

Evolution of semelparity in Mount Kenya lobelias

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Summary

Two closely related long-lived rosette plants in the genus *Lobelia* occur on alpine Mount Kenya. *Lobelia telekii* grows in drier sites and is semelparous (dies after first reproduction). *Lobelia keniensis* grows in wetter sites and is iteroparous (flowers repeatedly). I used long-term data to evaluate two related models of the evolution of semelparity ('reproductive effort' and 'demographic'), and found evidence to support only one. Eight years of population data indicate that a simple mathematical model accurately describes the demographic conditions that have favoured the evolution of semelparity. In drier sites, *Lobelia* individuals flower so infrequently and suffer such high mortality between reproductive episodes that the probability of future reproduction is outweighed by the greater fecundity associated with semelparity

Keywords: semelparity, life history, *Lobelia*, reproductive effort, demography.

Introduction

Why are the life histories of some plants and animals characterized by a single, massive, fatal reproductive episode? This life history is called semelparity, and the alternative, repeated reproduction, is called iteroparity. Semelparity is taxonomically and ecologically widespread. Many invertebrates are semelparous. Salmon and lamprey are examples of vertebrate semelparity. The plants we call annuals and biennials are semelparous. Long-lived semelparous plants occur in at least 20 genera, and include such well-known examples as some yuccas and agaves (century plants) and many bamboos.

Table 1. Estimates of the relative allocation to reproduction of semelparous and iteroparous short-lived plants. *Oryza perennis* and *Ipomopsis aggregata* data are from intraspecific comparisons; all other comparisons are interspecific. Values for *Hypochoeris* were calculated assuming a stable age distribution.

Species	Semelparous/Iteroparous	Reference
<i>Oryza perennis</i>	2.9	Sano <i>et al.</i> , 1980
<i>Oryza perennis</i>	5.3	Sano and Morishima, 1982
<i>Gentiana</i> spp.	2.2–3.5	Spira and Pollak, 1986
<i>Lupinus</i> spp.	2.2–3.2	Pitelka, 1977
<i>Helianthus</i> spp.	1.7–4.0 (–10.0)	Gaines <i>et al.</i> , 1974
Temperate herbs	2.8–2.9 (means)	Struik, 1965
Old field herbs	1.7 (mean)	Abrahamson, 1979
<i>Ipomopsis aggregata</i>	1.5–2.3	Paige and Whitham, 1987
<i>Sesbania</i> spp.	2.1–2.3	Marshall <i>et al.</i> , 1985
<i>Hypochoeris</i> spp.	2.4–3.7	Fone, 1989

Why would death after reproduction be so often favoured by natural selection? A clue is provided by empirical evidence that semelparous plant species have a higher reproductive output per episode than iteroparous species (Table 1 and refs. therein; Salisbury, 1942; Primack, 1979; Smith, 1983). It is to be expected that an organism that puts all available resources into reproduction will have a higher reproductive output than an organism that withholds some resources for future growth and survival. There exists a trade-off between high initial reproduction and continued (future) reproduction. Therefore, the key question becomes: under what conditions does the increase in initial fecundity associated with semelparity more than make up for the loss of possible future reproductive episodes?

I will review two theoretical approaches explaining the evolution of semelparity, and test them with eight years of reproductive and demographic data from two species of giant rosette lobelias on Mount Kenya. I will present evidence that a simple mathematical model accurately describes the demographic conditions that have favoured the differential evolution of iteroparity and semelparity in these *Lobelia* species.

A short review of theory

The evolution of semelparity has been the subject of a number of theoretical treatments (Schaffer, 1974; Charnov and Schaffer, 1974; Schaffer and Gadgil, 1975; Schaffer and Rosenzweig, 1977; Bell, 1976, 1980; Young, 1981). All assume a trade-off between present and future reproduction. As cited above, this trade-off has been repeatedly demonstrated with comparisons of closely related annual and perennial plants. Theoretical models numerically or graphically describe the conditions under which a given increase in present fecundity will more than make up for the loss of future reproductive episodes.

The two models described below are not mutually exclusive; in fact, they are mathematically related. However, they examine different proximate causes, and are empirically tested with different data sets and analyses. It is, therefore, appropriate to consider these models separately.

Reproductive effort model. One approach considers the shape of the curve representing the trade-off between present and future reproduction, as expressed by different relationships between reproductive effort and its attendant benefits and costs (Schaffer, 1974; Schaffer and Gadgil, 1975; Schaffer and Rosenzweig, 1977). Of particular interest has been the prediction that semelparity will be favoured when greater benefits of reproduction come at higher levels of reproductive effort, i.e. when relative reproductive success is an ever-increasing function of reproductive output (Fig. 1). For example, if a 10% increase in reproductive effort results in more than a 10% increase in reproductive success, then this increase will be favoured by natural selection (everything else being equal, e.g. assuming that the costs of increased reproductive effort do not rise as quickly as the benefits). If this differential holds over all levels of reproduction, natural selection should favour putting all resources into reproduction, withholding none for future growth and survivorship, i.e. semelparity.

One way to evaluate this model in a particular system is to examine differences in reproductive success among different-sized inflorescences and the causes of variation both in inflorescence size and in reproductive success. If one finds that (genetically based) differences in reproductive effort (inflorescence size) *cause* differences in relative reproductive success, then natural selection can act directly on this reproductive effort, and therefore on life history.

A pattern of selection for ever-increasing reproductive effort has been implicated in yuccas and agaves (Schaffer and Schaffer, 1977, 1979). Pollinators preferentially visited taller inflorescences in 'semelparous' species, and percent fruit set was positively correlated with inflorescence height in these species. In contrast, both pollinator preference and percent fruit set were

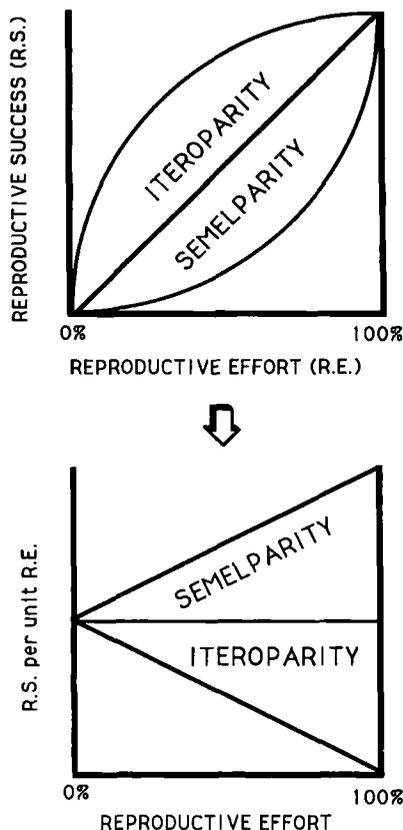


Figure 1. Reproductive Effort Model. Putative life history consequences of the relationship of reproductive effort (RE) and current reproductive success (RS). This is a simplified version of a more general model (Schaffer and Rosenzweig, 1977) that also incorporates the shape of the negative relationship between RE and future RS (survivorship, mostly). The part of the model presented here assumes that this relationship is linear, or more precisely, that the relationship between RE and current RS dominates the relationship between RE and future RS. This version of the model is the one tested by Schaffer and Schaffer (1977, 1979).

independent of inflorescence size in congeneric iteroparous species. If fruit set were pollinator limited in the semelparous species, these patterns would provide evidence that differential pollinator behaviour could have shaped life history evolution in *Yucca* and *Agave*. However, experimental studies on the semelparous species *Yucca whipplei* (Udovic, 1981; Udovic and Acker, 1981; Acker, 1982a) and *Agave chrysantha* (Sutherland, 1982) indicated that fruit set was usually limited by resources, and rarely if ever limited by pollinators. Therefore, the observed patterns of maternal reproductive success in these semelparous yuccas and agaves were probably not due to differential pollinator behaviour (cf. Pyke 1981). Nonetheless, the reproductive effort model remains a possibility for other systems, and even for *Yucca* and *Agave*, if pollinator-limited male success or rare years of pollinator-limited fruit set select for taller inflorescences only in the semelparous species (Acker, 1982b).

Demographic model. The second class of models is demographic, and ask: under what

Demographic Models

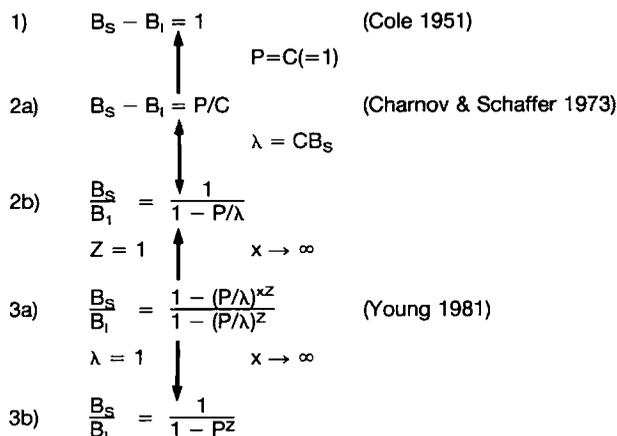


Figure 2. The history and development of demographic models of the evolution of semelparity and iteroparity. B_s = fecundity of the semelparous life history, B_i = fecundity of the iteroparous life history, P = yearly adult survivorship, C = juvenile survivorship, λ = population growth rate, Z = years between reproductive episodes, and x = number of reproductive episodes before senescence.

demographic conditions does a switch to the greater initial fecundity of semelparity become favoured? (Charnov and Schaffer 1973; Bell, 1976, 1980; Young, 1981; Orzack and Tuljapurkar, 1989). They confirm what intuition tells us, i.e. semelparity is more likely to evolve when future reproduction is unlikely, infrequent, or relatively unimportant. Specifically, semelparity tends to be favoured by high population growth rate, low adult survivorship, longer intervals between reproductive episodes, and early senescence (Fig. 2). None of these models has been tested with empirical data. In the discussion, I will give details of the demographic model I tested with data from Mount Kenya lobelias.

Mount Kenya lobelias

Distribution, life history and growth form

Two species of giant rosette plants in the genus *Lobelia* occur abundantly above treeline on Mount Kenya, separated along a resource gradient related to soil moisture (Young, 1984, 1990). The semelparous *Lobelia telekii* occurs on well-drained slopes at elevations of 3500 to 5000 m. The iteroparous *Lobelia keniensis* occurs in moist valley bottoms and on moorland slopes at elevations of 3300 to 4600 m. *Lobelia telekii* is restricted to the drier, less-vegetated sites, and *L. keniensis* is restricted to the wetter, more-vegetated sites (see Fig. 3).

The following observations are based on over eight years' study of the alpine Mount Kenya *Lobelia* species (Young, 1984, 1985, 1990). Rosettes grow slowly from germination to reproductive size over a period estimated to be 40–60 years for both species. Inflorescences are terminal and a rosette invariably dies after flowering. Semelparous plants are unbranched; iteroparous plants are branched. Individuals of *Lobelia telekii* are virtually always (> 99.9%) unbranched, single rosette plants. Individuals of *Lobelia keniensis* are usually (> 95%) branched, forming clones with several rosettes.

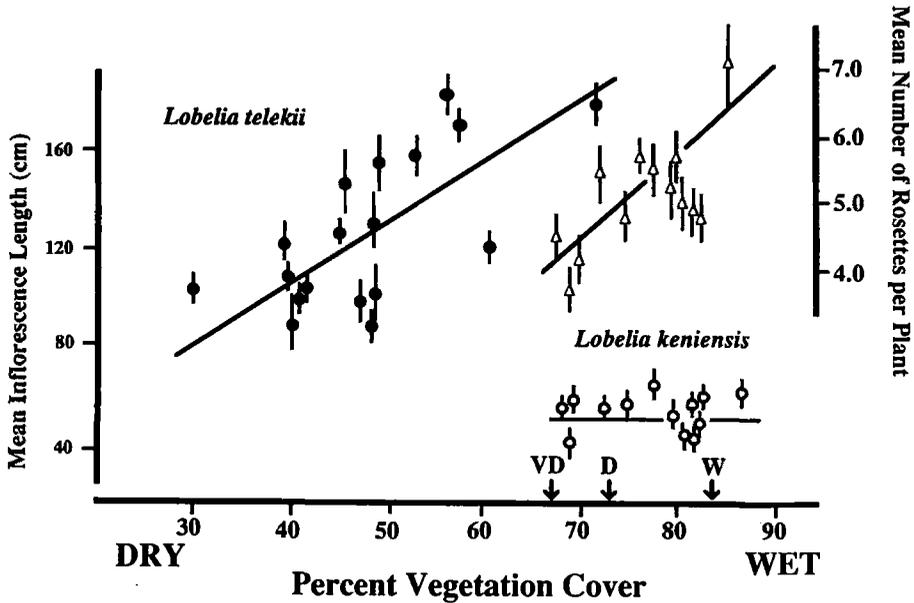


Figure 3. Mean inflorescence size and mean number of rosettes per reproductive plant in populations on Mount Kenya *Lobelias* along an environmental gradient. Solid circles = *L. telekii* inflorescence height, open circles = *L. keniensis* inflorescence height, and open triangles = number of rosettes per reproductive *L. keniensis* plant. Bars represent one standard error. W and D show the ecological positions of the wetter and drier *L. keniensis* demographic populations, and VD the very dry outlying *L. keniensis* population.

In the semelparous *L. telekii*, the resources of the entire plant go into reproduction, with both the stem and root system being converted into an inflorescence that may exceed 3 m in length. No side rosettes are produced at reproduction; the entire plant dies. In the iteroparous *L. keniensis*, side rosettes are produced prior to first reproduction and throughout life, independent of flowering episodes. Only the portion of the stem nearest the flowering rosette is consumed during flowering, producing an inflorescence that rarely exceeds 1 m in length. The flowers of both species are densely packed throughout the inflorescence and are pollinated primarily by birds, such as the Scarlet-tufted Malachite Sunbird and the Mountain Chat (Young, 1982). There is virtually no pre-dispersal seed predation.

Methods

Surveys of populations along the soil moisture gradient

This research was carried out in the upper Teleki Valley at 3900–4200 m altitude on the western side of Mount Kenya National Park in the Republic of Kenya, between 1977 and 1986. I have been monitoring populations of over 1000 marked individuals of each species since February 1978. These included over 200 *L. keniensis* adults in a set of relatively wetter and drier plots (Fig. 3). In addition, I marked and monitored a population of 100 plants, including 30 adults, at a very dry outlying site from 1983 to 1986. These target populations were surveyed every six weeks for growth, mortality, and reproduction. For details of sites and demographic methods, see Young (1984).

In December 1981, 31 populations (18 of *L. telekii* and 13 of *L. keniensis*) were surveyed

throughout the soil moisture gradient to obtain estimates of mean inflorescence size and the mean number of rosettes per reproductive plant. In each population, 22–34 reproductive plants were surveyed. For each surveyed plant, the total length of the inflorescence containing flowers was measured and (in *L. keniensis*) the number of vegetative rosettes was counted. The percentage vegetation cover was estimated at the site of each population by sampling four points around each surveyed plant.

Estimating total seed crops in various inflorescences

The seed crops of eleven *L. telekii* plants and seven *L. keniensis* plants were estimated. Ten rosettes of each species were randomly selected in March 1979 as they began to flower. These inflorescences were located near the demographic plots for each species. Three inflorescences of *L. keniensis* and one of *L. telekii* were blown down by high winds before they could be completely sampled. Two very small *L. telekii* inflorescences were included in July 1979. The length of each inflorescence was measured and the number of vegetative rosettes on each *L. keniensis* plant was counted.

Seed pods were sampled as they matured. One pod was collected from each of four compass directions around the inflorescence, beginning at the bottom and thereafter at 10 cm vertical intervals. Pods were collected just before seeds began to disperse and their seeds counted. Up to nine months elapsed between collection of the first and last pods, depending on inflorescence size.

Because the density of pods and their average seed set varied systematically within inflorescences (Young, 1990), it was necessary to weight mean seed set per pod by the number of pods in each 10 cm vertical interval on each inflorescence. After subsampling was complete, the total number of pods in each 10 cm interval was counted. The mean number of seeds per pod in each 10 cm interval was multiplied by the total number of pods in that interval, and the seed set estimates summed over all intervals to estimate the total number of seeds produced by each inflorescence. Differences in pod density within inflorescences were not due to pod abortion, but to the initial spacing of pods. On each *L. telekii* inflorescence, seed counts were made for 18–49 (mean = 28) pods; on each *L. keniensis* inflorescence, seeds counts were made for 11–27 (mean = 15) pods. A total of over 100 000 seeds were counted.

To estimate wet and dry reproductive biomass, five inflorescences of each species were weighed in the field. Care was taken to select inflorescences at similar reproductive stages, because inflorescences dry out with age. Subsamples of 100–200 g were cut from halfway up different sized inflorescences, weighed, dried at 95° C for 24 h, and weighed again.

Results

The results are summarized in Table 2. Spatial variation in percentage vegetation cover is strongly positively correlated with dry season soil moisture in the upper Teleki Valley on Mount Kenya ($r = 0.86$, $N = 18$, $p < 0.001$, Young, 1990). The amount and availability of most mineral nutrients also increased along this gradient. Comparative demographic data from wet and dry sites in wet and dry seasons imply that soil moisture was the key resource for Mount Kenya *Lobelia*, but that in any case the gradient from drier, less-vegetated sites to wetter, more-vegetated sites was one of increasing resource availability (Young, 1984). Because percentage vegetation cover changed little throughout the sampling period, it was possible to use it as an estimate of location of populations along the soil moisture gradient.

The response of each species to the soil moisture gradient with respect to mean inflorescence length and mean number of rosettes per reproductive plant is shown in Fig. 3. All *L. telekii*

Table 2. Ecological, life history, demographic and reproductive traits of *Lobelia telekii* and *Lobelia keniensis* on Mount Kenya.

Trait	<i>Lobelia telekii</i>	<i>Lobelia keniensis</i>
Life history	Semelparous (monocarpic)	Iteroparous (polycarpic)
Habitat	Dry rocky slopes	Moist valley bottoms
Growth form	Unbranched	Branched
Reproductive output	Larger inflorescences, more seeds.	Smaller inflorescences, fewer seeds.
Variation in inflorescence size	Highly variable, increases with soil moisture.	Relatively invariable, independent of soil moisture.
Demography	Virtually no adult survivorship.	Populations in drier sites have lower adult survivorship and less frequent reproduction.
Variation in number of seeds per pod	Strongly positively correlated with inflorescence size.	Independent of inflorescence size, positively correlated with number of rosettes.
Effects of pollinators	Increased seed quality, but not seed quantity.	Increased seed quality, but not seed quantity.

plants in this survey were unbranched and mean inflorescence length was significantly positively correlated with percentage vegetation cover ($r = 0.68$, $N = 18$, $p < 0.001$). In contrast, *L. keniensis* mean inflorescence length was essentially constant across this gradient ($r = 0.05$, $N = 13$, $p > 0.40$). However, the mean number of vegetative rosettes per reproductive *L. keniensis* plant was significantly positively correlated with percentage vegetation cover ($r = 0.70$, $N = 13$, $p < 0.01$). Less than 1% of the reproductive *L. keniensis* plants had more than one inflorescence at the time of this survey.

Mean inflorescence length was significantly greater across all sites in *L. telekii*, the semelparous species, than in *L. keniensis*, the iteroparous species (129 ± 7 cm vs 54 ± 2 cm, $p < 0.001$). These interspecific differences in life history, growth form, and inflorescence size exist even in sites where *L. telekii* and *L. keniensis* occur together.

Inflorescence length was a good predictor of both wet and dry reproductive biomass in both species. Total wet biomass of an inflorescence was strongly positively correlated with its length (*L. telekii*, $r = 0.98$, $N = 5$, $p < 0.01$; *L. keniensis*, $r = 0.96$, $N = 5$, $p < 0.01$). The ratio of dry biomass to wet biomass was relatively constant for each species (*L. telekii*, $D/W = 0.130 \pm 0.016$, SD; *L. keniensis*, $D/W = 0.112 \pm 0.004$).

The number of seeds per pod ranged from zero to 700 in *L. telekii* and from zero to 1400 in *L. keniensis*. The total estimated seed crops for the surveyed inflorescences are shown in Table 3. Estimated seed crops for *L. telekii* ranged from zero to 1.3 million, depending on inflorescence size ($r = 0.92$, $N = 11$, $p < 0.01$). Estimated total seed crops in *L. keniensis* ranged from 43 000 to 450 000 and were also correlated with inflorescence size ($r = 0.59$, $N = 7$, $p < 0.05$).

The total number of pods on an inflorescence was a simple linear function of inflorescence length (*L. telekii*, $r = 0.99$, $N = 11$, $p < 0.001$; *L. keniensis*, $r = 0.98$, $n = 7$, $p < 0.01$). Therefore, any variation in total seed set not explained by linear function of inflorescence size was due to variation in the mean number of seeds per pod. In *L. telekii*, the mean number of seeds per pod was strongly positively correlated with inflorescence size ($r = 0.90$, $N = 11$, $p < 0.01$). Taller *L. telekii* inflorescences (which tended to occur in wetter sites) produced more seeds per pod than shorter inflorescences (which tended to occur in drier sites). Therefore total seed set

Table 3. Fecundity estimates for individuals of *Lobelia telekii* (L.t.) and *Lobelia keniensis* (L.k.).

	Inflorescence length (cm)	Estimated dry biomass (g)	Number of seeds per pod	Number of pods	Estimated seed set	Vegetative rosette number
L.t.	10	32	0	0	0	
L.t.	15	49	0	50	0	
L.t.	90	593	138	1890	261 000	
L.t.	93	613	185	2026	375 000	
L.t.	110	725	145	2210	331 000	
L.t.	115	758	229	2189	501 000	
L.t.	120	791	233	2024	472 000	
L.t.	125	824	276	2431	671 000	
L.t.	145	956	212	2427	514 000	
L.t.	202	1331	237	3607	867 000	
L.t.	202	1331	360	3686	1 327 000	
L.k.	17	38	381	113	43 000	5
L.k.	50	198	265	403	110 000	7
L.k.	64	254	792	568	450 000	11
L.k.	65	258	375	422	157 000	*
L.k.	65	258	595	516	307 000	10
L.k.	72	285	477	588	280 000	6
L.k.	72	285	400	559	224 000	5

* There were several clones in one clump; it was not possible to count the number of rosettes.

in semelparous *L. telekii* was an ever-increasing (concave) function of inflorescence size (cf. Fig. 1). In *L. telekii*, a doubling of inflorescence size was associated with a four-fold increase in seed set.

In *L. keniensis* there was no significant relationship between inflorescence size and the average number of seeds per pod ($r = 0.32$, $N = 7$, $p > 0.40$), indicating a simple linear relationship between inflorescence size and seed set. However, the average number of seeds per pod in *L. keniensis* was positively correlated with the number of rosettes per plant ($r = 0.81$, $N = 6$, $p < 0.05$). *Lobelia keniensis* plants with more rosettes (which tended to occur in wetter sites) produced more seeds per pod than plants with fewer rosettes (which tended to occur in drier sites).

I calculated mean adult survivorship and the mean number of years between reproductive episodes for *L. keniensis* populations in two sites from eight years of demographic data. Mean annual survivorship was calculated as the eighth root of total survivorship (proportion of the population surviving eight years). In the wetter site, nine out of 97 adult plants died between 1978 and 1986, for a mean annual survivorship of 0.988. In the drier site, 12 out of 98 adult plants died over the same interval, for a mean annual survivorship of 0.984. In the outlying (very dry) site, three out of 30 adults died over a three and a half year period, for a mean annual survivorship of 0.972.

The frequency of flowering per rosette was independent of the number of rosettes per plant in both long-term sites (Table 4). Because rosettes flowered less frequently and there were fewer rosettes per plant in the drier site than in the wetter site, the estimated number of years between reproductive episodes was greater in the dry site, 13.9 yr, than in the wet site, 7.2 yr (Table 4). In the outlying site, I estimated a mean of 16 years between reproductive episodes. Therefore

Table 4. The number of inflorescences produced over an eight year period (1978–1986) by *Lobelia keniensis* plants with different numbers of rosettes, in wetter and drier sites.

Number of rosettes	WETTER SITE			DRIER SITE		
	<i>N</i>	<i>I</i>	<i>I/R</i>	<i>N</i>	<i>I</i>	<i>I/R</i>
2	26	15	0.29	13	5	0.19
3	12	6	0.17	16	5	0.10
4	14	11	0.20	17	10	0.15
5	7	4	0.11	17	10	0.12
6	6	7	0.19	6	3	0.08
7	5	4	0.11	9	2	0.03
8	1	1	0.12	2	2	0.12
9	2	3	0.17	3	4	0.15
10	4	4	0.10	2	2	0.10
11	3	4	0.12	1	1	0.09
12	2	4	0.17			
13	4	6	0.12	1	2	0.15
15	1	3	0.20			
Total <i>I/R</i>			0.164			0.111
Mean number of rosettes per plant \pm 95% conf. (from Young, 1984)		6.0 \pm 0.8		5.2 \pm 0.6		
Mean number of years between flowering		8.1		13.9		

N = number of plants, *I* = number of inflorescences produced, and *I/R* is the number of inflorescences produced per rosette.

survivorship between reproductive episodes (P^Z) was 0.966 in the wetter site, 0.878 in the drier site, and 0.64 in the outlying site. Both adult survivorship and frequency of reproduction decreased with decreasing soil moisture.

Discussion

In semelparous plants, all of the transferable resources of the individual can be devoted to reproduction, withholding little or nothing for the maintenance of vegetative structures. As a result, semelparous *L. telekii* exhibits greater reproductive output per flowering episode than its iteroparous relative, *L. keniensis*. Along a gradient from low to high soil moisture, semelparous *L. telekii* produces larger inflorescences. This pattern is similar to that of another long-lived semelparous rosette plant, *Yucca whipplei*, where inflorescences are larger in moister sites (Udovic, 1981).

In *L. keniensis*, inflorescence size does not increase with increasing soil moisture, but the number of rosettes per plant does. The number of rosettes per *L. keniensis* plant is proportional to the number of inflorescences produced through time (Table 4). Therefore as resource availability increased along a natural gradient, iteroparous *L. keniensis* plants kept reproductive output per episode constant, but flowered more frequently. Similarly, in a study of annual and perennial *Sesbania* species, reproductive output per episode was shown to be more variable and

more sensitive to resource availability in the semelparous species than in the iteroparous species (Marshall *et al.*, 1985). This is because semelparous plants have fewer options in response to increased resource availability. Where iteroparous species are able to divert some resources at the time of flowering to future growth and reproduction, semelparous plants put all available resources into flowering (see Van Andel and Vera, 1977). Resource allocation in 'weedy' and 'non-weedy' forms of *Antennaria parlinii* also show these patterns (Michaels and Bazzaz, 1989).

Reproductive effort model

In Mount Kenya *Lobelias*, seed set per pod was positively correlated with inflorescence size in the semelparous species, but not in the iteroparous species. Similarly, in 'semelparous' *Yucca* and *Agave* species, the percentage of fruits that matured was positively correlated with inflorescence size, whereas in the iteroparous species, the percentage of fruit set was independent of inflorescence size (Schaffer and Schaffer, 1977, 1979). As Schaffer and Schaffer point out, if these patterns are driven by external causes that are influenced by inflorescence size itself, they could represent an important force in life-history evolution (as outlined in the introduction to this paper).

If pollinators limit seed set, differential pollinator behaviour could produce these patterns. However, experimental studies carried out in 1979–1980 showed that seed set was not pollinator limited in Mount Kenya *Lobelia* species (Young, 1982). Therefore, pollinator behaviour did not explain differences in seed set among *Lobelia* inflorescences. Although pollinator visitation did increase *Lobelia* seed germination rates (Young, 1982), there were no significant correlations between inflorescence size and seed germination rates in either *L. telekii* or *L. keniensis* (Young, 1990). Therefore, I have not been able to implicate pollinator behaviour (or the reproductive effort model) as a causal factor in the evolution of semelparity in *Lobelia telekii*.

The differences in patterns of reproductive success in Mount Kenya *Lobelia* species do not reveal an underlying set of selective forces favouring either semelparity or iteroparity, but rather these differences are likely to be the result of the observed life-history differences. In semelparous *L. telekii*, taller inflorescences were found in moister sites and taller inflorescences had more seeds per pod. In iteroparous *L. keniensis*, inflorescence size was independent of both soil moisture and relative seed set. However, *L. keniensis* plants with more rosettes were found in moister sites and produce more seeds per pod than plants with fewer rosettes. Therefore, seed set in Mount Kenya *Lobelias* was apparently resource limited. This resource limitation was expressed as reproductive success related to inflorescence size in the semelparous species, and as reproductive success related to clone size in the iteroparous species because of the different ways that these two species respond to an environmental resource gradient (Table 2).

A demographic explanation for the evolution of semelparity in Mount Kenya lobelias

Several mathematical models quantify, for particular combinations of demographic parameters, the relative increase in fecundity that must be associated with an evolutionary switch from iteroparity to semelparity in order for semelparity to be favoured (Fig. 2). I will use a model (Young, 1981; Equation 3a in Fig. 2) that allows for variation in the frequency of iteroparous reproduction, because *Lobelia keniensis* does not flower every year and, as I have shown above, its flowering frequency is correlated with the key environmental gradient (soil moisture) separating the two *Lobelia* species on Mount Kenya. This model assumes similar pre-reproductive development times for the semelparous and iteroparous life histories. Demographic data indicate that this is a reasonable assumption for Mount Kenya *Lobelias* (Young, 1984, 1990).

The model may be simplified by assuming that long-term population sizes are stable ($\lambda = 1.0$)

and that the clonal iteroparous species experiences no senescence ($x \rightarrow \infty$). Both of these assumptions are reasonable; these populations are in relatively stable alpine communities, and eight years of demographic data do not indicate any pattern of senescence in these clonal plants. In addition, the results reported below are relatively robust against relaxation of these assumptions. For example, if the iteroparous *Lobelia* populations increase by 50% each generation, or if there is senescence after only ten reproductive episodes, the relationship modelled here changes by less than 10%.

The model, thus simplified, becomes:

$$\frac{B_S}{B_I} = \frac{1}{1 - P^Z} \quad \text{(Equation 3b in Fig. 2)}$$

where B_S = the fecundity of the semelparous life history,
 B_I = the fecundity of the iteroparous life history,
 P = mean yearly adult survivorship (iteroparous),
 Z = mean number of years between reproductive episodes (iteroparous life history), and therefore
 P^Z = the mean survivorship between reproductive episodes.

This model can be applied equally to systems with short-lived (annual and biennial) or long-lived semelparous species. For an iteroparous genotype in an environment where it experiences an average survivorship between reproductive episodes equal to P^Z , this equation quantifies how

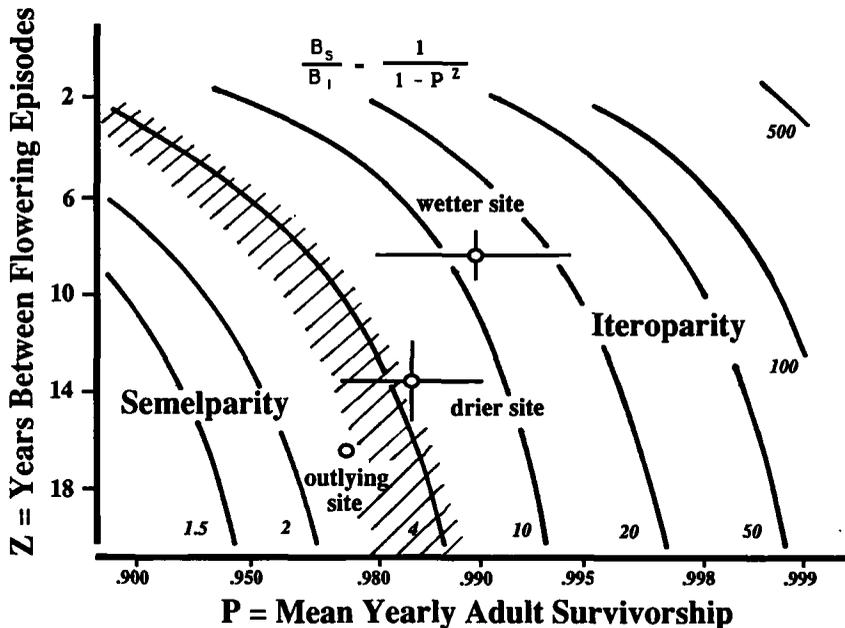


Figure 4. Demographic location of the three *Lobelia keniensis* populations monitored on Mount Kenya, relative to the putative evolutionary boundary between semelparity and iteroparity in this system. See text for details. Bars represent 95% confidence limits. Differences in mean annual survivorship between the upper two populations were not significant ($p \sim 0.30$), but did contribute to significant ($p < 0.001$) overall differences between these populations. Due to small sample size ($n = 30$), and short survey period (three and a half years), I did not estimate confidence limits for the outlying population.

great an increase in fecundity (B_S/B_I) must be associated with an evolutionary switch to semelparity to overcome the loss of future reproduction. If the actual increase in fecundity associated with a switch to semelparity is greater than the value of $1/1-P^Z$ in a given environment, then the evolution of semelparity will be favoured. If it is less, iteroparity will be favoured. I have previously suggested that differences in adult survivorship and frequency of reproduction may hold the key to life-history evolution in Mount Kenya *Lobelias* (Young, 1981, 1984). Only now do I have demographic data on these long-lived plants covering a long enough time to test this prediction. The years 1979–1986 on Mount Kenya were representative of the great year to year variation in rainfall that characterizes East Africa; since records began in 1932, only 1939 was drier (as measured by river flow) than 1980, and only 1961 and 1968 were wetter than 1977 (Leibengut, 1986).

A graphical presentation of this demographic model appears in Fig. 4. Each solid-curved line is an isocline representing all combinations of adult survivorship (P) and years between reproductive episodes (Z) that produce a given value of B_S/B_I . As adult survivorship and frequency of reproduction decrease, the increase in fecundity associated with semelparity needed to overcome the loss of future reproduction also decreases, and it becomes increasingly likely that semelparity will evolve.

To evaluate this model in the present case, it is first necessary to estimate how great an increase in fecundity is expected to be associated with a switch from iteroparity to semelparity in Mount Kenya *Lobelias*. I have estimated the expected reproductive output per episode of the two species near the ecological species boundary. By using the measured relationships between inflorescence size, clone size, location along the environmental gradient, and seed set for both species, I produced two estimates of B_S/B_I (Table 5). I estimate that at their ecological boundary, semelparous *L. telekii* produces 3–4 times as many seeds and 4–5 times as massive an inflorescence as does iteroparous *L. keniensis*. Given that these two species have diverged both morphologically and physiologically in their different habitats, it may be more appropriate to compare the more basic currency of reproductive output (grams reproductive biomass) than to compare how each of these species convert that output into seeds. In any case, I think it likely that the expected increase in fecundity associated with semelparity in Mount Kenya *Lobelias* is three- to fivefold, over iteroparity (cf. Table 1).

The hatched portion of Fig. 4 represents B_S/B_I values of 3–5. The model therefore predicts that in *Lobelia* populations experiencing demographic conditions placing them above and to the right of this area, iteroparity will be favoured because a semelparous life history will not produce an increase in fecundity great enough to offset the loss of future reproduction. However, in those populations experiencing demographic conditions placing them below and to the left of the shaded area, the likelihood of future reproduction is low enough that a three- to fivefold increase in present fecundity results in greater reproductive success, even though it means forfeiting future reproduction. Therefore, it is appropriate to think of the hatched area in Fig. 4 as an evolutionary boundary between semelparity and iteroparity in Mount Kenya *Lobelias*.

Table 5. Mean reproductive output near species boundary

	<i>Lobelia telekii</i>	<i>Lobelia keniensis</i>	$\frac{B_S}{B_I}$
Inflorescence dry weight (g)	990–1120	180–260	3.8–6.3 (4–5)
Seeds per inflorescence	600 000–800 000	150 000–250 000	2.4–5.3 (3–4)

I cannot examine variation in adult survivorship or frequency of reproduction in *L. telekii* because it has already evolved semelparity. However, I can examine how these parameters vary among iteroparous populations of *L. keniensis* located different distances along the environmental gradient from the ecological boundary between the two species.

I have eight years of demographic data for two *L. keniensis* populations. These populations have been plotted in Fig. 4, based on their mean values of adult survivorship and frequency of reproduction. Their locations along the environmental gradient are shown in Fig. 3. In the wetter sites, with higher survivorship and more frequent reproduction, the model predicts that the evolution of semelparity would be favoured if it could produce a thirteenfold increase in fecundity. This is far higher than can be achieved, and so in this environment the model predicts that iteroparity will continue to be favoured. In the drier population, adult survivorship is lower and reproduction per individual is less frequent, so semelparity would be favoured if it could produce only five times the output of the iteroparous life history. This is at the upper limit of the attainable increase in fecundity that is estimated to be associated with a switch to semelparity.

Three and a half years of data from the outlying (very dry) *L. keniensis* population (Fig. 4) indicate that adult survivorship and frequency of reproduction are even less than in the dry population. A switch to semelparity in this site would be favoured if less than a threefold increase in fecundity would result, a likely possibility for Mount Kenya lobelias. This population is located beyond the normal range of *L. keniensis* in a drier habitat within the ecological range of *L. telekii*.

Therefore, as we examine iteroparous *L. keniensis* populations nearer and nearer the ecological boundary between the two *Lobelia* species, we also approach the evolutionary boundary between iteroparity and semelparity as described by the demographic model. I suggest that this simple mathematical model accurately describes the demographic conditions that have favoured differential life-history evolution in Mount Kenya *Lobelias*.

Semelparity in *L. telekii* has been favoured by natural selection in those severe habitats where future reproduction is so unlikely that putting all resources into first reproduction is the most productive evolutionary strategy. Many other long-lived semelparous rosette plants also live in severe habitats, such as in tropical alpine areas (Andean *Puya*, *Draba* and *Espeletia*, Hawaiian *Argyroxiphium*, and Canary Island *Echium*), in subalpine areas (New Guinea *Harmsioplanax*, North American *Frasera* and *Hymenoxys*, and Hawaiian *Lobelia*), in deserts (New World *Yucca* and *Agave*), and as epiphytes (neotropical *Tillandsia*). It remains to be seen whether the present model also applies to these species. I suspect that this kind of demographic approach will also apply to the evolution of semelparity in annuals and biennials.

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