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AGE-SPECIFIC DEMOGRAPHY IN *PLANTAGO*: VARIATION AMONG COHORTS IN A NATURAL PLANT POPULATION

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Abstract. The major starting point to life history analysis is the schedule of reproduction and mortality; hence, knowledge of age-specific demographic dynamics is needed. The key ingredients to studies on age-specific demography must include large cohorts of individuals of known age, an accurate accounting of all individuals, and an experimental design to facilitate a separation of age-dependent and age-independent dynamics.

In this study with *Plantago lanceolata*, multiple, large cohorts were planted over four successive years, and the individuals were censused monthly for nearly five years. Longitudinal analysis showed seasonal variation in demography that was correlated with maximum temperature and cumulative precipitation. Cross-sectional analysis of the different cohorts showed variation across cohorts in age-specific demography. The cohort with the lowest juvenile mortality had the highest adult mortality and the lowest fecundity, suggesting that there is an interdependence of demographic patterns across life stages and that the history of mortality within a cohort may be critical to late-age demographic patterns.

Key words: *age-specific mortality; cohort variation; demography; natural population;* Plantago lanceolata; *ribwort plantain.*

INTRODUCTION

One of the critical issues in life history theory is addressing how natural selection has molded the way that reproduction and mortality depend on age (Charlesworth 1980). Addressing this theory requires evaluations of age-specific birth and death rates. In natural populations, the causes of age-specific trends are potentially a confounding of internal trade-offs and environmental effects. Environmental influences can vary either in space or in time (cf. Moloney 1988, Vavrek et al. 1997), and these influences may mask age-dependent changes that are attributable to internal factors. Age-dependent changes in mortality and reproduction may also be difficult to discern because declining sample sizes in advanced-age classes can reduce the precision of mortality estimates. In order to identify age-dependent demographic patterns, large populations with multiple cohorts of known age must be followed for their entire life span.

The advantage of using plants to study demography in natural populations is that individuals can be marked and followed for their entire life span with minimal disturbance to the surrounding biotic community and minimal effort per individual, facilitating the use of large sample sizes. Additionally, unlike most animal studies, there are no statistical uncertainties associated with the mark and recapture of individuals in the population. However, despite this relatively easy experimental system, data on age-specific demography in plants is currently very limited. Except for studies with short-lived annual plants, for which mortality is closely tied to reproduction or extrinsic climatic conditions at the end of the growing season, there is very little known about age-specific demography (for a review, see Roach 1993). This paucity of data was recently noted by Silvertown et al. (2001), who reviewed the life tables and fecundity schedules of 65 species of iteroparous perennial plants to evaluate the current state of evidence for the evolution of senescence in plants. To do their analysis, they were forced to convert stage-projection matrices to age for many species. Furthermore, many studies had very small sample sizes, making the age-specific demographic patterns difficult to evaluate.

In this study, multiple cohorts were planted over four successive years to facilitate the separation of age-dependent and age-independent dynamics. The comparative analysis of different-aged cohorts shows that historical differences in mortality among cohorts has a major impact on demographic patterns.

MATERIALS AND METHODS

Plantago lanceolata (ribwort plantain) is a short-lived perennial that germinates in the fall and spring, and flowers in midsummer. It is herbaceous with a basal rosette that remains green all year; thus, the demography of individuals can be easily followed. The "natural" habitat for *P. lanceolata* is a mown field. The field site for this study was located in Durham, North Carolina, on a long-term research site, which had been maintained as a mown field for over 50 yr.

Seeds, from which the experimental plants were derived, were collected from the same field where the experiment was conducted. Large sample sizes are re-

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quired to identify age-dependent mortality in a natural population, thus, for the initial cohort, 10 000 individuals were planted into the field. Within this cohort, there was a genetic substructure that included 250 individuals from each of 30 families, and 50 individuals from another 50 families. Sets of seeds collected from a particular individual growing in the field constitute a "family." They share a female parent, and given that this species is self-incompatible and wind pollinated, the seeds within a family are most likely half-siblings (half-sibs). Previous demographic studies in natural populations of both plants and animals have shown relatively high mortality at the earliest stages of the life cycle. In order to ensure that the experimental plants for this study survived this period of high risk, individuals were planted into the field, not as seeds, but as six-week-old seedlings. In order to guarantee a complete design, two seeds from the same family were planted in each of the 10 000 small (3.4 × 12.3 cm), deep, "zipset" pots (Monarch Manufacturing, Salida, Colorado, USA). The seedlings were then thinned shortly after emergence to one centrally located seedling per pot. They were grown in the National Phytotron at Duke University, Durham, North Carolina, a controlled growth facility, under cool conditions for six weeks. In order to acclimate the seedlings to ambient conditions, the seedlings were moved outside the greenhouses a few days prior to planting. Thus, the seedlings for this experiment were of uniform age, yet of sufficient size and condition to maximize survival during transplantation. To keep the plants in as natural a condition as possible, the seeds were planted and the seedlings were grown in sterilized field soil that had been collected from the same field where the seed had been collected and the seedlings were to be planted. The soil was mixed with sand to improve drainage.

Individual seedlings were planted and marked with minimal disturbance to the surrounding biotic community. Each plant was marked with an identification label, and wrapped with plastic-coated wire to distinguish it from the surrounding vegetation. The seedlings were planted in a randomized block design, with replication of genotypes within and among blocks. Each block was 23 × 24 m^2, and within each block, plants were located 15 cm apart in 10 staggered rows each 10 cm apart. This spacing was sufficient to avoid competition between individuals and is within the natural density in this field. Individuals were censused every four weeks for mortality, and mature inflorescences were collected weekly during the reproductive period to quantify reproduction. Age-specific fecundity was estimated as the number of inflorescence spikes produced by an individual.

This initial cohort was transplanted into the field in April 1997. With only one, even-aged cohort, it is not possible to determine whether changes in mortality patterns over time are due to the advancing age of the cohort or to environmental/seasonal changes experienced by the cohort. Additional cohorts of 10 000, 2000, and 5000 seedlings were planted in April 1998, 1999, and 2000, respectively. During each year, the same protocol was used to raise the seedlings prior to planting. In order to minimize the effects of spatial location across cohorts and to maintain density within the plots, half of the individuals of the 1998 and 2000 cohorts were planted within the same spatial blocks as those used for cohort 1, in locations where cohort 1 individuals had died. The other half was planted in new blocks immediately adjacent to the old blocks. All of the individuals in the 1999 cohort were planted within the original blocks used for cohort 1. The census of all cohorts was done concurrently, and the plants were followed until October 2001, when the field site was no longer available.

Mortality was calculated as $q(x)$, the number of deaths between age x and $x + 1$, divided by the number of individuals alive at age x. Monthly mortality was standardized to 31-d intervals to reflect minor variation in the number of days included in the census interval. The mortality by reproductive class was calculated for each cohort and year as the percentage mortality from June to December. This was calculated for nonreproductive individuals and for four reproductive quartiles derived from the frequency distribution of the number of inflorescences for each cohort and year.

Meteorological data, including daily minimum, maximum, and average temperature, and precipitation, was obtained from the State Climate Office of North Carolina at North Carolina State University, Raleigh, North Carolina.[2] The West Durham weather station is located just a few miles from the field site. The relationship between the field mortality data and the weather data was analyzed using additivity and variance stabilization procedures for regression (AVAS; Tibshirani 1988) in S-Plus (MathSoft 1999). This analysis computes a form of nonlinear regression that transforms both the dependent and independent variables to produce an additive model with constant residual variance.

Results

A longitudinal analysis of the mortality of the four cohorts showed seasonal and yearly variation (Fig. 1a). For all cohorts, mortality consistently peaked during the summer months and was separated by a period of substantially lower mortality during the winter and early spring. An analysis of several temperature measures showed that the monthly mean maximum temperature explained a large proportion of the seasonal fluctuation in mortality when mortality was log transformed (Fig. 2a). An AVAS analysis of cohort 1 showed that the influence of the maximum temperature on log mortality is a two-step function with a minimal effect below 21°C, and a steep log-linear increasing effect with every degree of increase in temperature above 21°C. The

[2] URL: ⟨http://www.nc-climate.ncsu.edu⟩

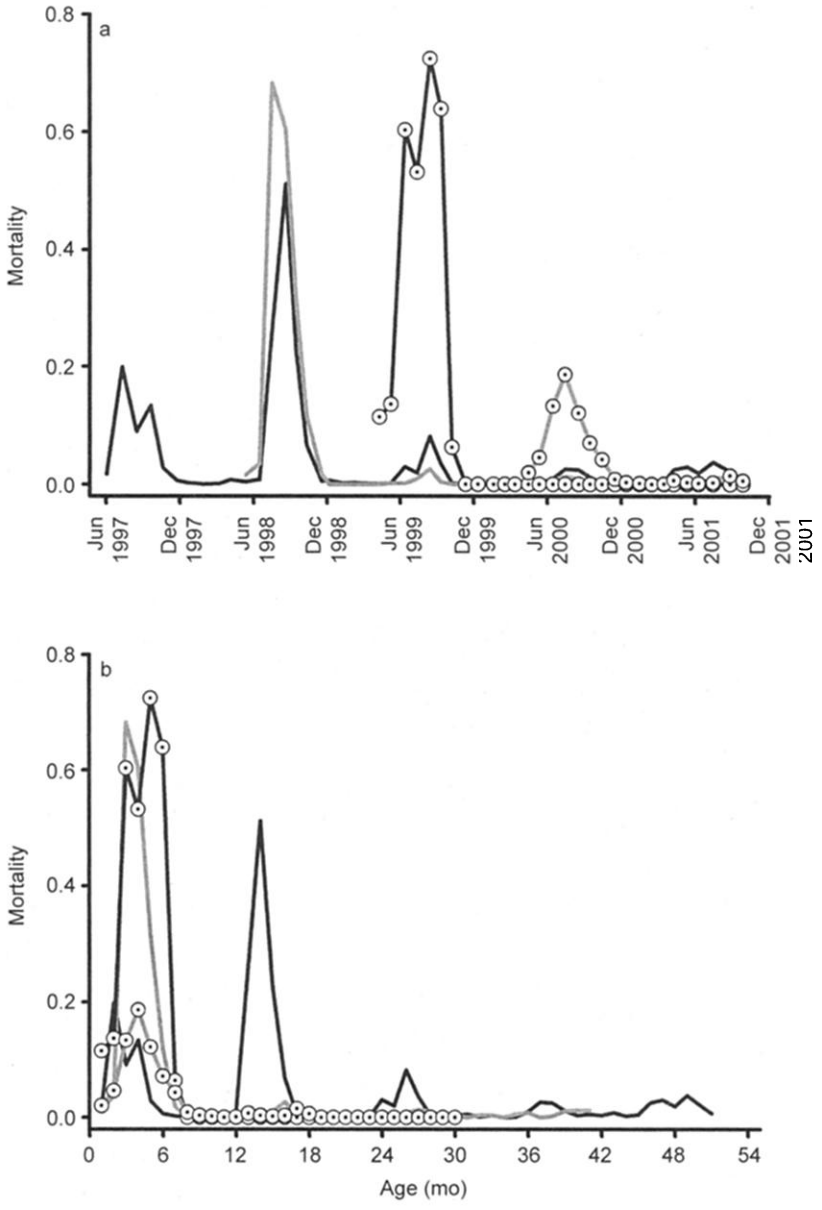

FIG. 1. Mortality of four cohorts of *Plantago lanceolata*: (a) mortality over time, and (b) mortality by age. Symbols and lines for the different cohorts are as follows: cohort 1 (black solid line), cohort 2 (gray solid line), cohort 3 (black line with open symbols), and cohort 4 (gray line with open symbols). For a description of mortality calculations see *Materials and Methods*.

AVAS-transformed model for cohort 1 had an R^2 of 0.50. An analysis of several different precipitation measures, including monthly cumulative precipitation and the length of "no-rain" intervals, showed that the cumulative precipitation for 40 d prior to a census was the best measure to explain variation in log mortality (Fig. 2b). An AVAS analysis of the log mortality of cohort 1 showed that mortality was high when precipitation was low, and that when the cumulative precipitation increased, mortality decreased linearly up until the cumulative precipitation was ~11 cm. When cumulative precipitation was added to the AVAS-transformed model with mean maximum temperature, the R^2 value increased to 0.77. Separate analyses were also done for cohorts 2 and 4, and they both showed similar influences of temperature (above 21°C) and cumulative precipitation (below 11 cm) on log mortality. Cohort 3 was not analyzed with respect to the weather variables because very few individuals in this cohort lived beyond their first summer.

Whereas temperature and precipitation could explain a large proportion of the within-year fluctuation in mortality, this was not true among years. The mortality curves showed interannual variation in mortality, yet

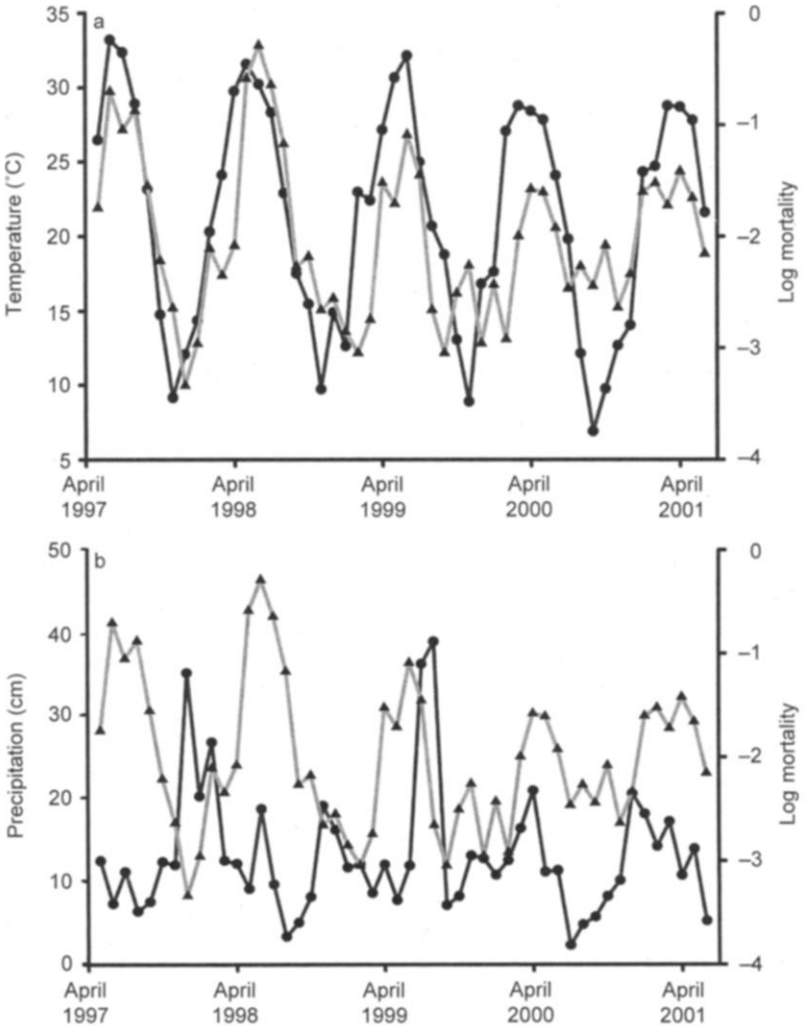

FIG. 2. Weather variables and log mortality of *Plantago lanceolata* at the study site for five years: (a) monthly mean maximum temperature (circles with black line) and log mortality (triangles with gray line), and (b) cumulative precipitation 40 d prior to census time (circles with black line) and log mortality (triangles with gray line).

this variation was not correlated with yearly variation in weather variables (Fig. 2a, b). The highest mortality occurred in summer 1998, yet the weather during this year was not extreme. Similarly, the years with relatively low mortality across all cohorts (1999–2001) did not show any unique temperature or precipitation patterns.

In addition to seasonal and yearly variation in mortality, there was also variation across ages for the different cohorts (Fig. 1b). The most striking difference among the cohorts was that mortality was the highest at the juvenile stage for all cohorts except cohort 1. For cohort 1, mortality was highest in the second year. The age-specific pattern of mortality after reproductive maturity was much lower for those cohorts suffering high mortality during their juvenile period (Table 1). Cohorts 2 and 3 both showed extreme mortality during their first year and relatively low mortality after reproductive maturity. Cohort 4 showed a relatively low juvenile mortality, similar to cohort 1.

The percentage of nonreproductive individuals was highest in the first year of reproduction for all cohorts (Table 2). Across cohorts, this first-year percentage of nonreproductive individuals was highest for cohort 1. It was also higher for cohort 4 than for cohort 2 (χ^2,

TABLE 1. Yearly mortality of *Plantago lanceolata* by cohort at the study site in Durham, North Carolina.

Cohort	Juvenile	Year 2	Year 3	Year 4	Year 5
1	0.47	0.77	0.19	0.11	0.14†
2	0.94	0.06	0.04	0.05†	
3	0.99	0	0†		
4	0.51	0.04†			

Note: For a description of mortality calculations see *Materials and Methods*.

† Year 5 calculations are only for six months.

TABLE 2. Percentage of nonreproductive individuals of *Plantago lanceolata*, and mean number of inflorescences (±1 SE) of reproductive individuals, by cohort and year at the study site in Durham, North Carolina.

	1998		1999		2000		2001	
Cohort	Nonreproductive (%)	Inflorescences (no.)	Nonreproductive (%)	Inflorescences (no.)	Nonreproductive (%)	Inflorescences (no.)	Nonreproductive (%)	Inflorescences (no.)
1	49.4	5.3 ± 0.8	23.8	10.2 ± 0.3	14.5	17.5 ± 0.6	35.7	18.6 ± 0.9
2			33.7	10.1 ± 0.5	4.7	21.7 ± 0.8	11.2	16.0 ± 0.8
4							41.2	8.8 ± 0.3

$P < 0.0001$, in both cases). An analysis of reproductive individuals showed that cohort 1 individuals had lower fecundity in their first year compared to cohort 2 (GLM, Independent Contrasts, $P < 0.001$, Table 2). Cohort 4 also had low first-year fecundity that was significantly lower than the fecundity of the individuals from the older cohorts flowering in 2001 (GLM, Independent Contrasts, $P < 0.001$, Table 2). In addition to different percentages and levels of reproduction, there were differences across cohorts in mortality by reproductive class (Table 3). In its first year of reproduction (1998), individuals within cohort 1 with the largest number of inflorescences had the highest mortality. Individuals with minimal or no reproduction had lower mortality. For cohort 1 in its second year of reproduction, this hierarchy was reversed such that the class of individuals with the highest level of reproduction had the lowest mortality. The major difference between cohorts 1 and 2 in their pattern of survival by reproduction was that in its first year of reproduction, the highest mortality in cohort 2 was found in the nonreproductive individuals. This pattern of mortality by reproductive classes for cohort 2 was consistent across all three years of reproduction. The mortality by reproductive class could not be calculated for cohort 4 because the study was terminated shortly after this cohort had reproduced for the first time. Cohort 3 had too few individuals survive to reproduction to be included in any of the analyses of reproductive patterns.

The differences among cohorts 1 and 2 were also analyzed with respect to genetics and spatial location. Cohort differences could arise if there were genetic variation among individuals across cohorts combined with significant genotype by environment interaction. An additional analysis of mortality was done using only individuals from overlapping half-sib families. This analysis included 30 families and a total of 4090 and 3993 total individuals from cohorts 1 and 2, respectively. A comparison of the yearly mortality by cohort, using this reduced data set of overlapping families, did not show any change in the pattern of mortality across years as reported in Table 1 (χ^2, $P > 0.5$, for all cases). This suggests that the different patterns of mortality across cohorts cannot be explained by any differences in the initial genetic composition of the two cohorts because similar patterns of mortality were found, both within and among cohorts, when the analysis was restricted to overlapping half-sib families.

The analysis of spatial differences among cohorts also does not significantly change the patterns of mortality across years. Half of the individuals in cohorts 2 and 4 were planted in new blocks immediately adjacent to the blocks used for cohorts 1 and 3. For both cohorts, the mortality was lower in these new blocks, suggesting that there is spatial heterogeneity within the field site (χ^2, $P < 0.0001$, in both cases). Yet, this spatial heterogeneity did not have a significant effect on the mortality patterns across cohorts. For cohort 2, yearly mortality in the new blocks was 0.90, 0.06, 0.04, and 0.05, respectively, up to year 4. These values do not significantly change the pattern of differences in mortality across cohorts that are presented in Table 1.

TABLE 3. Percentage mortality of *Plantago lanceolata* six months after reproduction by reproductive class, cohort, and year at the study site in Durham, North Carolina.

	Cohort 1			Cohort 2		
Year	Reproduction	No./class	Mortality (%)	Reproduction	No./class	Mortality (%)
1998	0	908	10.57			
	1 (1–2)	275	9.82			
	2 (3–4)	218	10.55			
	3 (5–7)	211	16.11			
	4 (>7)	196	16.33			
1999	0	202	19.80	0	174	10.34
	1 (1–4)	221	7.24	1 (1–4)	93	1.08
	2 (5–7)	198	6.57	2 (5–8)	89	3.37
	3 (8–13)	225	7.56	3 (2–12)	75	0
	4 (>13)	215	4.19	4 (>12)	86	3.49
2000	0	139	30.94	0	23	13.04
	1 (1–6)	221	5.43	1 (1–9)	109	3.54
	2 (7–12)	202	8.42	2 (10–18)	116	2.52
	3 (13–22)	189	3.21	3 (19–28)	113	1.74
	4 (>22)	207	1.93	4 (>28)	116	0
2001	0	207	30.54	0	52	13.46
	1 (1–4)	148	6.08	1 (1–4)	105	7.62
	2 (5–11)	120	1.67	2 (5–11)	106	2.83
	3 (12–26)	130	3.08	3 (12–22)	104	2.88
	4 (>26)	137	0	4 (>22)	99	0

Notes: Reproductive class "0" designates nonreproductive individuals, and classes 1–4 designate the quartiles from the frequency distribution of the number of inflorescences. The number of inflorescences in each quartile is given in parentheses. A chi-square test of mortality across reproductive classes for each cohort and year was significant at $P < 0.001$ in all cases, except 1998, in which case $P < 0.03$.

For cohort 4, juvenile mortality in the new block was 0.27, which was significantly lower than the 0.51 value reported for the entire population (χ^2, $P < 0.0001$). Again, however, this does not alter the relative pattern of mortality across cohorts.

Discussion

In order to understand how natural selection has acted to shape mortality patterns in natural populations, it is important to do experiments under the same environmental conditions that the population has experienced for many generations of selection. Yet, these environmental conditions may mask age-dependent patterns. The longitudinal demographic patterns in this study clearly demonstrate that seasonal weather patterns are an important determinant of mortality. This seasonal variation in mortality may be due to the direct effects of temperature and moisture, or to indirect effects of other biotic factors that may be induced by these seasonal environments. Similar season-dependent demographic patterns have been shown in other studies (cf. Vavrek et al. 1997). For example, a seasonal cycle of mortality was found for mature *Ranunculus repens* and to a lesser extent for *R. bulbosus* and *R. acris* (Sarukhan and Harper 1973). They suggested that variation in risk of mortality was associated with active growth and the demands for limited resources, and that the rigors of variation in climate had only minimal direct effects on the dynamics (Sarukhan and Harper 1973). In other studies with *P. lanceolata*, seasonal variation in mortality has been found (Sagar 1959, as cited in Sarukhan and Harper 1973), and the range of mortality found in this study is similar to that found in other demographic studies using this species (cf. Mook et al. 1989, Van Tienderen and Van Der Toorn 1991).

What is unique about this study is the comparative analysis of cohorts. The experimental design made it possible to follow large cohorts of individuals either longitudinally to evaluate season- and age-specific dynamics, or cross-sectionally to compare cohorts of different ages sharing the same environment. The most striking difference among cohorts was the low mortality in year 1 followed by a high mortality in year 2 (1998) for cohort 1. For all of the other cohorts, the highest mortality was in the first year. The weather variables, temperature and precipitation, explained the within-season variation in mortality, but did not explain the unique pattern of age-specific mortality for cohort 1. It is possible that other weather variables, or other unmeasured environmental factors, could have explained this yearly variation. Alternatively, cohort differences in age-specific demography may be caused by historical differences. Cohort 1 showed only 50% mortality at the juvenile stage, but cohorts 2 and 3 showed 94% and 99% mortality, respectively. This difference in mortality at the juvenile stage may partially explain the cohort differences in mortality, because lower mortality at the juvenile stage may result in the persistence of more frail individuals into the second year. A cohort or population with a greater proportion of frail individuals may then show a higher mortality at later ages as the frail individuals die (Vaupel and Yashin 1985). Comparative age-specific reproduction across cohorts supports this hypothesis. In particular, in the first year of reproduction, cohort 1 had both a lower percentage of individuals reproducing and a lower reproductive output than cohort 2 did, suggesting that there were proportionally more frail individuals at later ages. Cohort 1 also showed an unusual pattern of mortality across reproductive classes. In the first year of reproduction, those individuals with the largest number of inflorescences had the highest mortality. Whereas this mortality may not be a true mortality "cost" to reproduction because it may have been confounded with external factors, it was a pattern that was not apparent for cohort 2 and it had important long-term demographic consequences. If the study had not been terminated prematurely, cohort 4 might have been a test of this hypothesis that different levels of selective mortality at the juvenile stage can have an impact on later age demography. This last cohort showed a relatively low mortality of 51% in its first year, similar to cohort 1. Cohort 4 then showed a very high percentage of nonflowering individuals in its first year of reproduction and low fecundity. Unfortunately, because the experiment had to be terminated, it could not be determined whether the mortality of this fourth cohort would have increased at the end of its second year. The results from this study suggest that there is an interdependence of demographic patterns across life stages. The cohorts in this study had an overlapping genetic composition and were planted in adjacent blocks within the same field, yet they had radically different demographics. Whatever chance events caused the unusually low mortality in the first year for cohort 1 also shaped the subsequent mortality patterns and apparent interactions between mortality and reproduction. Moreover, these delayed life history effects were dichotomous in the sense that the cohort that did best as a juvenile did worse at later life stages. This negative correlation of demography across life stages is in contrast to other demographic studies in which adverse environmental conditions experienced by a cohort early in life have been shown to have continued adverse effects on the demography and reproduction later in life (cf. Lindstrom 1999, Gaillard et al. 2000, but see Rose et al. 1998, Forchhammer et al. 2001).

This study used longitudinal tracking of a large number of individuals. The alternative technique that has been commonly used in both plant and animal studies is to construct survival curves from a cross-sectional sampling of the population where a single sample of individuals are aged on the basis of recognizable life stages, morphological traits, or size. The data are then extrapolated to a stable age distribution. However, var-

iance in vital rates across time dictates that demographic models of long-lived individuals cannot be approximated by differences in representation of age classes in a single sample (Nakaoka 1996). The results of this study show that variation in the history of cohorts within a population may be critical to the dynamics of the population, yet these differences in cohort history would not have been apparent without the longitudinal monitoring of several different cohorts.

An additional advantage of a multiple-cohort design is that it makes it possible to distinguish age- and environment-dependent dynamics. With cohort 1 alone, one would conclude that this *P. lanceolata* population contains a large proportion of individuals who are monocarpic and die after the first year of reproduction. For those who survive, there is a lower, intermediate, mortality rate. Alternatively, if the study had included only cohort 2 or 3, one would conclude that juvenile mortality in this species is extremely high and that those few individuals who survive to the adult stage have a very low mortality rate at later ages. Clearly, multiple cohorts are needed to get a true understanding of the demography of a particular species. Even with only two cohorts, the age-dependent nature of the dynamics may be misleading. In a preliminary analysis of the first three years of this experiment with cohorts 1 and 2 only, it was concluded that there was possible evidence for aging in this species and it was manifest as an age by environment interaction (Roach 2001). Further analysis with more years and more cohorts has now demonstrated that the higher mortality of cohort 1 was an anomaly. The higher late-life mortality in cohort 1 appears to have been a function of the unusually low mortality during the first year.

In previous studies, the lack of multiple-aged cohorts has made it difficult to interpret not only late-age mortality dynamics, but also the age-dependent nature of the dynamics. In one of the few studies that has documented increases in age-specific mortality in a longitudinal study of a perennial plant in its natural environment, Canfield (1957) found evidence for increased mortality with increasing age in several tussock range grasses (see Roach, *in press*). However, the apparent increase in mortality at later ages may have been caused by the environmental conditions that were particularly bad in those years. The Canfield study has been cited as the best evidence from field data for a senescent mortality pattern in plants (Harper 1977, Watkinson 1992, Roach 1993). Yet, an increase in age-specific mortality rate is indicative of senescence only if it is caused by an internal physiological deterioration and not by a deterioration of the environment. Distinguishing the causes of change in age-specific mortality to determine if in fact there is evidence for senescence in a natural population is a problem not only for plant studies, but also for studies with animals. Acceleration of mortality rates has been documented in several surveys of mammal and bird populations (Promislow 1991, Gaillard et al. 1994, Ricklefs 1998), but it is not clear whether this effect is the result of increases in external or internal causes of death (Zwaan 1999). In order to determine whether senescence affects the demographic dynamics in *P. lanceolata*, a detailed regression model is needed to separate the age-independent and age-dependent influences on mortality. This analysis will be presented in a future paper (D. A. Roach and J. Gampe, *unpublished data*).

For any species, plant or animal, in its natural population, there are many factors that may influence an individual's risk of mortality. These factors include, but are not limited to, abiotic factors ranging from weather to fine-scale spatial variation, and biotic factors, such as size, growth, and costs of reproduction. The analysis presented here has focused on the population- and cohort-level mortality dynamics. The results of this study suggest that, contrary to the assumptions of many demographic models, successive life stages are not independent. The comparative analysis of the cohorts in this study shows that within a population there may be variation in age-specific mortality and reproduction that is caused not only by variation in the abiotic and biotic environments, but also by variation in the demographic history of different cohorts.

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