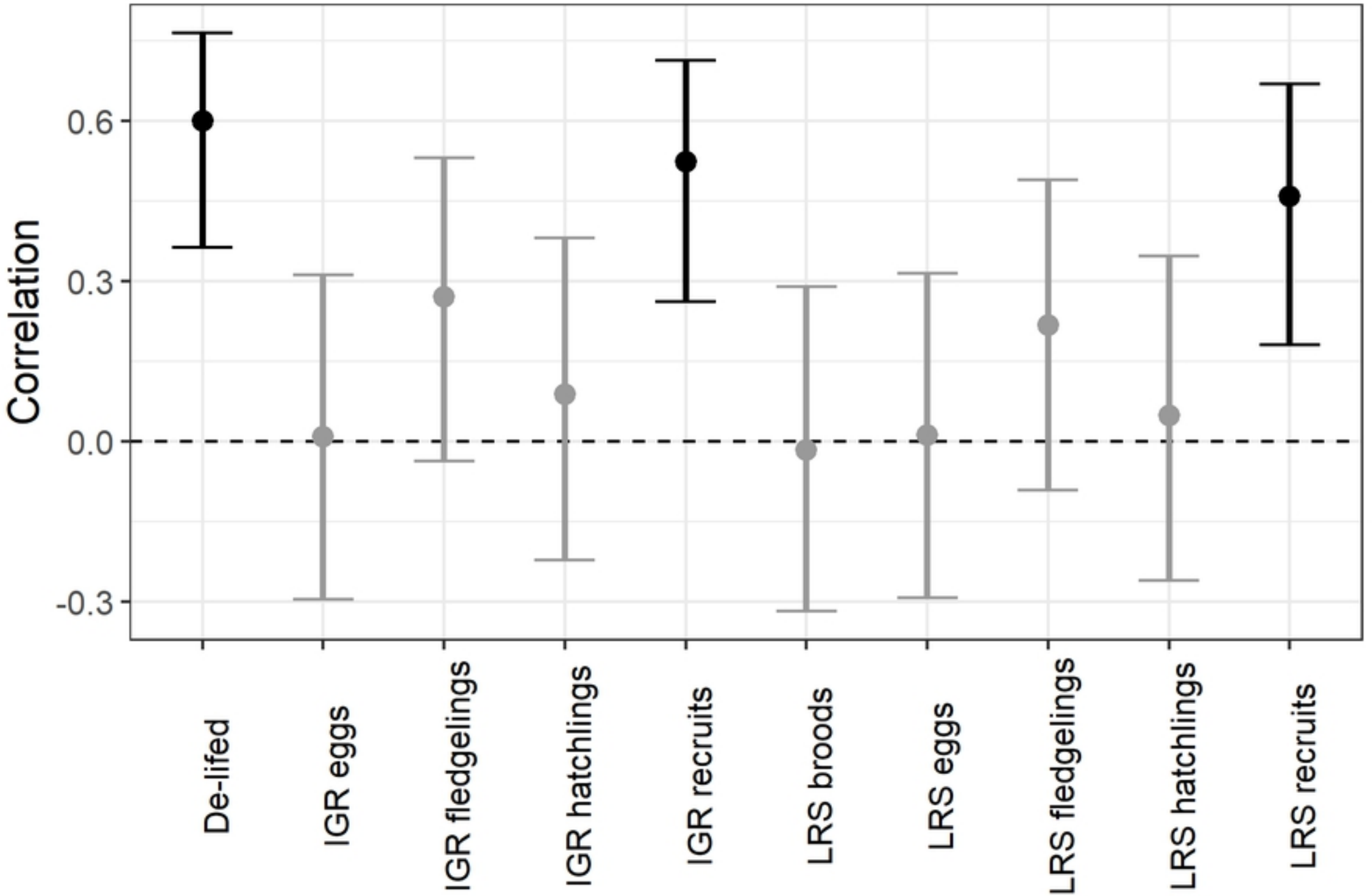
Correlation
0.6
0.3
0.0
-0.3
De-lifed
IGR eggs
IGR fledgelings
IGR hatchlings
IGR recruits
LRS broods
LRS eggs
LRS fledgelings
LRS hatchlings
LRS recruits

Figure 2

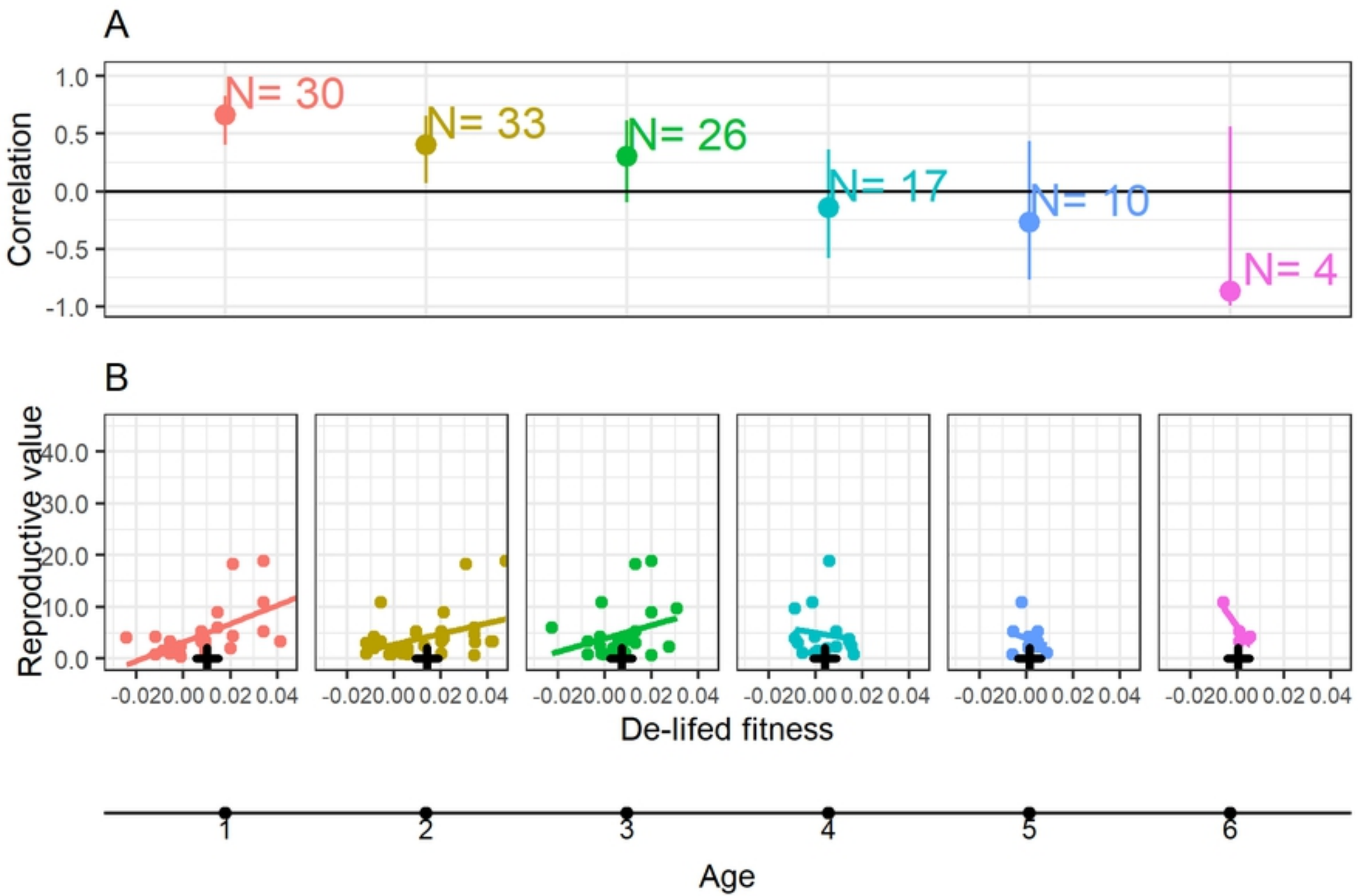
A
Correlation
1.0
0.5
0.0
-0.5
-1.0
N= 30
N= 33
N= 26
N= 17
N= 10
N= 4
B
Reproductive value
40.0
30.0
20.0
10.0
0.0
-0.020.00 0.02 0.04
De-lifed fitness
1
2
3
4
5
6
Age

Figure 3

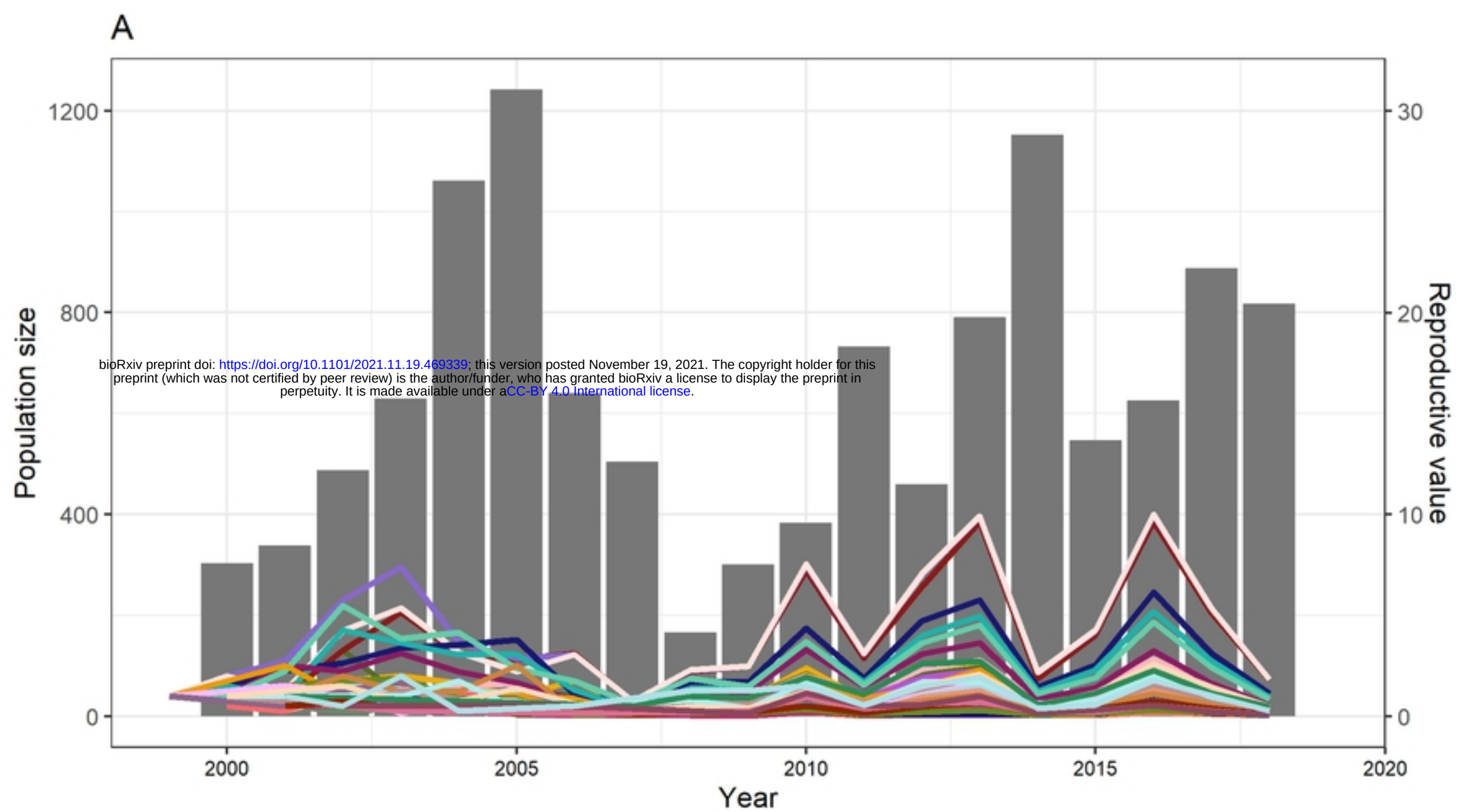

Figure 1