



Sex and the cost of reproduction through the life course of an extremely long-lived herb

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Abstract

Despite being central concepts for life history theory, little is known about how reproductive effort and costs vary with individual age once plants have started to reproduce. We conducted a 5-year field study and estimated age-dependent reproductive effort for both sexes in the extraordinarily long-lived dioecious plant *Borderea pyrenaica*. We also evaluated costs of reproduction on vital rates for male and female plants, both by examining effects of differences in individual reproductive effort under natural conditions, and by conducting a flower removal experiment, aimed at decreasing reproductive effort. Reproductive effort was fairly constant and independent of age for males, which may reflect a strategy of adjusting overall reproductive output by spreading reproduction over the life course. Females had a higher total effort, which first increased and then decreased with age. The latter may be a response to an increasing reproductive value—an inverse of a terminal investment—or a sign of reproductive senescence due to an age-related physiological decline. Seed production was lower in plants with higher previous reproductive effort and this effect increased with age. We found no evidence for costs of reproduction on other vital rates for either sex. Experimental flower removal only resulted in progressively more negative effects on flower production in older male plants, whereas female vital rates were unaffected. Overall, this study demonstrates that not only sex, but also age influences resource allocation trade-offs and, thus, plant life history evolution.

Keywords Ageing · Demographic senescence · Life history · Reproductive effort · Reproductive value

Introduction

Reproduction is necessary for persistence of all species. Investing resources into producing offspring has short- and long-term consequences, and the optimal investment

strategies depend on the abiotic and biotic environment. As a result, there is a substantial variation of reproductive strategies in terms of when to start, how often to reproduce, and how much to invest. Reproductive effort, the proportion of an organism's resources allocated to reproduction (Samson and Werk 1986), may be expected to change over the life span of individuals as an evolutionary response to changes in reproductive value [the expected average contribution of individuals of a given age to future population growth rate (Caswell 2001)]. However, although some studies have documented increases in reproductive effort with age for young plants (Lacey 1986; Ehlers and Olesen 2004), little is known about how reproductive effort changes with age in polycarpic plants that have started to reproduce. In species where survival decreases with advancing age (actuarial senescence), such as birds and mammals, future reproduction events become progressively less certain, and a progressive increase in reproductive effort could be expected to maximize fitness (Williams 1966; Pianka and Parker 1975). In particular, a large investment into reproduction very late in life has been called 'terminal investment' (Williams 1966)

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and seems to be common in animals (Galimberti et al. 2007; Descamps et al. 2007, but see Clutton-Brock 1984; Velando et al. 2006). Alternatively, reproductive senescence may accompany actuarial senescence, that is, reproductive effort may decline throughout an organism's life span due to physiological decline (Thomas 2013).

Plants show a wide variation in life span (Ehrlén and Lehtilä 2002), but few studies have investigated late-life changes in reproductive effort. Koenig and colleagues (2017) found no evidence for terminal investment, in terms of that trees of eight *Quercus* species in California that died during the study had invested more into reproduction compared to surviving trees. In most investigated species, reproductive investment has been found to be relatively constant over age for established plants of similar size (Dahlgren and Roach 2017). However, we are not aware of studies explicitly investigating how reproductive effort and reproductive value change with age. For some plants, such as the extremely long-lived species *Pinus longaeva* and *Borderea pyrenaica*, increases in reproductive value due to increases in survival may occur (Hiebert and Hamrick 1983; García et al. 2011). In these species, where future reproduction becomes more certain with age, we may expect a decrease in reproductive effort as plants become older.

Likewise, reproductive “costs” (lowered future reproduction, growth and survival; Stearns 1992; Roff 1992) may change over life spans. The concept of resource allocation trade-offs is central to life-history theory and reproductive costs have been shown in many taxa, including long-lived plants (Obeso 2002; Sletvold and Ågren 2015). Changes in the cost of reproduction over age could occur if individuals either senesce or become physiologically more robust as they age. However, little is known about how effects of reproduction on future performance change with age.

In dioecious organisms, reproductive effort and costs usually differ between sexes, and female plants often appear to invest more into reproduction than males (Meagher and Antonovics 1982a). A lower reproductive effort in males than in females would imply that male plants have more resources to invest in growth and survival (Stearns 1992). However, female plants may compensate for the higher reproductive investment by reproducing less frequently, delaying the onset of reproduction, and increasing their reproductive investment from low levels in young plants. If male reproduction is less costly, we may thus expect earlier reproduction and overall flatter age trajectories of reproductive effort than in females.

In this study, we used observational demographic data recorded over 5 years and field experiments to examine age- and sex-dependent reproductive effort and costs of reproduction in the long-lived dioecious herb *Borderea pyrenaica*. Age determination in our study species is possible because of a morphological characteristic of the tubers, offering an

unusual opportunity to explore how reproductive parameters change over the life course of individuals. Our data set included almost seven hundred individuals of ages up to 260 years in an ecologically stressful but stable alpine scree environment in the central Pyrenees. Previous studies did not find evidence of demographic or physiological senescence in this plant, but instead showed that reproductive value increased with age for both sexes (García et al. 2011; Morales et al. 2013) and that males tend to flower more frequently than females (García and Antor 1995b). Here, we tested the following three hypotheses: (a) reproductive effort is similar in males and females over their life courses, because the higher investment per reproductive event in females is balanced by a lower frequency of reproductive events; (b) reproductive effort decreases with age in both sexes because the reproductive value increases, but the decrease in males is less pronounced because they have a lower overall effort; (c) reproductive costs are age dependent and decrease with age after that individuals have attained their maximum size and have more resources to invest into reproduction, again the decrease being less pronounced in male plants.

Materials and methods

Study system

Borderea pyrenaica (Dioscoreaceae) is a small relict species endemic to limestone screes in the Central Pyrenees, usually at altitudes higher than 1800 m a.s.l. Pollinators include ants, flies and lady beetles, fruit set is high and there is no evidence for pollen limitation (García et al. 1995). By the latter half of May, each plant has grown one short above-ground stem, flowering begins in late June and fruit dispersal in early September. At the end of the growing season, this stem dies back, leaving behind a scar on the tuber (García and Antor 1995a). Counting the number of scars gives an age estimate. Sex of reproductive individuals is usually easily identifiable throughout the growing season as flowers remain on the plant. Males start reproducing at younger ages (10–20 years) than females (15–35 years), have a larger number of flowers, and flower more frequently (almost every year) than females (García and Antor 1995b).

Data collection and preparation

Data were collected yearly from 1995 to 1999 in the Pineta valley (42°41'N, 0°06'E; 2000 m a.s.l.), located in the central Pyrenees. The density of *B. pyrenaica* in this population varies considerably, reaching up to a few hundred plants per square metre (García et al. 2011). Individuals were carefully mapped to be relocated in successive years (aboveground

parts wilt in fall), and for each plant and year we recorded state (dead or alive), sex (vegetative, male or female), number of leaves, length of the longest leaf, number of flowers in males, and the number of fruits and seeds within each fruit in females. Aerial vegetative biomass (“size” hereafter) was estimated for all plants as $\log(\text{number of leaves} \times \text{leaf length}^2)$. Tubers were collected the final year of the study and were weighed and aged. Due to a severe drought that made male flowers die back early in the season and counts unreliable, the number of flowers in males was not recorded in 1999. Age estimates for individuals of unknown age but known size were imputed for both sexes based on generalised additive models (GAM) of age on size (García et al. 2011).

The analyses were based on two demographic data sets: observational data on 518 individuals during the period 1995–1999 which was analysed previously to investigate changes in flowering probability, flower number, seed number and reproductive value with age (García et al. 2011), and experimental data on 181 reproductive individuals of both sexes, whose reproductive effort was manipulated by flower removal both in 1996 and 1997. Experimental plants were assigned to one of two treatments: (1) control (no treatment) and (2) flower removal (in both years for individuals that flowered the second year, otherwise only in the first year). We conducted the experiment because we expected costs of reproduction to potentially be obscured by positive correlations between reproduction and plant condition.

To convert our measures of size and reproductive output into dry weights (g), we also collected aerial parts of 32 female and 32 male reproductive plants, counted the number of fruits and male flowers, estimated size as defined above, and dried and weighed reproductive and vegetative parts separately. The dry weights were then regressed on corresponding counts of fruits or male flowers, or size, and the regression coefficients were used to translate field recordings of number of fruits, male flowers and size into corresponding dry weights (Online Resource 1).

Age trajectories of reproductive investment and effort

Reproductive investment (weight of reproductive parts) and reproductive effort (proportion of aerial biomass allocated to flowers and fruits for males and females) were regressed on age using generalised additive models, which allow flexible nonlinear patterns reflecting potential non-monotonic changes in reproductive effort and investment with age. Each individual plant was assigned one value of reproductive investment or effort, being the sum of values for each year. We did not include tuber biomass in these calculations, as this was only measured once, at the end of the study. However, aerial and tuber biomass were tightly correlated

(Online Resource 2), and our estimates of aerial reproductive investment and effort should, therefore, be proportional to values based on plant total biomass. We applied the default thin-plate smoothing splines in the “gam” function of the package “mgcv” for the statistical software R. Initially, models including all individuals were fitted, but since sex and the interaction term of sex and age had statistically significant effects on trajectories of flower number, seed number and size ($p < 0.05$), separate models were fitted for the two sexes.

Effects of flower removal

Generalised linear models (GLMs) were used to examine age-specific effects of flower removal for males and females separately. Treatment, individual age, and the interaction between treatment and age were used as predictor variables. Size in the previous year was also included as a covariate. We tested effects on five response variables: tuber biomass in the final year of the study, and size and fecundity in 1998 and 1999. Size was set to zero for plants that were dormant in 1 year and for 14 plants that did not emerge in the last year. Death is a very rare event in this species. Thus, survival was not modelled, and the potential effects of treatment on dormancy and survival are included in the analyses of size. Models of tuber biomass and size were fitted as ordinary linear regression models, in GLMs with “identity” link functions and Gaussian error distributions. Fecundity was first analysed as total seed number and male flower number in all individuals (reproducing or not), in models with log link functions and quasi-Poisson error distributions (accounting for overdispersion relative to the Poisson distribution). Female fruit number and seed number were strongly correlated (Online Resource 3). Effects on fecundity were also examined for separate components: flowering probability, flower and fruit number in flowering individuals, and seed number in female plants that produced fruits. Both methods yielded similar results, and only the models of seed number and male flower number for all individuals are presented. Wald tests were used to calculate p values.

Observational study of costs of reproduction

Data from the observational study were used also to examine the cost of reproduction, in terms of relationships between past reproduction and current vital rates. The response variables were the same as in the analyses of the experimental flower removal study and were analysed using the same types of regression models. All individuals that flowered at least once during the study were included in analyses. The total numbers of seeds produced per female (Online Resource 4) and flowers produced per male (Online Resource 5) in 1995, 1996 and 1997 were regarded as measures of reproductive

investment and used as predictor variables, together with age and size the previous year.

Results

Generalised linear models indicated that for all ages, females invested more biomass into reproduction per year than males, also when accounting for the lower frequency of reproductive events in females (Fig. 1a, b). The pattern was similar for reproductive effort (Fig. 1c, d).

There were also sex differences in the age trajectories of reproductive investment and effort. In male plants, there was a continuous increase in reproductive investment with age. In contrast, in females there was an early increase in reproductive investment, followed by a decline starting at ages of about 70 years, when individuals attained their maximum size. The divergence of age trajectories between sexes was slightly more pronounced for reproductive effort (Fig. 1c,

d). In males, there was no apparent increase with age in reproductive effort, whereas reproductive effort decreased in females at ages above 70 years. The decreases in female reproductive investment and effort above 70 years were statistically significant (Online Resource 6).

Experimental flower removal did not affect size or seed production in female plants in the short term (Table 1). In males, flower removal reduced size in 1998, but not in 1999. There was also an interactive effect of age and treatment on male flower number: flower removal resulting in lower flower number in plants older than 40 years (median and mean ages were 65 and 80.5, respectively), and effects of treatment being larger in older plants (note that effects in Table 1 are the effects of not receiving the flower removal treatment, i.e. of an increased reproductive investment, and thus corresponding to effects of increased reproductive investment in Table 2).

The results of the observational study suggest an age-dependent cost of reproduction for female plants: fecundity

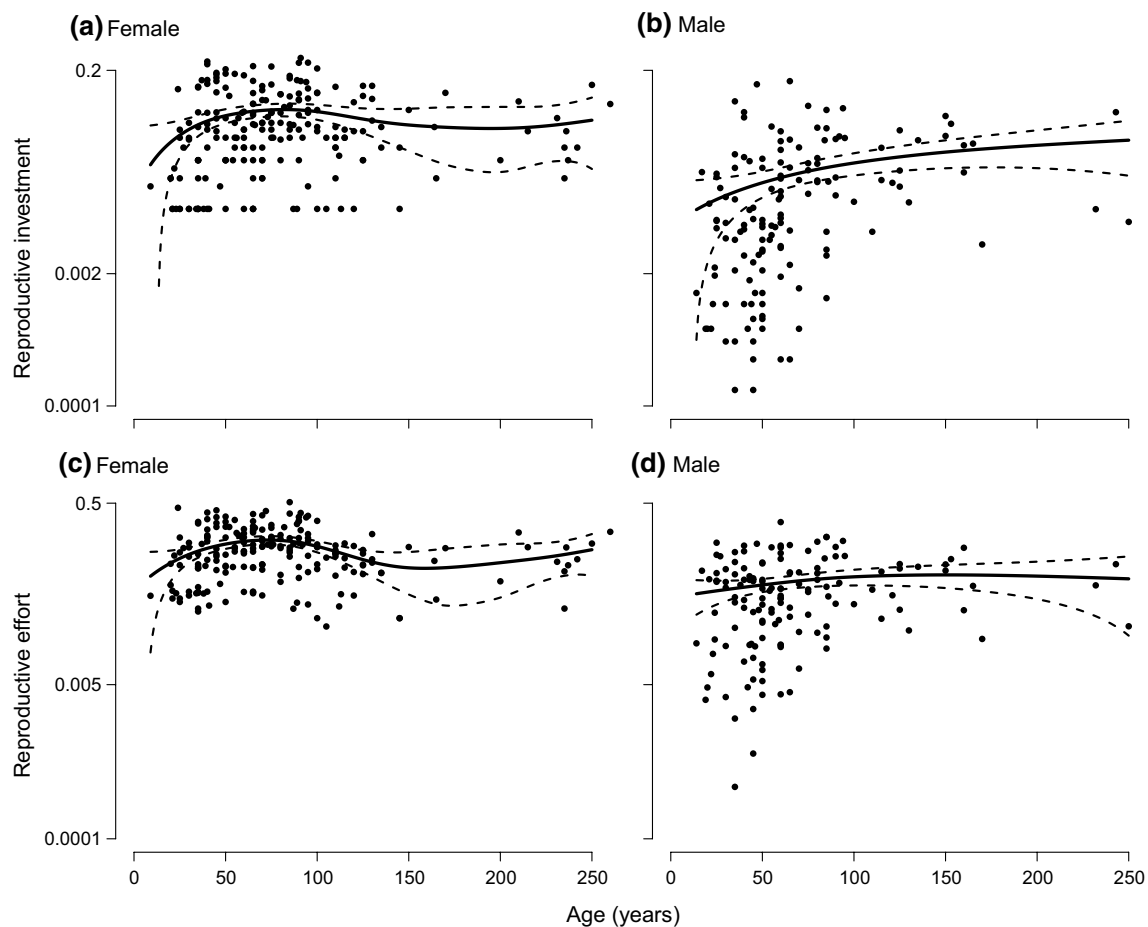


Fig. 1 Reproductive investment measured as (\ln) weight of reproductive structures (g) and reproductive effort (proportion of plant biomass invested in reproductive elements) over individual age for **a, c** female and **b, d** male individuals of *Borderea pyrenaica*, respectively.

Each point represents an individual plant's summed reproductive investment or effort over the entire observation period. Continuous lines represent spline fits of GAM models and dashed lines represent the 95% confidence intervals

Table 1 Effects of experimental flower removal, age (years) and their interactions on seed number, size (aerial biomass) and tuber biomass for male and female plants of *Borderea pyrenaica*

	High RI (no flower removal)	Age	High RI × age
Female plants			
Seed number 1998			
Seed number 1999			
Size 1998		(0.002)	
Size 1999		0.004	
Tuber biomass 1999		0.010	
Male plants			
Flower number 1998	−0.322	−0.004	0.0079
Size 1998	0.260		
Size 1999			
Tuber biomass 1999	(−0.507)	0.024	(0.0065)

Statistically significant ($p < 0.05$) regression coefficients for generalised linear models of the effects of no flower removal (vs. flower removal; corresponding to a high reproductive investment (RI) in order for signs to be comparable with Table 2) are presented without parentheses. Terms borderline significant at $0.05 < p < 0.10$ are presented within parentheses. Size in the previous year was accounted for by its inclusion as a covariate in all models

Table 2 Relationships of observed reproductive investment (RI), age (years) and their interactions with seed number, size (aerial biomass) and tuber biomass for male and female plants of *Borderea pyrenaica*

	RI	Age	RI × age
Female plants			
Seed number 1998		0.010	
Seed number 1999	0.018	0.005	−0.00038
Size 1998	0.005	0.003	
Size 1999	(0.005)	(0.003)	(−0.00010)
Tuber biomass 1999	0.006 (0.001)	0.011 (0.010)	(0.00007)
Male plants			
Flower number 1998	0.002 (0.001)	0.005 (−0.002)	(0.00002)
Size 1998			
Size 1999	(0.001)		
Tuber biomass 1999	0.005	0.015	

Statistically significant ($p < 0.05$) regression coefficients for generalised linear models are presented without parentheses. Terms borderline significant at $0.05 < p < 0.10$ are presented within parentheses. Reproductive investment for observational data was quantified as the biomass of the number of fruits in females, and flowers in males in the preceding years (see “Methods”). Average size over the same years was accounted for by its inclusion as a covariate in all models

(in 1999 but not 1998) was lower in plants with higher previous reproductive effort and this negative effect of previous reproduction increased with age (Table 2; note that model predictions based on both main effects and the interaction term are that, except for plants with combinations of low

previous reproduction and low age, effects of increasing previous reproduction are negative). For other response variables, our analyses suggested overall positive effects of having a higher previous reproduction in both sexes (Table 2). Female plants with higher previous reproductive investment had higher aerial biomass in 1998 and tuber biomass in 1999. However, older females with higher previous reproductive effort also tended to have a lower aerial biomass in 1999 and this effect became stronger with increasing age ($p = 0.095$). Male plants with higher previous reproductive investment had a higher tuber biomass and subsequent flower number, with a tendency ($p = 0.07$) of increasingly positive relationship between previous reproductive effort and flower number with age.

Discussion

Our results show that reproductive effort and costs of reproduction are age dependent in the long-lived *Borderea pyrenaica* and that age trajectories differ between male and female plants. Males had an overall lower reproductive effort than females and were hardly affected by plant age, while female reproductive effort first slightly increased and then decreased with age. Also costs of reproduction were age dependent in females. Late-life age dependence of reproductive effort has been shown previously for animals (e.g. Ericsson et al. 2001), but not in plants, and we are not aware of any previous study with plants suggesting age-dependent reproductive costs.

In *Borderea pyrenaica*, the greater reproductive effort per reproductive event in females than in males is not fully compensated for by a lower frequency of female reproductive events. Sex differences in reproductive effort may reflect differing strategies of resource allocation. In polygynous animals, males appear to invest more resources into reproduction than females through high costs of traits favouring competition for mates (Promislow et al. 1992; Clutton-Brock and Isvaran 2007). Male plants do not compete in other ways than by increasing pollen (flower) production, and females often invest more resources than males into reproductive tissue (Meagher and Antonovics 1982b). The higher female reproductive effort in *B. pyrenaica* is somewhat surprising given the lack of differences in growth or survival between sexes (García et al. 2011). It is possible that our measure of reproductive effort is not fully adequate, since it is only based on biomass and does not account for nutrient concentrations. Moreover, quantifying reproductive effort is difficult in our study species because both male inflorescences and female fruits are photosynthetically active. However, we would not expect higher nutrient concentrations in male tissues than in females, and despite that fruits might contribute to energy acquisition during ripening, resources invested

in fruits are eventually lost at dispersal whereas nutrients may be resorbed from male inflorescences after the growing season. As a result, we expect the identified difference in reproductive effort to be conservative.

Also the shape of age trajectories of reproductive effort differed between sexes. One explanation of the observed differences in both overall effort and the shape of trajectories between sexes may be that a lower effort, per flower and also over their life course, allows males to spread their reproduction more evenly over their life spans than females. That females show lower reproductive effort early in life may be because the high minimum cost of reproduction, in terms of producing one fruit, makes it optimal for females to stay non-reproductive for a longer period than males. Our observation of a lower effort with advancing age in older female plants may be explained by the fact that their reproductive value seems to increase with age due to increasing survival (García et al. 2011). Under these circumstances, it should not be beneficial for individuals to invest more resources into reproduction as they age if such investments affect survival negatively, because future reproduction becomes gradually more certain (Williams 1966). The observed tendency of decreasing reproductive effort with age could also simply be a consequence of physiological decline (Thomas 2013), even though no evidence of such declines has been detected previously in this species (Morales et al. 2013).

Our results regarding reproductive costs, in terms of effects of previous reproduction on vital rates, may at first glance seem contradictory. In our experimental study, we found no effect of flower removal on females and a negative effect on male plants. Small effects of a 2-year treatment for plants that can live longer than two centuries and have a prominent storage organ (tuber) are not surprising (Ehrlén and van Groenendael 2001; Obeso 2002; and see also Aragon et al. (2009) for effects on a short-lived plant). However, we still expect to detect age-dependent costs if the effect of age is strong. For male plants, it appears that negative effects of removing photosynthetic tissue associated with inflorescences outweighed any positive effects of reduced reproductive investment on future vital rates. It is possible that the treatment had negative effects also in females, which cancelled out positive effects of reduced reproductive effort. However, in several other studies flower removal has led to increases in future reproduction or in other vital rates (Hartemink et al. 2004). Analysing the observational data, we found some positive relationships between high reproductive effort and future vital rates, which are likely a result of reproductive effort being positively correlated with plant condition (Obeso 2002). However, we also found that older female plants produced more seeds after having a lower previous reproductive effort, indicating a cost of reproduction, and that this effect increased with plant age. The fact that we did find evidence for an age-dependent cost

of reproduction, despite the short study period in relation to the maximum life span of this plant, suggests to us that costs may be substantial. Taken together, and also considering the observed differences in reproductive investment and effort over the plants' life course, these results may illustrate causes of differences in life history strategies among sexes. Males maintain a fairly constant reproductive effort as they age, but at the cost of becoming frailer at higher ages, as indicated by the larger negative effect of the treatment in older males. Females, on the other hand, having higher costs per reproductive event than males, and a larger reproductive effort that first increases (young females) but then decreases (old females) seem to adjust their fecundity to their resource state.

In conclusion, the age dependence of reproductive effort and reproductive costs, and the differences between sexes shown in this study, suggests that age and sex shape plant life history strategies. *Borderea pyrenaica* shows an increasing survival and reproductive value with advancing age, and no evidence for an increase of investment into reproduction at high ages, but instead a slight decline in female reproductive effort after reproductive maturity. This pattern may either be a response to an increasing reproductive value, or the consequence of physiological decline. More demographic studies considering plant ageing are needed to understand plant life history diversification and how this is affected by resource allocation trade-offs.

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Author contribution statement MBG and JE designed the experiments. MBG carried out the field work. All authors conceived the specific study questions. DAS and JPD conducted the statistical analyses. DAS wrote the first draft of the manuscript and all other authors contributed substantially with revisions.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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