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LOBELIA TELEKII HERBIVORY, MORTALITY, AND SIZE AT REPRODUCTION: VARIATION WITH GROWTH RATE¹

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Abstract. Size-specific life tables are often used in plant and animal demography when age-specific tables cannot be assembled or are less predictive. However, age \times stage interactions may confuse the interpretation of size-specific life tables. I demonstrate here several age \times stage interactions in the demography of *Lobelia telekii*, a long-lived semelparous rosette plant on Mount Kenya. Analysis of 4 yr of demographic data indicated that slower growing plants were more subject to herbivory, more likely to die, and tended to flower at a smaller size, than faster growing plants in the same population. If overlooked, these effects would cause overestimation of both plant age and the variance in generation time, when such estimates are based on size-specific life tables. Because these patterns parallel large-scale temporal and spatial trends in *L. telekii* demography related to soil moisture availability, I suggest that slow-growing plants occupied less favorable microsites than fast-growing plants.

Key words: herbivory; hyrax; *Lobelia*; Mount Kenya; plant demography; predation; size-specific life tables.

INTRODUCTION

Size- or stage-specific life tables are often used in demography and have two main advantages over age-specific life tables. First, in many long-lived organisms the ages of individuals are not known and can only be inferred from size and documented transition times (Lord 1959, Laws 1966, Inouye and Taylor 1980, Smith 1981, Young 1984). Second, size is a better predictor of fate than is age for several short-lived herbs (Werner 1975, Werner and Caswell 1977, Gross 1981). Size-specific life tables, however, have shortcomings. Information of ecological and evolutionary interest, such as population growth rate, requires data that can be accurately related in time. Hence the attempts to infer age from size-specific data. An additional problem with size-specific life tables is illustrated in *Dipsacus sylvestris*, in which there are age \times stage interactions (Werner and Caswell 1977). Hubbell and Werner (1979) and Law (1983) have developed demographic models that incorporate both age and size, showing the importance of considering age \times stage interactions.

Differences in herbivore preference among plant populations have been related to differences in the environment (Wellington et al. 1950, White 1969, 1974, 1976, Mattson and Addy 1975). Within-plant herbivore preferences have been related to leaf age and palatability (Reichle et al. 1973, Milton 1979, Coley 1980). However, few studies have examined herbivore preferences among individual plants within populations (Farentinos et al. 1981).

I examined the fates of *Lobelia telekii* plants with

different demographic histories to explore age \times stage interactions, including herbivore preferences.

SPECIES, STUDY AREA, AND METHODS

Lobelia telekii is a long-lived semelparous plant endemic to alpine East Africa. Plants grow for an estimated 40–70 yr before producing a terminal inflorescence and dying. On Mount Kenya *L. telekii* occurs from 3500 to 5000 m altitude, primarily on dry rocky slopes.

Since February 1978, I have collected demographic data on *L. telekii*, including rosette size and records of mortality, herbivory, and reproduction, at 6-wk intervals. In an initial demographic analysis of Mount Kenya lobelias (Young 1984), I showed that significant edaphic differences between wetter and drier sites were reflected in the plants' demography. Because more plants were sampled in the wetter sites than in the drier sites (705 vs. 237), I restrict my analysis here to plants in the wetter sites, all of which were within 100 m of each other.

I have previously shown that the length of the largest leaf (measured to the nearest 5 mm) is a good estimator of rosette size (total leaf area) and a good predictor of plant fate in *L. telekii* (Young 1984). For most analyses below, growth rates (changes in leaf length) of plants were calculated for the first 15 mo (February 1978 to May 1979) and were compared to their fate from May 1979 to November 1981. I estimated the average transition time through each size class by calculating the time it would take for a rosette to grow into the next size class, were it growing at the average rate for rosettes in that size class. These estimated transition times were then summed over a range of size classes (1.0 to 21.0 cm) to get a total estimated transition time.

Mount Kenya rock hyrax (*Procapra johnstoni mack-*

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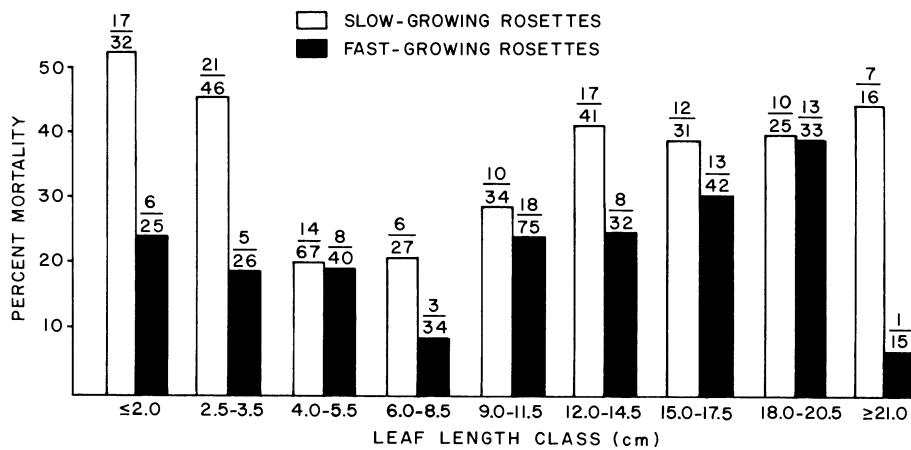


FIG. 1. Size-specific mortality from May 1979 to November 1981 for rosettes that had either grown more slowly than the mean (□) or more quickly than the mean (■) during the period February 1978 to May 1979. Leaf length was measured to the nearest 5 mm. The fraction above each bar is the number of deaths divided by the number of plants in the size class. Sample sizes are far from equal because the modal growth class was often near the mean.

inderi), marmot-sized mammals native to Mount Kenya, feed on *Lobelia telekii*. This feeding takes two forms on vegetative plants. First, hyrax may sample a few young leaf tips. This herbivory does not result in plant death. Second, hyrax may kill the plant by removing all the leaves and eating the meristem and pith of the subterranean stem. Intermediate levels of herbivory are rare. *Lobelia telekii* rosettes are protected by a bitter-tasting latex, and I have not observed any other animal feeding on them to any extent.

RESULTS

Growth rate and subsequent mortality

Slow-growing rosettes were more likely to die than fast-growing ones. Mortality rates of rosettes growing faster than the mean growth rate for a size class were uniformly lower than rates for rosettes with below-average growth (Fig. 1, $\chi^2 = 9.0$, $df = 1$, $P < .01$). Similarly, the average size-specific growth rates (from February 1978 to May 1979) for rosettes that died between May 1979 and November 1981 were usually less than the growth rates of rosettes that survived until Novem-

ber 1981 (Table 1). As a result, the estimates of size-specific growth from February 1978 to May 1979 were uniformly lower when all rosettes were included than when only those rosettes surviving to November 1981 were included ($\chi^2 = 8.0$, $df = 1$, $P < .01$). This differential mortality was still expressed fully 2 yr after the initial growth measurements were made. The estimated time for a rosette to grow from a leaf length of 1.0 cm to 24.0 cm consistently decreases as rosettes that die further and further into the future are excluded from growth measurements (Table 2). These growth rates are for a relatively wet period when growth rates were relatively high; the transition times should not be taken as estimates of total prereproductive development time.

The death of rosettes with leaf length ≥ 12 cm was mainly due to hyrax predation, while smaller rosettes succumbed mostly to internal bud death, wilting, and burial under mudslides. Predation was most severe between May and November 1981. Hyrax distinguish among individuals of *L. telekii*. The rosettes killed by hyrax in the latter half of 1981 had grown significantly

TABLE 1. Mean growth (change in leaf length for the period February 1978 to May 1979) of rosettes with different fates, by size class. N = number of rosettes.

Rosette size class (leaf length measured to the nearest 0.5 cm)	Change in leaf length (cm)					
	All rosettes		Rosettes that survived until November 1981 (or flowered)		Rosettes that died between May 1979 and February 1980	
	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N
≤2.0	0.25 ± 0.08	57	0.38 ± 0.11	34	0.17 ± 0.08	9
2.5-3.5	0.58 ± 0.07	72	0.73 ± 0.09	45	-0.10 ± 0.10	5
4.0-5.5	0.56 ± 0.08	107	0.59 ± 0.08	85	0.00 ± 0.41	4
6.0-8.5	0.50 ± 0.08	123	0.54 ± 0.08	105	-0.50 ± 0.00	2
9.0-11.5	0.47 ± 0.09	109	0.54 ± 0.12	80		0
12.0-14.5	0.83 ± 0.11	74	0.88 ± 0.15	47	0.83 ± 0.44	3
15.0-17.5	0.83 ± 0.11	73	0.94 ± 0.12	48	-1.25 ± 0.75	2
18.0-20.5	0.83 ± 0.15	59	0.83 ± 0.20	36		0
≥21.0	0.59 ± 0.24	31	1.09 ± 0.17	23		0

TABLE 2. The estimated time for a rosette to grow from leaf length 1.0 cm to leaf length 21.0 cm, based on mean growth rates of rosettes from February 1978 to May 1979, excluding those rosettes that eventually died during various subsequent periods.

	Including all rosettes	Excluding those rosettes that died between		
		May 1979 and Feb 1980	May 1979 and May 1981	May 1979 and Nov 1981
Estimated transition time (yr)	54.0	50.4	46.4	43.6
Overestimate compared to minimum (%)	24	16	6	...

more slowly over the previous 42 mo than rosettes that escaped predation (Table 3). Hyrax sampled virtually all larger rosettes during this time.

Growth rate and size at reproduction

Faster growing *L. telekii* plants flowered at a larger size, on average, than slower growing plants (Fig. 2, $r = 0.50, P < .01$). Among rosettes in the 15.0–17.5 cm class, the February 1978 to May 1979 growth rates were significantly less for plants that flowered before November 1981 than for plants that remained vegetative throughout the same period (Table 3). However, among rosettes with leaf length ≥ 21.0 cm, the February 1978 to May 1979 growth rates were significantly greater for plants that flowered before November 1981 than for plants that remained vegetative (Table 3). These results imply that (a) among smaller rosettes, faster growing individuals were less likely to flower than slower growing individuals, and (b) among larger rosettes, faster growing individuals were more likely to flower than slower growing individuals. The former is to be expected if faster growing plants flower at a larger size than slower growing plants.

Hyrax predation on flowering rosettes reflects this interaction between growth rate and size at reproduction. From February 1978 to May 1981 hyrax preferentially attacked smaller reproductive plants; this preference was consistent throughout the study period (Table 4). These results are consistent with the observations that (a) hyrax select slower growing plants, and (b) slower growing plants flower at a smaller size.

TABLE 1. Continued.

Change in leaf length (cm)			
Rosettes that died between February 1980 and May 1981		Rosettes that died between May 1981 and November 1981	
$\bar{X} \pm 1 \text{ SE}$	N	$\bar{X} \pm 1 \text{ SE}$	N
0.00 \pm 0.17	13	0.00	1
0.38 \pm 0.13	16	0.50 \pm 0.13	6
0.29 \pm 0.30	12	0.92 \pm 0.15	6
0.35 \pm 0.28	10	0.42 \pm 0.20	6
0.08 \pm 0.08	12	0.41 \pm 0.23	17
0.23 \pm 0.23	13	0.40 \pm 0.21	10
0.45 \pm 0.22	11	1.08 \pm 0.31	12
0.83 \pm 0.44	3	0.85 \pm 0.21	20
-0.20 \pm 0.34	5	-1.83 \pm 1.36	3

DISCUSSION

Age \times stage interactions in L. telekii demography

The importance of age \times stage interactions in natural populations of *Dipsacus sylvestris* was inferred by Werner and Caswell (1977), who found that stage-specific life tables gave consistently higher estimates of population growth rates than did age-specific tables. Age \times stage interactions are expressed as differential fates of individuals with different growth rates; within a size class, older individuals have grown more slowly than younger individuals. It is likely that a plant is more sensitive to factors that influence its growth rate than to age itself. It is therefore appropriate to examine interactions between fate and growth rate as indicators of age \times stage interactions.

Higher mortality of slower growing rosettes results in overestimation of the ages of individuals when such estimates are based on mean transition times (Table 2). This overestimation occurs because rosettes in any size class do not represent a random subsample of smaller (i.e., younger) rosettes from a previous time period. On average, the surviving rosettes grew faster when they were smaller than the average smaller rosette.

The true variance in generation time in *L. telekii* is likely to be less than that inferred by differences in size at reproduction (see Inouye and Taylor 1980). The

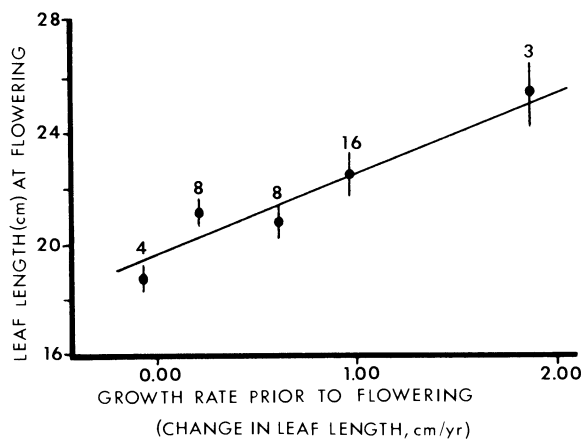


FIG. 2. The relationship between *Lobelia telekii* rosette size (leaf length) at reproduction and the plant's previous mean yearly growth rate. The vertical bars represent $\pm 1 \text{ SE}$, and sample sizes are shown above each bar.

TABLE 3. Mean growth (change in leaf length, cm) of larger rosettes with various fates. *N* = number of rosettes.

Size class (leaf length to the nearest 0.5 cm)	Growth of plants before predation by hyrax*						Growth of plants that survived or flowered and died†	
	Rosettes killed by hyrax		Rosettes not killed by hyrax		Student's <i>t</i> (killed vs. not killed)		Rosettes that survived	
	$\bar{X} \pm 1 \text{ SE}$	<i>N</i>	$\bar{X} \pm 1 \text{ SE}$	<i>N</i>	<i>t</i>	<i>P</i>	$\bar{X} \pm 1 \text{ SE}$	<i>N</i>
	Mean growth (change in leaf length, cm)						Mean growth	
12.0–14.5	0.45 ± 0.60	11	1.36 ± 0.26	44	1.48	.07	(no flowering in this size class)	
15.0–17.5	0.15 ± 0.53	10	1.85 ± 0.26	37	2.98	<.01	1.01 ± 0.12	40
18.0–20.5	0.72 ± 0.32	20	2.23 ± 0.30	22	3.45	<.01	0.71 ± 0.27	26
≥21.0	-0.83 ± 1.45	3	1.25 ± 0.32	4	1.59	.09	0.56 ± 0.22	8

* Growth measured February 1978 to May 1981. Predation occurred May to November 1981.

† Growth measured February 1978 to May 1979. Survival May 1979 to November 1981.

tendency for slower growing plants to flower at a smaller size than faster growing plants means that the difference in ages of reproduction of larger and smaller rosettes is less positive than would be estimated by assuming similar growth rates. Larger flowering plants may even be younger on average than smaller flowering plants. In two studies of invertebrate animals, faster growing individuals reproduced earlier and at a larger size than slower growing individuals (Wolda 1970:Fig. 4, Robertson and Salt 1981). Data from other plant taxa suggest similar patterns (Hubbell and Werner 1979, Inouye and Taylor 1980, Gross 1981).

The age × stage interactions shown here for *L. telekii* would not account for the pattern exhibited by *Dipsacus sylvestris* (Werner and Caswell 1977), in which stage-specific life tables produced higher estimates of population growth rates than age-specific life tables. The overestimation of plants' ages by size-specific models would result in a lower estimated population growth rate. The tendency for faster growing plants to flower at a larger size does mean that a size-specific model will tend to overestimate age at reproduction for these individuals, but this appears to be offset by the model's underestimation of the ages of smaller reproductive rosettes.

Growth rate and herbivory

I have previously shown a substantial increase in hyrax predation of *L. telekii* plants during a prolonged

dry period (Young 1984). Such an increase could be the result of: (a) a change in the needs of hyrax, with an increased need in the dry season for resources provided by *L. telekii*; (b) the hyrax being forced to rely on *Lobelia* as more palatable plants become less available; or (c) *L. telekii* plants becoming more palatable as they become more stressed. These possibilities are not mutually exclusive; any or all of them could act. However, hyrax preference for slower growing plants implies that the palatability of *Lobelia* increased. The increased mortality associated with hyrax attack was not due to slower plants' inability to recover, but because severe herbivory, which is always fatal, was directed towards slower growing plants.

In examining insect outbreaks on stressed plant populations, White (1969, 1974, 1976) suggested that an increased nitrogen content in stressed plants may make them more rewarding to insect herbivores. However, it is as likely that decreased herbivore defence in stressed plants is the key factor (Mattson and Addy 1975). In one of the few examinations of differences in herbivore attack among individuals of a population, Farentinos et al. (1981) provided a posteriori evidence that pine trees attacked by squirrels were lower in monoterpenes than unattacked trees in the same population.

In general, *L. telekii* populations in drier sites and during drier weather exhibited slower growth, higher mortality, and a smaller size at reproduction than populations in wetter sites or during wetter weather (Young

TABLE 4. The size at flowering for rosettes either killed by hyrax or not, for the total time period analyzed, the wet period, and for the dry period. *N* = number of rosettes. The average size at flowering was significantly greater in the wet period than in the dry period ($t = 2.79$, $P < .05$).

Time period	Leaf length at flowering (cm)							
	All flowering rosettes		Flowering rosettes killed by hyrax		Flowering rosettes not killed by hyrax		Student's <i>t</i> *	
	$\bar{X} \pm 1 \text{ SE}$	<i>N</i>	$\bar{X} \pm 1 \text{ SE}$	<i>N</i>	$\bar{X} \pm 1 \text{ SE}$	<i>N</i>	<i>t</i>	<i>P</i>
Total (February 1978 to May 1981)	20.7 ± 0.4	55	18.8 ± 0.4	25	22.5 ± 0.5	30	5.24	<.001
Wet (February 1978 to May 1979)	22.9 ± 0.9	16	18.5	1	23.2 ± 0.9	15	5.49	<.001
Dry (February 1980 to May 1981)	20.4 ± 0.5	28	19.3 ± 0.4	18	22.4 ± 0.9	10	4.44	<.001

* Comparing rosettes killed by hyrax vs. those not killed by hyrax.

TABLE 3. Continued.

Growth of plants that survived or flowered and died†			
Rosettes that flowered and died		Student's <i>t</i> (flowering vs. surviving)	
$\bar{X} \pm 1 \text{ SE}$	<i>N</i>	<i>t</i>	<i>P</i>
Mean growth (no flowering in this size class)			
0.56 ± 0.11	8	2.02	<.05
1.22 ± 0.21	9	1.07	.15
1.37 ± 0.21	15	2.46	<.05

1984). I hypothesize that the demographic differences among individuals within the wetter sites reported here were due to similar microsite effects. Rosettes in more favorable microsites (within the wetter site population) were characterized by faster growth, lower mortality, less herbivory, and a larger size at reproduction than rosettes in less favorable microsites.

It is not clear why slower growing plants flower at a smaller size than faster growing rosettes. There are several possibilities. (A) Because slower growing rosettes were more likely to die than faster growing rosettes, natural selection may have favored relatively early reproduction for plants that find themselves in less favorable microsites. The cost of delaying flowering until a larger rosette size is attained would be greater in sites with higher mortality. (B) Less favorable microsites may not be able to support larger rosettes. If rosettes flowered at some maximum attainable size, then slower growing rosettes would flower at a smaller size than faster growing rosettes. (C) *L. telekii* rosettes all flower at a similar age, with faster growing rosettes flowering big and slower growing rosettes flowering small.

Clearly, size alone does not provide the best predictor of plant fate in *L. telekii*. The condition of a plant, and thus its fate, are related to both plant size and growth rate. The concept of 'minimum size at reproduction,' while accurately describing empirical data, obscures the fact that there is also a minimum age at reproduction, and that the physiological phenomenon of flowering is sensitive to some combination of a plant's size and its growth rate. Only through long-term studies of marked plants, and a conscious effort to identify such patterns, will it be possible to determine the generality of these patterns.

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