

Longitudinal analysis of *Plantago*: adaptive benefits of iteroparity in a short-lived, herbaceous perennial

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Abstract. Theory suggests that iteroparity may confer greater fitness than semelparity in situations in which temporal environmental variation is high and unpredictable. Variable age-specific mortality, density dependence, and other factors may also favor iteroparity over semelparity. Here, we empirically test the adaptive benefits of greater numbers of reproductive years in a study of reproductive schedules in an experimental population of a short-lived polycarpic perennial, *Plantago lanceolata*. A large experimental population was established that included four cohorts with similar genetic structure. Individuals were censused for mortality, size, and reproduction for seven years. Plants experienced variable numbers of reproductive years, but one or two years were most common (~46.7% of the population reproduced only once). The probability of flowering at least once prior to death was determined strongly by extrinsic, environmental or intrinsic but environmentally influenced variables, including early-life size, cohort, and block, but also varied with a number of interactions involving paternal lineage. Maternal effects explained small but significant components of the variance in the number of reproductive years among individuals in each cohort, while paternal effects were significant in only two cohorts. Number of reproductive years contributed significantly to fitness in this system, more so than all other variables tested, although most of the variation in relative fitness may be attributed ultimately to environmental influences. We suggest that the high proportion of each cohort composed of plants reproducing only once may be due to environmental constraints on either growth or size. Such environmental influences, particularly on early life size, may result in small but important indirect effects on fitness.

Key words: *inflorescence; iteroparity; Plantago lanceolata; reproductive schedule; reproductive timing; semelparity; Virginia, USA.*

INTRODUCTION

Reproductive schedules cause and are a result of complex interactions of life history relationships, population dynamics, and environment. Work on this topic was originally spurred by Laurent Cole's proposition that the perennial growth habit, in which organisms live and reproduce for more than one year, represents little fitness advantage over the annual habit (Cole 1954). Cole's hypothesis is at odds with the commonness of biennial and perennial plants (Silvertown 1983, 1986) and rests on the assumptions of no age-specific mortality and no density dependence. Models breaking these assumptions suggest that delayed reproduction and iteroparity may indeed be favored under some conditions (Charnov and Schaffer 1973, Bulmer 1985). Others have suggested that iteroparous perenniality may be favored under a range of other conditions, including factors such as the duration of the reproductive season (Iwasa and Cohen 1989), size at maturity (Baskin and

Baskin 1979), the duration of the juvenile stage (Stearns 1992), correlations among life history traits (Orzack and Tuljapurkar 1989), stochastic environmental variability (Harper and White 1974, Orzack and Tuljapurkar 1989), and the extent and timing of temporal variability in survival with respect to age (Bulmer 1985). Longer life spans in general also appear to be more common under a range of ecological conditions, including even the type of community in which an organism typically lives (Ehrlén and Lehtilä 2002).

Though theoretical work on the significance of different reproductive schedules is substantial, empirical studies have focused mostly on obligately semelparous organisms, including monocarpic plants. Fitness in monocarpic perennials has been found to be a function of growth, probability of flowering, probability of survival, and reproductive output (cf. Metcalf et al. 2003). Here, size acts as an important determinant in the optimal flowering strategy because of its importance in determining the probabilities of flowering and survival (Harper and White 1974, Lacey 1986, Wesselingh and de Jong 1995). The optimal reproductive schedule in a monocarpic perennial can be thought of as the schedule that optimizes reproduction in the face of environmental variation and increasing mortality risk with age and is

Manuscript received 24 March 2009; accepted 22 May 2009.
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mediated by size and the marginal impact of growth (Lacey et al. 1983, Metcalf et al. 2003).

The evolutionary ecology of reproductive schedules is much less understood in iteroparous organisms than in semelparous organisms. In polycarpic perennials, plants that reproduce multiple times during their lifetime, reproduction may be delayed for many years and the probability of flowering often correlates positively with size and either positively or negatively with future survival (Law 1979, Bierzychudek 1982, Shefferson 2006). Because polycarpic perennials may flower any number of years within their life span, the number of reproductive years may be subject to selection. In turn, the optimal age of reproduction may vary with the number of reproductive events, because these plants do not need to “put all of their eggs in one basket” as a monocarpic plant would. In iteroparous animals, years of reproduction may also vary with conditions experienced in early life, because of the effects of such conditions as the age at first reproduction, the onset of aging, and fitness (Metcalf and Monaghan 2001, Nussey et al. 2007). Reproductive timing in polycarpic perennials should be adaptively plastic in response to temporal and spatial variability in the environment. At the extreme end of temporal variability, multiple reproductive events may result in a “spreading of risk” similar to a bet-hedging trait (Slatkin 1974, Gillespie 1977), in which the effort put into reproduction in any given year is lower than possible in order to increase the number of later reproductive opportunities.

Here we assess adaptive effects of iteroparity by assessing the fitness consequences of different numbers of reproductive years in an experimental population of the short-lived, polycarpic perennial *Plantago lanceolata*. In our experimental population, four cohorts with similar genetic structures were planted in the same environment. Because they were planted in different years, they had different environmental histories through their life cycles. We hypothesize that these different environmental histories should result in different reproductive schedules across cohorts and have different fitness consequences even though each cohort has a similar genetic background.

METHODS

Field methods

Plantago lanceolata L. is a short-lived, polycarpic perennial monocot with a widespread, holarctic distribution. It is commonly found in disturbed habitats. The plant produces a basal rosette from which it grows one or more long inflorescences. In central Virginia, USA, flowering may occur from April to September, though May to August is most common.

We obtained *Plantago* individuals from a wild population in Shadwell, Virginia. We then bred five unique sets of sires and dams in the greenhouse according to a modified North Carolina II breeding design (Comstock and Robinson 1948, 1952, Lynch and

Walsh 1998) in which each set was composed of four sires bred fully factorially with each of two dams. This design resulted in a total of 40 parental combinations with ~800 seeds each. Seeds from each resulting lineage were split into four cohorts, which were sequentially planted in the greenhouse and grown until seedlings. The protocol established in an earlier study (see Roach 2003) for raising seedlings, planting, and marking individuals was also used for this study. Seedlings of uniform age (approximately six weeks) were planted in a randomized block design with replication of genotypes and cohorts (see Plate 1). Plants were located 15 cm apart in rows each 20 cm apart within an approximately 75 × 45 m² area. This spacing was sufficient to avoid competition between individuals and is within the natural density of the field. The analysis presented here is for a subset of 21 406 plants from a larger experimental population (“large families” only; see Roach et al. 2009). The different cohorts were planted as follows: October 2000, cohort 1, 6654 plants; October 2001, cohort 2, 7892 plants; October 2002, cohort 4, 3258 plants; and in the spring, April 2002, cohort 3, 3602 plants. This study includes data from the time of planting until December 2007, by which time ~92% of the experimental plants had died. Mortality was censused monthly. Additionally, we measured size, as the total number of leaves per plant, in May and November of each year. Leaf number is highly correlated with aboveground biomass ($r = 0.70$, $P < 0.0001$, $n = 80$; D. A. Roach, unpublished data). Mature inflorescences were counted and collected per plant throughout the flowering season.

Analytical methods

We first assessed basic patterns in reproductive schedule across cohorts. We began by calculating the number of reproductive years that *Plantago* individuals experienced. We also sought to explore the variation in age at first reproduction by assessing year of reproduction in plants that reproduced only once prior to death. A year of reproduction was defined as any year in which at least one inflorescence was produced. We then tested for genetic and environmental impacts on probability of flowering at least once prior to death via logistic regression in SPSS 16.0 for Windows (SPSS, Chicago, Illinois, USA), in which the probability of flowering was dependent upon size toward the start of the first growing season (hereafter referred to as early-life size), life span (given in weeks), paternal lineage, cohorts, and block. In cohort 3, we skipped flowering in the first growing season and instead began with the second growing season, because these plants were planted after their first growing season had already begun. Also, all plants surviving through the end of the study were set at a life span equivalent to having died in December 2007, in order to simplify analyses (total numbers of plants still alive in December 2007 by cohort, cohort 1, 353; cohort 2, 711; cohort 3, 500; cohort 4, 551).

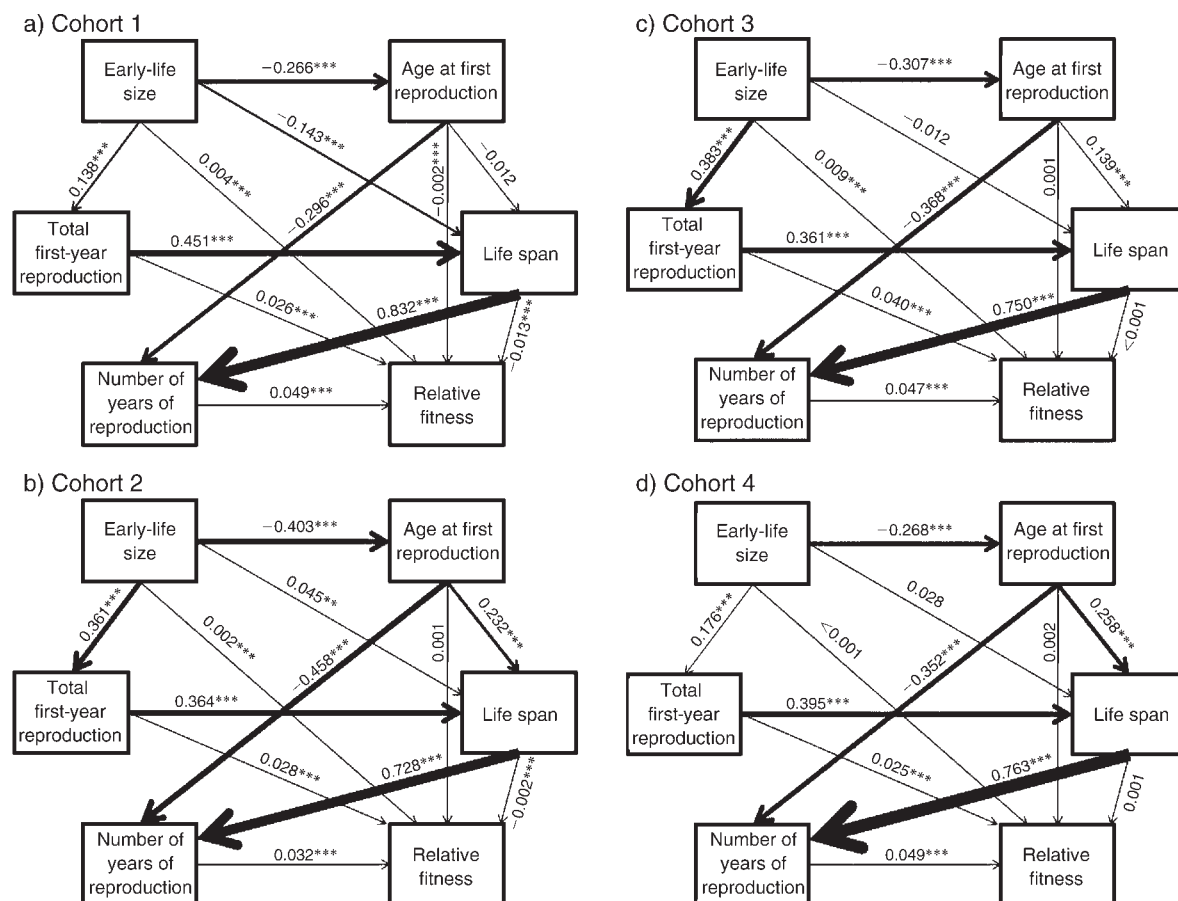


FIG. 1. Path diagrams resulting from structural equation modeling of factors affecting relative fitness in four cohorts of an experimental population of *Plantago lanceolata* in Shadwell, Virginia, USA. Factors tested include size attained in the first year of life (i.e., early-life size), age at first reproduction, total first-year reproduction, life span, and the number of reproductive years. Here, early-life size is an exogenous variable, while all other variables are endogenous. Arrow thickness indicates strength of causality. Asterisks indicate significance (no asterisk, $P > 0.05$).
 * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

We next asked whether there was evidence of heritable genetic variation in number of reproductive years. We assessed genetic components of variance in the number of reproductive years among plants using variance components estimation via the VARCOMP procedure in SPSS 16.0 for Windows (SPSS, Chicago, Illinois, USA). Here, the number of reproductive years was modeled as a function of dam, sire, and dam \times sire interaction as random factors in an ANOVA-style analysis with type 1 sum of squares estimation and no intercept. The number of reproductive years was standardized to a mean of 0 and a standard deviation of 1. Significant genetic variation was inferred if both paternal and maternal components of variance were significant, while maternal effects were inferred if maternal components were significantly greater than paternal components.

We explored the factors determining fitness via path analysis (Scheiner et al. 2000, Scheiner et al. 2002) using the AMOS package for SPSS 16.0 for Windows. The

model determining relative fitness included early-life size, age at first reproduction (in years), total reproduction in the first growing season, life span (in weeks), and the number of years of reproduction (Fig. 1). Total reproduction in the first year is the number of inflorescences produced in that year (Roach 2003). Relative fitness is the total number of inflorescences produced throughout life, standardized within each cohort to a range of 0 to 1 (i.e., 0 inflorescences = 0 fitness, and the fitness of the plant with the most inflorescences produced = 1). All variables other than relative fitness were standardized to a mean of 0 and a standard deviation of 1.

RESULTS

Cohorts varied in size and reproductive schedule. Plants in cohort 1 grew to the largest size in their first year, while plants in cohort 3 grew to the smallest (size in November following first growing season, cohort 1, 15.40 ± 0.185 leaves; cohort 2, 11.16 ± 0.170 leaves;

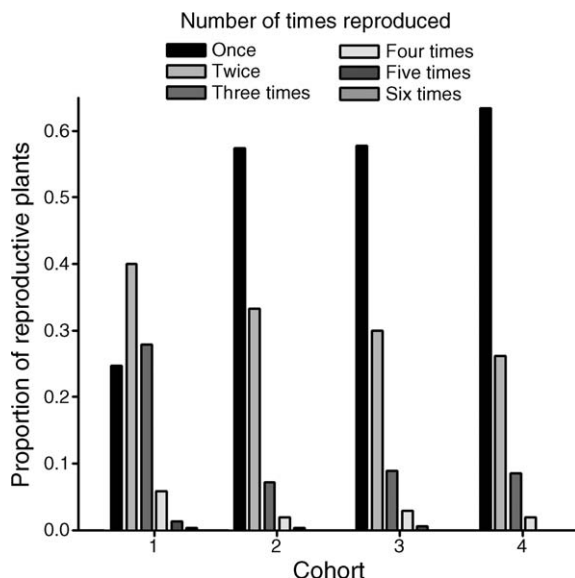


FIG. 2. Proportion of individuals flowering from one to six times, by cohort, in an experimental population of *Plantago lanceolata*. In this analysis, each year of flowering is considered to be a single reproductive event.

cohort 3, 8.23 ± 0.195 leaves; cohort 4, 8.92 ± 0.260 leaves). Plants in cohort 1 were most likely to reproduce twice while plants in all other cohorts were most likely to reproduce only once prior to death (Fig. 2). Plants that only reproduced once in their lifetimes did so primarily in the first or second year, with plants in cohort 1 reproducing evenly among those ages, plants in cohort 2 reproducing mostly at age 2, and plants in cohorts 3 and 4 reproducing mostly in their first year (Fig. 3). Plants that reproduced only once prior to death lived approximately one extra year after flowering (cohort 1, 1.2 ± 0.2 yr; cohort 2, 1.2 ± 0.1 yr; cohort 3, 1.4 ± 0.1 yr; cohort 4, 1.4 ± 0.1 yr; mean ± 1 SE).

The probability of flowering was strongly determined by size and life span in our study, with cohort and block also significant (Table 1). Sire was not a significant main effect. However, significant cohort \times sire, sire \times size, and sire \times life span interactions suggest that the probability of flowering does have some genetic variation and in particular that plant genotypes respond plastically to different environments (Table 1). Significant cohort \times size and block \times size interactions likewise suggest that the influence of size on reproductive schedules differs with environments (Table 1).

The variance in the number of reproductive years among plants was strongly environmentally determined, though not entirely so. Small, intrinsic components of variance explained significant portions of the total variance in all cohorts (Table 2). Of these, maternal effects were significant and strong relative to paternal effects in all cohorts (cohort 1, $F_{10,15} = 3.257$, $P = 0.019$; cohort 2, $F_{10,15} = 3.799$, $P = 0.010$; cohort 3, $F_{10,15} = 3.930$, $P = 0.009$; cohort 4, $F_{4,20} = 5.313$, $P = 0.004$)

(Table 2). Paternal components were significant only in cohorts 2 and 3, suggesting minor levels of heritable, additive genetic variance (Table 2).

Path analysis suggested that number of reproductive years significantly determined relative fitness via direct paths in all cohorts and did so more than any other tested factor in all cohorts (Fig. 1, Appendix). Early-life size had a significantly negative influence on the age at first reproduction and a significantly positive influence on the amount of reproduction in the first year (Fig. 1, Appendix). Further, greater reproduction in the first year of life led to longer life span and greater relative fitness (Fig. 1, Appendix), suggesting no cost of reproduction. Earlier age at first reproduction led to a greater number of reproductive years, as did longer life span (Fig. 1, Appendix). Greater reproduction in the first year of life led to greater overall fitness, as did increased number of reproductive years (Fig. 1, Appendix).

A number of effects varied among cohorts, suggesting the importance of environmental variation both on development and fitness. Early-life size had a significantly negative effect on life span in cohort 1, but a significantly positive effect in cohort 2, and no significant effects in cohorts 3 and 4 (Fig. 1, Appendix). Age at first reproduction had a significantly positive effect on life span in cohorts 2, 3, and 4, but not in cohort 1 (Fig. 1, Appendix). Early-life size in the first year had a significantly positive effect on relative fitness in cohorts 1, 2, and 3, but not in cohort 4 (Fig. 1, Appendix). Age at first reproduction had a small but significantly negative effect on relative fitness in cohort 1, but no effect in the other cohorts (Fig. 1, Appendix). Life span had a small but significantly negative effect on relative fitness in cohorts 1 and 2, but no significant effect in cohorts 3 and 4 (Fig. 1, Appendix).

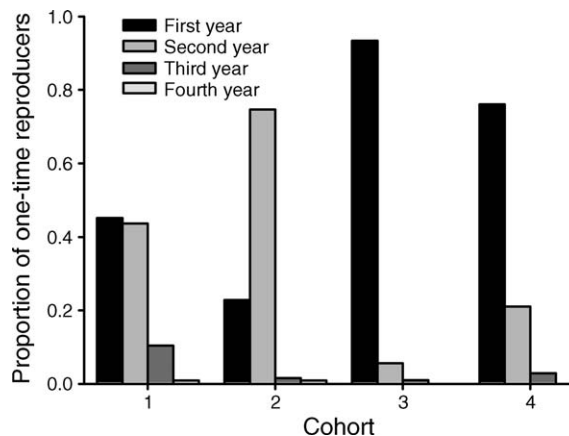


FIG. 3. Proportion of plants reproducing only once in their lifetimes that flowered each year after planting, per cohort, in an experimental population of *Plantago lanceolata*.

TABLE 1. Logistic regression of the probability of flowering as a function of early-life size, life span, block, cohort, and paternal lineage in four cohorts of an experimental population of *Plantago lanceolata* in Shadwell, Virginia, USA.

Factor	$b \pm SE$	Wald coefficient	df	P
Cohort		10.363	3	0.016
Block		34.599	16	0.005
Sire		22.793	19	0.247
Size	0.432 ± 0.096	20.143	1	<0.001
Life span	0.118 ± 0.019	40.019	1	<0.001
Cohort \times block		64.244	38	0.005
Cohort \times sire		87.814	57	0.005
Cohort \times size		54.358	3	<0.001
Cohort \times life span		25.705	3	<0.001
Block \times sire		292.253	304	0.676
Block \times size		66.633	16	<0.001
Block \times life span		48.222	16	<0.001
Sire \times size		39.196	19	0.004
Sire \times life span		63.385	19	<0.001
Size \times life span	-0.003 ± 0.001	26.356	1	<0.001

Notes: The coefficient b refers to the logit-untransformed regression coefficient. Sire, cohort, and block are categorical variables and so no coefficient is given.

DISCUSSION

Temporally variable environments can produce dramatic differences in optimal reproductive timing in monocarpic perennials (Lacey et al. 1983, Rees et al. 1999, 2004). We suggest that this may happen in short-lived polycarpic perennials such as *Plantago lanceolata* because we found genetic variation, relationships between life history traits varying across cohorts, and differential reproductive scheduling across years and cohorts (Tables 1 and 2, Appendix). In the monocarpic triennial *Daucus carota*, variation in the year of reproduction was determined by both genetic and habitat variation (Lacey 1986). In a recent study of an experimental population of the monocarpic evening primrose, *Oenothera biennis*, genetic variation in annual vs. biennial reproductive strategy was found (Johnson 2007).

Plantago individuals may benefit from iteroparity by fine-tuning their reproductive response to their environment. Reproductive traits in *Plantago* may often be plastic because of the influence of temporal variability in such traits on several key components of fitness (Lacey and Herr 2005). Further, a variety of environmental influences can cause variation in reproductive timing even within a growing season, including the heights of surrounding vegetation and the timing of disturbance events (van Tienderen and van der Toorn 1991a, b, Hautek ete et al. 2002). Such plasticity in reproductive schedules, and in life histories in general, is supported by the dramatic differences among cohorts. Cohort 1 in particular showed greater life span and fitness with earlier age of reproduction, but the opposite patterns occurred in the other cohorts (Appendix). Such patterns may be the result of plants in cohort 1 growing to nearly

twice the size of plants in other cohorts while in their first year. Further, plants that reproduced only once had a post-reproductive life that averaged more than one year and thus they could have reproduced another time. Among-cohort differences in the timing of reproduction among plants, particularly among paternal lineages, reinforce that perenniality may allow the plant to deal with year-to-year environmental stochasticity (Metcalfe et al. 2003). Such plasticity may be an important determinant of *Plantago*'s distribution, due to the advantages it confers in the colonization of novel habitats (Williams et al. 1995, Maron et al. 2004).

The optimal reproductive schedule in *Plantago lanceolata* is likely to be influenced strongly by early-life environment. The design of this experimental population, with individuals from different cohorts having the same genetic structure and sharing the same environment, showed cohort variation in a number of key reproductive traits. The environment is likely to influence *Plantago*'s fitness via immediate impacts on growth during these early months. This may be partially due to greater mortality in early ages, a condition thought to favor the evolution of iteroparity and longer life span (Bulmer 1985, Orzack and Tuljapurkar 1989, Stearns 1992). Thus, good environmental conditions should result in quicker attainment of the critical size required for flowering (Lacey 1986). However, we suggest that large size may also be detrimental under some conditions, for example if good environmental conditions lead to high growth in the first year, that in turn may lead to higher levels of intraspecific competition. Nonetheless, in this experiment, individuals were spaced at a distance to avoid such competition, although

TABLE 2. Variance components determining the number of reproductive years in four cohorts of an experimental population of *Plantago lanceolata*.

Source	SS	df	MS	Proportion of variation explained	P
Cohort 1					
Dam	77.348	10	7.735	0.008	0.021
Sire	35.620	15	2.375	<0.001	0.515
Sire \times dam	36.329	15	2.422	0.009	0.001
Error	6502.588	6614	0.983	0.983	
Cohort 2					
Dam	146.061	10	14.606	0.015	<0.0001
Sire	57.681	15	3.845	0.006	0.031
Sire \times dam	21.169	15	1.411	0.002	0.117
Error	7669.442	7852	0.977	0.977	
Cohort 3					
Dam	136.365	10	13.637	0.031	<0.001
Sire	52.045	15	3.470	0.012	0.047
Sire \times dam	15.598	12	1.300	0.004	0.176
Error	3397.252	3565	0.953	0.953	
Cohort 4					
Dam	22.591	4	5.648	0.012	0.048
Sire	21.258	20	1.063	-0.011 (0)	0.814
Sire \times dam	18.265	11	1.660	0.008	0.073
Error	3194.803	3223	0.991	0.991	



PLATE 1. *Plantago lanceolata* seedling, with identification tag, shortly after planting in the field site. Photo credit: D. Roach.

natural *Plantago* individuals also occurred within field plots.

Strong maternal effects determining the number of reproductive years suggest the importance of nongenetic means of inheritance in determining reproduction and reproductive schedules. Maternal environment impacts many kinds of traits important to the fitness of organisms, ranging from aspects of metabolism tied to cellular structures, to seed chemical composition, to fruit characteristics (Roach and Wulff 1987, Mousseau and Fox 1998). Although maternal effects dominate the early life of plants more than they do the later life (Weiner et al. 1997), nonetheless maternal effects can be long-lasting, as they are in determining the number of reproductive years experienced by plants (Roach and Wulff 1987).

Our work reinforces that in iteroparous perennial plants, greater numbers of reproductive years typically lead to greater fitness (Lacey et al. 1983, Silvertown 1983, 1986). However, long-lived herbaceous perennials have more variable fecundity than shorter-lived perennials (García et al. 2008), most likely owing to a need to maintain fitness via high adult survival (Sæther and Bakke 2000, Miller et al. 2008). Although *Plantago lanceolata* is an iteroparous perennial, in our study 46.7% of reproducing individuals only reproduced once and did so overwhelmingly in the first or second years of life. Thus, the adaptive benefits do not mesh with the

commonality of single reproductive bouts. One possible reason may be that the reproductive schedule of this plant is at least partially determined by spatial differences in microhabitat. Under limited nutrients, some plants may not reach the proper threshold sizes necessary to ensure multiple reproductive bouts (Wilbur and Collins 1973, Lacey 1986). Another possible scenario is that plants reproducing only once may minimize the variance in fitness over generations, leading to increased geometric mean fitness relative to plants reproducing more often. Such a bet-hedging strategy may result in fewer reproductive episodes yielding higher fitness under some conditions and could be verified via a multiple cohort study conducted over multiple generations. We suggest further work to clarify this apparent contradiction.

ACKNOWLEDGMENTS

We thank and acknowledge the huge contributions of all of the technicians and undergraduates at the University of Virginia who spent long hours in the field gathering data. This project involved many people and unfortunately there were too many to name them all individually. We are also grateful to E. Lacey, J. Dudycha, M. Aikens, S. Goodrich, E. Yoshizuka, S. Felker, and two anonymous reviewers for providing helpful critiques of earlier drafts of the manuscript. Financial assistance was provided by the National Institutes of Health (P01-AG8761) to D. A. Roach.

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APPENDIX

Path coefficients from structural equation modeling of relative fitness in *Plantago lanceolata* (*Ecological Archives* E091-033-A1).