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BIRD VISITATION, SEED-SET, AND GERMINATION RATES IN TWO SPECIES OF LOBELIA ON MOUNT KENYA¹

Truman P. Young²

Seed-set in natural plant populations may be limited by pollinators, resources, or seed predators. Bierzychudek (1981) found pollinator numerical limitation of seed-set to be common in natural populations. However, many plant species are capable of self-pollination when pollinators are absent (Proctor and Yeo 1973); in others natural levels of outcrossing are sufficient for full seed-set, and seed-set appears to be resource limited (Primack and Lloyd 1980, Udovic 1981, Udovic and Aker 1981). In most pollination studies of natural plant populations, numerical seed-set is the only measure of reproductive success, although recent studies have shown that other factors such as seed size, germination rates, and seedling success may be affected by the degree of outcrossing (Price and Waser 1979, Schoen 1982). Such effects have long been known for crop plants (Crumpacker 1967). This paper reports an attempt to determine the importance of pollinators for the seed production of two species of *Lobelia* on Mount Kenya.

Two species of rosette plants in the genus *Lobelia* (family Lobeliaceae) occur in the alpine zone of Mount Kenya. *L. telekii* is primarily semelparous, and *L. keniensis* is primarily iteroparous. These two species are thought to be bird pollinated (Hedberg 1964). The morphology of the reproductive structures is such that birds, but no native insects, normally come into contact with the pollen source (T. P. Young, *personal observation*). The cylindrical inflorescences project above the surrounding vegetation, and the purple flowers secrete copious nectar. *L. telekii* has narrow, hairy bracts and is visited primarily by territorial individuals of the Scarlet-tufted Malachite Sunbird (*Nectarinia*

johnstonii). *L. keniensis* has broad glabrous bracts, and is visited by a variety of birds, including *N. johnstonii*, the Mountain Chat (*Pinarchroa sordida*), and the Slender-billed Chestnut-winged Starling (*Onag-nathus tenuirostris*).

The tall terminal inflorescences mature progressively upwards from the base. The five petals are united and open between the upper two petals to form a lower-lipped flower (Fig. 1). The style is enclosed by a tube formed of the five united filaments and anthers. This tube terminates in a brush that acts as a block to pollen release. Dehisced pollen collects inside the distal end of the filament tube. When the brush is pushed back by the forehead of a visiting bird, pollen is released. I have observed white pollen on the foreheads of *P. sordida* and *O. tenuirostris* visiting *L. keniensis* flowers. The male state of the flowers lasts up to 2 wk. The style lengthens during this time, and is finally exerted from the filament tube. The stigmas separate and become receptive several days later, and begin to dry up after 2–4 wk. Seeds develop in a pair of inferior ovaries and are wind dispersed over a period of many weeks. The time from the first appearance of the flowers to final dispersal of seeds is ≈12–18 mo, depending

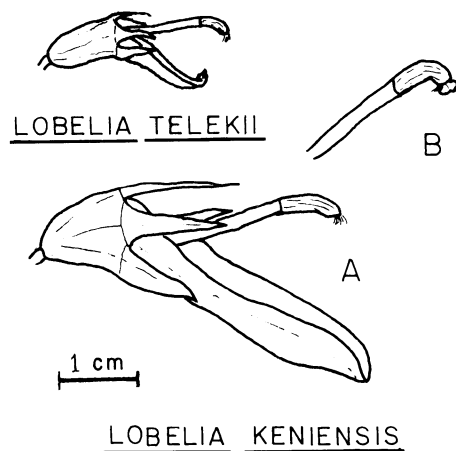


FIG. 1. The flowers of *L. telekii* and *L. keniensis*. *L. keniensis* filament tube shown in the male state with pollen brush (A), and in the female state with exposed receptive stigma (B).

on inflorescence size. Predispersal seed predation is apparently limited to damage by hyrax (*Procavia capensis mackinderi*), a small mammal that eats entire flowers and pods of *L. telekii* (T. P. Young, *personal observation*).

Methods

In March 1979, I selected 10 pairs of plants of each species in which the inflorescences had just begun to appear from the central leaf bud. I selected pairs for similar habitat and rosette size. Cylindrical cages of 2.5-cm (one-inch) wire mesh were placed over one randomly selected inflorescence of each pair. Approximately 20 h of observation showed that these cages exclude all birds. Of the 40 inflorescences, 8 were blown down by high winds before the experiment was complete.

From March to September the following manipulations were carried out on certain flowers of each inflorescence on both caged and uncaged plants:

- 1) flowers were emasculated, and no pollen transfers made;
- 2) flowers were emasculated, and pollen from the same inflorescence was applied later by hand when the stigmas were receptive (from younger flowers higher on the inflorescence);
- 3) flowers were emasculated, and pollen from a different plant was applied later;
- 4) pollen from the same inflorescence was applied to the stigmas of intact flowers; and
- 5) pollen from a different plant was applied to the stigmas of intact flowers.

Treatments 1–5 were carried out on groups of five flowers at each of four compass directions around the inflorescence, and at two to three different heights. The relative orientation of the treatments was randomized within each group of five flowers. In all, ≈ 1000 flowers were manipulated. A sixth treatment class was represented by the hundreds of unmanipulated flowers on each inflorescence.

Emasculations were done before each flower opened. The upper two petals were separated, and the filament tube removed from around the style. Both the male and the female structures of the flower were immature at this stage. Emasculations did not visibly damage styles or stigmas. Artificial pollination was done by collecting pollen and depositing it by hand in a manner similar to that presumed for birds, with the back of the finger simulating a bird's forehead. Flowers were visited every 2–4 wk. Visual inspection of the stigmas indicated that caging prevented visible pollen deposition, and that artificial pollination greatly increased the amount of pollen on the stigmas, when compared to uncaged flowers that were not hand pollinated. This

increased pollen load will be referred to as overpollination.

As the pods matured from October 1979 to May 1980, they were collected before they could dehisce, stored, and counted. Pods of unmanipulated flowers were subsampled throughout each inflorescence. Flowers in which stigmas had desiccated or were damaged before pollen application could be carried out were rejected.

For each treatment combination, the mean number or seeds per pod was calculated for each inflorescence. Data were log transformed, making the variances homogeneous. Analysis of variance was carried out.

In July 1980, seeds from several caged and uncaged inflorescences were collected. All the seeds from each of these two treatments were pooled, and divided into three sets of 100 seeds each. The 12 sets (6 for each species) were placed on moist filter paper in individual Petri dishes, kept at 25°C, and counted as they germinated over a period of 4 wk. Since pods for the other treatments (1–5) were limited and collected only prior to dehiscence, no germination tests were done on them. The germination rates of seeds from caged and uncaged inflorescences of both species had small variances, and were compared with a *t* test.

Results

The results of the seed counts for the 12 treatment combinations in each species are shown in Fig. 2. Approximately 270 000 seeds were counted from 1200 pods. The results of a statistical analysis of the various effects are shown in Table 1.

Lobelia telekii. There were no differences in seed-set among the different emasculations treatments. Three-way analysis of variance showed that emasculations greatly reduced seed-set, regardless of other treatment ($F_{2,80} = 24.09$, $P < .001$). Two-way analysis of variance on intact flowers showed a significant interaction between caging and overpollination ($F_{2,40} = 5.43$, $P < .01$). Intact flowers that were both experimentally overpollinated and exposed to bird visitation (uncaged, treatments B and C) had significantly reduced seed-set when compared to intact flowers subjected to birds alone (uncaged, treatment A), overpollination alone (caged, treatments B and C), or neither (caged, treatment A).

The effect of caging alone was tested by comparing intact, untreated flowers from caged and uncaged inflorescences. The effect of overpollination was tested by comparing all three pollen treatments from intact flowers on caged inflorescences. Neither caging alone nor overpollination alone had a significant effect on seed-set (Table 1).

Lobelia keniensis. The results for *L. keniensis* par-

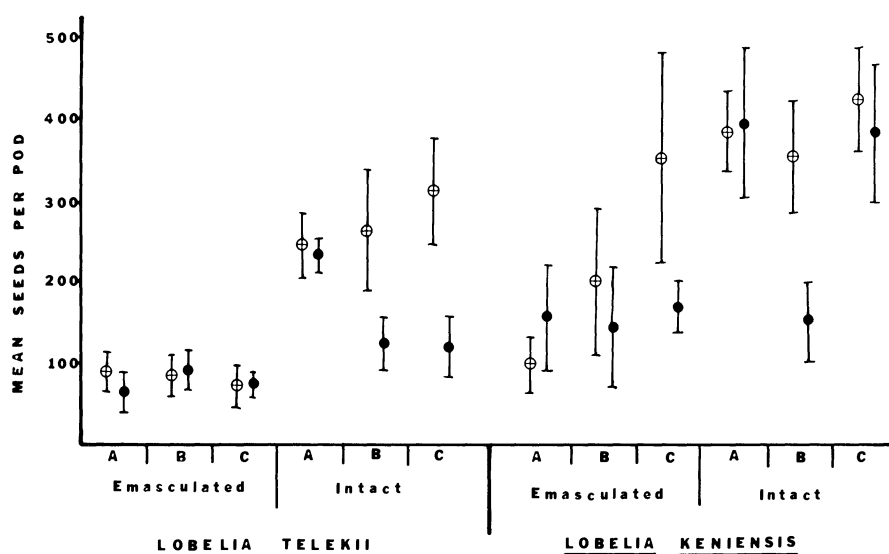


FIG. 2. Mean seed-set (\pm one standard error, calculated from untransformed data) for treatments on flowers of *L. telekii* and *L. keniensis*. \oplus are from caged inflorescences, and \bullet are from uncaged inflorescences. Pollen treatments were: A = no artificial pollination; B = pollen applied from the same inflorescence; C = pollen applied from a different plant.

allel those for *L. telekii* (Fig. 2 and Table 1). Emasculation significantly reduced seed-set, regardless of other treatments. However, emasculated flowers which were both caged and hand pollinated had greater seed-set than other emasculated treatments, with numbers approaching those of unemasculated flowers (Fig. 2). The interaction between caging and overpollination can be seen for both emasculated and intact flowers, although neither is significant. Again, caging alone or overpollination alone had no significant effect on seed-set (Table 1).

The result of the germination tests are shown in Table 2. Caging significantly reduced germination rates of seeds for both species. This reduction amounted to 48% in *L. telekii* and 31% in *L. keniensis*. Ninety percent of the seeds that germinated did so in the first 2 wks.

Discussion

Exclosure and overpollination experiments test the importance of pollen vectors in different ways. Exclosure experiments test whether the particular pollen vectors excluded are necessary for full seed-set (or maximal seed quality). Overpollination experiments test to what extent the pollen vectors present are sufficient. The caging data for Mount Kenya *Lobelia* spp. indicate that bird visitation was not necessary for flowers to produce normal seed numbers in 1979–1980. Since overpollinated flowers did not produce more seeds than naturally pollinated flowers, the natural

levels of pollination by bird or other vectors (even self-pollination) were sufficient for full seed production. However, bird visitation had a strong positive influence on the germination rates of the seeds produced by both species.

The data from *L. keniensis* imply that self-pollination occurs when major pollinators are absent. In caged inflorescences, artificially pollinated emasculated flowers produced more seeds than did emasculated flowers that were not pollinated. However, a low level of seed-set occurs in emasculated flowers of both species for which birds and artificial pollen sources

TABLE 1. Results of analysis of variance on the mean number of seeds per pod. Three-way ANOVA indicated strong emasculation effects, and two-way ANOVA on intact flowers showed an interaction between caging and overpollination. The effect of caging alone was tested by comparing unmanipulated flowers only on caged and open inflorescences. The effect of overpollination was tested by comparing all three pollen treatments on caged, intact flowers.

Treatment	<i>Lobelia telekii</i>	<i>Lobelia keniensis</i>
Emasculation	$F_{1,80} = 24.09^{***}$	$F_{1,81} = 22.02^{***}$
Caging	$F_{1,15} = 0.02$ (NS)	$F_{1,11} = 0.25$ (NS)
Overpollination	$F_{2,22} = 0.43$ (NS)	$F_{2,23} = 0.45$ (NS)
Caging \times overpollination	$F_{2,40} = 5.43^{**}$	$F_{2,39} = 1.96$ (NS)

** $P < .01$.

*** $P < .001$.

NS = not significant.

TABLE 2. Percent germination of seeds of unmanipulated flowers from caged and uncaged inflorescences, \pm one standard error. $N = 3$ for all samples. Compared by a t test.

Species	Uncaged	Caged	P	% Reduction
<i>L. telekii</i>	63.0 \pm 3.0	33.0 \pm 3.2	<.001	48
<i>L. keniensis</i>	89.3 \pm 2.7	61.8 \pm 2.7	<.001	31

were unavailable. This implies either a low level of pollen movement by vectors other than birds, such as wind or insects, or some capacity for apomixis.

The seed-set results were complicated by two experimental effects. First, emasculation greatly reduced seed-set, regardless of subsequent pollen treatment. This reduction of seed-set in emasculated flowers may have been due to desiccation of the exposed styles. The filament tube normally protects most of the style throughout its development, even after the anthers have fully dehisced their pollen. Relative humidity in the alpine zone of Mount Kenya may drop to as low as 15%. The stigmas of emasculated flowers develop more quickly and dried up sooner than stigmas on unemasculated flowers (T. P. Young, *personal observation*). Emasculation of flowers may have had less of an effect in *L. keniensis* than in *L. telekii* because *L. keniensis* is found in moister sites than is *L. telekii* (Young 1981), and therefore may be under less drought stress.

Second, an interaction between bird visitation and overpollination significantly reduced seed-set. I can think of no satisfactory explanation for this. One possibility is that birds, taking advantage of an unusually high abundance of pollen, damage overpollinated stigmas by feeding on them. Pollen has been found in the stomach of a *Nectarinia johnstonii* individual (Williams 1951), and pollen-eating birds can damage female flower parts to the point of floral abortion (Grant and Grant 1981). As stated earlier, densities of pollen on overpollinated stigmas were noticeably higher than on natural stigmas pollinated by birds alone. These increased densities of pollen may encourage feeding at stigmas by birds. Of course, there may be other explanations for this phenomenon. The data of Waser (1978), of Stephenson (1979), and of Willson et al. (1979) all apparently indicate a reduction of seed-set or fruit-set associated with hand pollination, but none discusses it (see Bierzychudek 1981).

Although bird visitation had no effect on seed numbers, it significantly increased the proportion of seeds that germinated under the conditions described in the Methods. Caging may have affected seed viability, seed dormancy (Schoen 1982), or both. Numerical seed-set is probably resource (water) limited in Mount Kenya

Lobelia spp. (Young 1981), and the primary significance of pollen transferred by birds may be that it affects the germination rates of their seeds.

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