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An exception to Darwin's syndrome: floral position, protogyny, and insect visitation in *Besseyia bullii* (Scrophulariaceae)

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Abstract Darwin pointed out that plants with vertical inflorescences are likely to be outcrossed if the inflorescence is acropetalous (flowers from the bottom up), the flowers are protandrous (pollen is dispersed before stigmas are receptive), and pollinators move upward on the inflorescence. This syndrome is common in species pollinated by bees and flies, and very few exceptions are known. We investigated flowering phenology and pollinator behavior in *Besseyia bullii* (Scrophulariaceae) and found that it did not fit Darwin's syndrome. The vertical inflorescence was acropetalous but the flowers were distinctly protogynous, so flowers with newly receptive stigmas appeared on the inflorescence above those with dehiscing anthers. A number of small insects visited *B. bullii*; bees in the family Halictidae (*Augochlorella striata* and *Dialictus* spp.) were most common. When insects moved between gender phases within inflorescences, they moved up more often than down (61% versus 39% of observations, respectively) but this difference was only marginally significant. Most visits were to male-phase flowers only, and this preference was more pronounced for pollen-foraging insects than for nectar-foraging insects. *B. bullii* was self-compatible, so its flowering characteristics potentially could result in considerable self-pollination. However, an average of 38% of the lowermost flowers opened before

any pollen was available on the same inflorescence; these "solo females" had a high probability of outcrossing (though fruit set was relatively low in the bottom portion of the inflorescence). Upper flowers may also be outcrossed because downward insect movement was not uncommon. Therefore protogyny in *B. bullii* may not necessarily lead to more selfing than would protandry.

Key words *Besseyia bullii* · Pollination · Protogyny
 Halictidae · Foraging behavior

Introduction

Based on his observations of "humble-bees" on the orchid *Spiranthes autumnalis* (now called *S. spiralis*), Darwin (1877, first published in 1862) recognized a three-part pollination syndrome:

1. The vertical inflorescence matures from the bottom up (is acropetalous).
2. The individual flowers are protandrous (functionally male before female).
3. The flowers are pollinated by insects that move from the bottom of the inflorescence to the top.

Darwin proposed that this combination of characters would typically result in insects arriving at an inflorescence with pollen, depositing pollen on the female-phase flowers at the base, and picking up more pollen from the male-phase flowers at the top before leaving the inflorescence.

As in other cases of dichogamy (the temporal separation of stigma receptivity and pollen presentation), a possible fitness advantage to Darwin's syndrome in self-compatible species is a high rate of outcrossing. However, the frequent occurrence of dichogamy in self-incompatible species argues for additional explanations

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(Faegri and van der Pijl 1979; Wyatt 1983; Lloyd and Webb 1986; Bertin 1993). A second advantage to dichogamy could be reduced interference between pollen export and receipt within the flower (Lloyd and Webb 1986), for example by reducing the clogging of stigmas by self-pollen (Bawa and Beach 1981; Lloyd and Yates 1982; Wyatt 1983). For both the "increased outcrossing" and the "reduced interference" hypotheses, the fitness advantage of dichogamy is increased when relatively more outcross pollen is deposited on stigmas. Darwin's syndrome appears to be a particularly effective means of achieving this result.

Recent reviews show that Darwin's syndrome is common in diverse angiosperm groups. Bertin and Newman (1993) reviewed the floral characteristics of plants that are pollinated by bees or flies, both of which are thought to move upward on inflorescences; 88.2% of bee- or fly-pollinated species are protandrous, but only 28.2% of species pollinated otherwise are protandrous. In addition, among bee- or fly-pollinated plants, protandry is more common in species with vertical inflorescences than with other types of inflorescence (Bertin and Newman 1993). Lloyd and Webb (1986) report eight genera in seven families that demonstrate Darwin's syndrome; they also point out that the combination of protogyny (flowers female before male) and basipetalous (top down) floral maturation would be functionally the same as Darwin's syndrome, and report one instance of this situation. Lloyd and Webb (1986) conclude that "there are no known cases of the two combinations of dichogamy and floral development that contradict Darwin's hypothesis" (i.e., protogyny with acropetalous development or protandry with basipetalous development).

We investigated the order of floral development and the pattern of insect visitation in inflorescences of *Besseyia bullii* (Eaton) Rydberg (Scrophulariaceae), and report that this species is clearly an exception to Darwin's syndrome: it has a vertical inflorescence that matures from the bottom up, is pollinated by bees, but has protogynous flowers.

Materials and methods

B. bullii is a rosette-forming perennial which usually occurs in prairies and savannas (Curtis 1959; Coffin and Pfannmuller 1988). Flowering occurs in the spring (May in Minnesota), when one or more flowering shoots of 15–40 cm are produced per basal rosette (Holmgren 1986). Each flower has four sepals, an irregular corolla, two stamens, and a single style with a capitate stigma (Holmgren 1986; Hufford 1992; see also Fig. 1). Fruits are dry, dehiscent capsules which contain many seeds (Holmgren 1986).

The current range of *B. bullii* includes only six states of the midwestern US, and it is considered rare in all of these. In Minnesota it is listed as an endangered species. Our study took place on McKnight Prairie (Goodhue County, Minnesota, 44° 30' 04" N, 93° 01' 40" W), a 14-ha prairie remnant which has been managed

by periodic spring burns since its purchase by Carleton College in 1963. McKnight Prairie includes several gravelly ridge-tops where populations of *B. bullii* occur.

Pollination and flowering phenology

In late April 1991, we chose 20 groups of 4 neighboring inflorescences that had not yet begun to flower; if there were multiple inflorescences per basal rosette, one was selected at random. We randomly assigned one member of each group to be (1) bagged and hand-selfed (to determine if *B. bullii* is self-compatible), (2) bagged and hand-outcrossed, (3) measured for floral phenology, and (4) used as an unmanipulated control.

Plants in the hand-pollination treatments were covered with bridal-veil cloth bags before flowering began; a styrofoam cup with most of the sides cut out was placed around each inflorescence within the bag to prevent contact between the bag and the flowers. Except during hand pollination, these inflorescences remained bagged until several days after the last flowers had opened. Plants were self-pollinated every 2–3 days by rubbing a camel-hair paintbrush over dehiscent anthers and then along the exerted stigmas (those visible beyond the petals) of the same inflorescence. Outcrossed plants were pollinated on a similar schedule, usually with pollen from two other plants. During cool or wet days, pollen was sometimes very difficult to obtain and some stigmas undoubtedly were not pollinated. Pollination treatments continued until each inflorescence had completed flowering.

Phenology data were taken from inflorescences every day throughout the flowering period. Daily measurements included the distance from the base of the inflorescence to the uppermost flowers with stigmas exerted and to the uppermost flowers with anthers exerted. The first appearance of female-phase and male-phase flowers on an inflorescence was usually unambiguous, but the end of flowering was sometimes difficult to determine. Generally we considered flowering to be complete when flowers within 3 mm of the top of the inflorescence had opened. Often a few flowers exerted stigmas or anthers after this time, but the number per day was very low.

On 12–13 June, after fruits were mature, inflorescences were collected and the number of flowers and fruits were counted. Any ovary that had expanded was considered a fruit; in most cases the fruits were large and of typical size, but some were smaller. To determine if fruit characteristics varied by position within the inflorescence, control inflorescences were divided into three equal lengths (top, middle, bottom) before counting.

Female-only phase

Because they were protogynous (see Results), the first flowers to open on an inflorescence were receptive before any pollen was available from the same inflorescence. We measured the extent of this female-only phase on 15 plants in 1991 and 17 plants in 1992, chosen haphazardly on the availability of preflowering inflorescences. The number of female-phase flowers was counted daily on each of these plants until the first anthers were exerted. The total number of flowers per inflorescence was counted after flowering was complete.

Insect observations

In May 1992, insect observations were made in a dense patch of flowering *B. bullii* on six clear days at times ranging from late morning to late afternoon. Observers lay down next to the patch to record data; insects seemed to behave normally once we were no longer standing or moving. As we watched, we recorded observations on a hand-held tape recorder for later transcription.

Insects were chosen for observation when they could be seen arriving at an inflorescence near the observer. We used data only from complete observations (i.e., when insects were visible from

arrival to departure); visits that lasted less than 3 s were not counted. The gender phase of the flowers being visited was recorded throughout the observation. If possible, we noted whether the insect was foraging for nectar (as evidenced by it probing deeply into the flower) or pollen (as evidenced by it gathering pollen from the exerted anthers). Insects were identified to morphotype as closely as possible during field observations. Several of the most common insects were collected for identification; nomenclature follows Moure and Hurd (1987).

Statistical analysis

All results are given as mean \pm 1 SE. Parametric statistics were used for most tests, and non-parametric alternatives were used for analysis of fruit set (because variance of percentages often changes with the mean) and insect visitation time (because data were not normally distributed). In the data on floral number and density at different inflorescence positions, the variance increased with the mean. Log transformation solved this problem, but the results were the same for transformed and untransformed data. Hence, only the analysis of untransformed data is given here.

Results

Flowering and fruiting patterns

The flowers of *B. bullii* were distinctly protogynous (Fig. 1; see also Hufford 1992). In the female phase, styles were exerted while anthers remained well hidden within the petals. In the male phase, anthers were exerted and dehiscent, and the styles remained exerted (and therefore may have remained receptive).

The vertical inflorescence consisted of 54.4 ± 2.9 flowers ($n = 54$, range = 12–103 flowers), which opened from the bottom up (acropetally; Fig. 2). At a given position in an inflorescence, anthers were exerted on average about a day later than the styles. As a result, an inflorescence typically had a band of female-phase flowers above a band of male-phase flowers. For individual inflorescences, the average time from the lowest flowers entering female phase to the highest flowers entering male phase was 7.6 ± 0.7 days ($n = 16$, range = 4–14 days). At the population level, flowering in 1991 began before 4 May and was complete by 21 May (Fig. 3). The peak of female flowering occurred before that of males, and many anthers dehiscent after 15 May when there were few newly receptive stigmas available in the population.

Within an inflorescence, the female-only phase averaged 1.81 ± 0.18 days ($n = 32$, range = 0–4 days). Because these first flowers had no access to pollen from the same inflorescence, we designated them "solo females". On average, $38.2 \pm 5.1\%$ of the flowers on an inflorescence were solo females, but this percentage was highly variable in the population (CV = 75.8%, range = 0–100%). The proportion of solo-female flowers was not correlated with the total number of flowers in the inflorescence (Spearman rank correlation, $P > 0.05$).

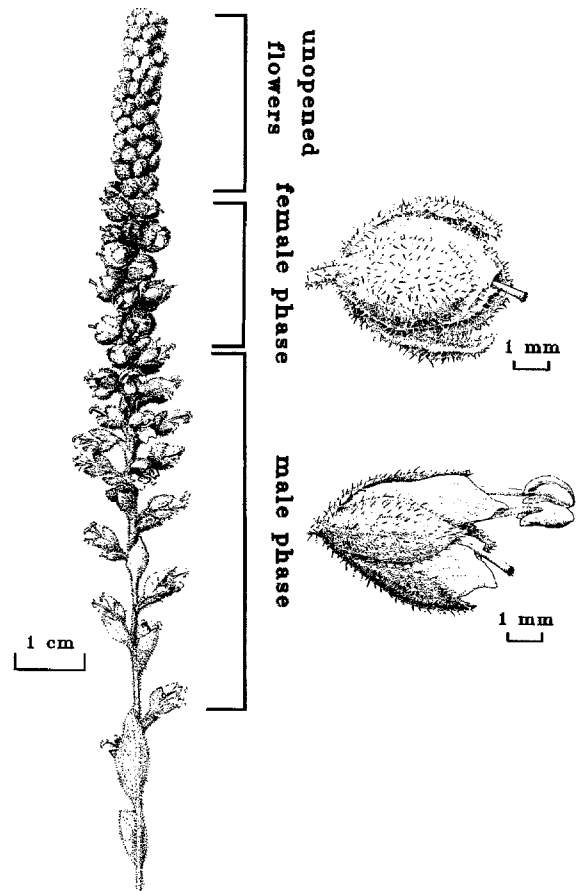


Fig. 1 *Besseyia bullii* inflorescence (left), female-phase flower (upper right), and male-phase flower (lower right). The inflorescence has a region of unopened flowers, of flowers in female phase, and of flowers in the male phase. Flowering is acropetal (i.e., proceeds from the bottom to the top of the inflorescence) and individual flowers are protogynous

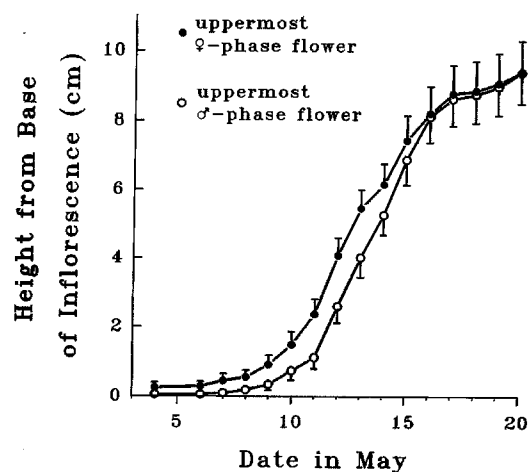


Fig. 2 Progression of female-phase and male-phase flowering within *Besseyia bullii* inflorescences in 1991. Distance from the base of 19 inflorescences was measured daily throughout the flowering period. Standard error bars are shown.

Flowers were progressively more densely packed toward the top of the inflorescence (Table 1; ANOVA,

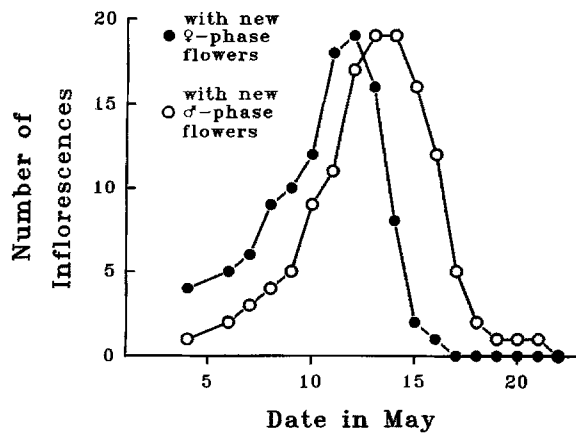


Fig. 3 Flowering phenology of *Besseyia bullii* in 1991 at McKnight Prairie. Twenty inflorescences were visited each day during the flowering period and scored for the presence of newly exerted stigmas or anthers. The last day of flowering was sometimes difficult to determine

$P < 0.001$); floral density in the top third of the inflorescence was 2.8 times greater than in the bottom third. Fruit set was not randomly distributed within the inflorescence (Table 1; Kruskal-Wallis test, $P < 0.001$). There was distinctly lower fruit set in the bottom third of the inflorescence.

Self-compatibility

The pollination treatments had a significant effect on fruit set (Kruskal-Wallis test, $P < 0.001$). There was no difference (nonparametric multiple comparison, $P > 0.50$) in fruit set between hand-selfed ($30.8 \pm 4.7\%$, $n = 20$) and hand-outcrossed inflorescences ($30.7 \pm 5.9\%$, $n = 15$), but fruit set in naturally pollinated inflorescences ($60.0 \pm 4.8\%$, $n = 19$) was significantly greater (nonparametric multiple comparisons, $P < 0.01$) than in either of these hand-pollinated treatments.

Insect behavior

During 1992 we made 261 complete observations (from arrival to departure) of individual insects visiting *B. bullii* inflorescences. There were a variety of insect

Table 1 Flower number, density, and fruit set at different positions within inflorescences of *Besseyia bullii* (mean \pm 1 SE shown, $n = 16$ for each position). Inflorescences were collected after fruits were mature and were divided into three approximately equal lengths for counting. There was a significant position effect on flower number (ANOVA, $P < 0.001$), flower density (ANOVA, $P < 0.001$), and fruit set (Kruskal-Wallis test, $P < 0.001$). Within a column, *supercripts* of different letters designate means that differ significantly ($P < 0.05$) by Tukey test (for flower number and density) or by nonparametric multiple comparison (fruit set)

	Flower number	Flower density/cm	Fruit set (%)
Top	$28.2^a \pm 2.2$	$9.22^a \pm 0.87$	$71.5^a \pm 6.2$
Middle	$19.4^b \pm 1.8$	$5.71^b \pm 0.47$	$66.3^a \pm 6.4$
Bottom	$11.7^c \pm 1.0$	$3.34^c \pm 0.28$	$27.2^b \pm 6.8$

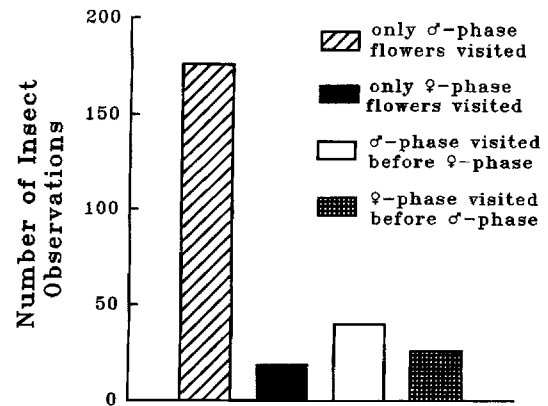


Fig. 4 Insect visitation behavior on *Besseyia bullii* inflorescences in 1992. If more than one gender phase was visited, observations were categorized by the gender phase visited first. Insects moved between gender phases more than once (e.g., male-female-male) in 17 of the 66 visits that included both gender phases. An observation was included only if the insect was visible from its arrival on an inflorescence until its departure

visitors, most of which were small native bees; seven distinct-appearing taxa (based on field observation) were recorded more than ten times. The most common visitors were *Dialictus* spp. (Halictidae; 28% of observations). Species of *Dialictus* were indistinguishable in the field; we collected four distinct species of *Dialictus*, but only *Dialictus vierecki* could be identified to species. Also common were *Augochlorella striata* (Halictidae; 15% of observations) and an unidentified bee (15% of observations). *Augochlorella striata* and most *Dialictus* species are generalist flower visitors, known to visit a large number of species (Mitchell 1960; Moure and Hurd 1987).

Insects visited only male-phase flowers in most (67.4%) visits to an inflorescence (Fig. 4). Horizontal movements around the circumference were typical of most visitors. In only 25.2% of the observations were both female-phase and male-phase flowers visited on the same inflorescence; in most of these cases, the insect made only one transition (male phase to female phase or vice versa), though in 6.5% of observations there were multiple transitions. When both phases were visited, there was a tendency to visit male-phase flowers before female-phase flowers ("bottom up", 60.6%) rather than to visit female-phase flowers before male-phase flowers ("top down", 39.4%), but the difference was only marginally significant ($P = 0.08$, G -test of goodness of fit, $n = 66$).

When both gender phases were visited on the same inflorescence, more time was spent visiting male-phase flowers (21.8 ± 7.9 s) than visiting female-phase flowers (11.5 ± 1.9 s; Wilcoxon's paired rank test, $P < 0.01$, $n = 66$). When only one gender phase was visited on an inflorescence, there was no difference in length of time of insect visits to male-phase and female-phase flowers (Mann-Whitney U -test, $P > 0.50$, $n = 195$).

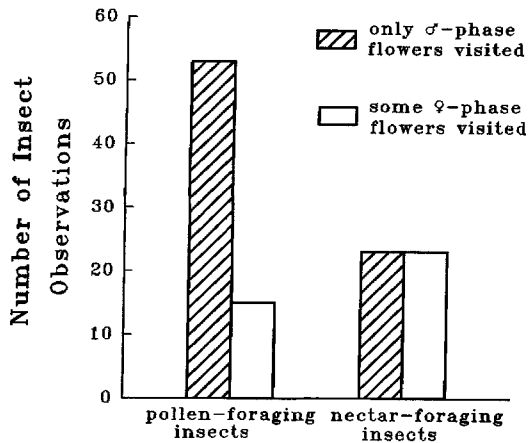


Fig. 5 Comparison of pollen-foraging and nectar-foraging insects on *Besseyia bullii*. Insect visits were categorized as either being exclusively to male-phase flowers (striped box) or as including at least some female-phase flowers (open box), either exclusively or in addition to male-phase flowers. The difference between foraging types was highly significant (G -test of independence, $P < 0.01$)

For about half ($n = 121$) of the insect observations, we were able to determine whether the insect was foraging for nectar or pollen. Insects were pollen-foraging in 56.2% of observations, nectar-foraging in 38.0%, and both in 5.8%. The two most common insect taxa differed in foraging behavior (Fisher's exact test, $P < 0.001$); *Dialictus* spp. foraged mostly for pollen (75% of observations, $n = 30$) and *Augochlorella striata* foraged mostly for nectar (87% of observations, $n = 23$). To compare the behavior of pollen-foraging versus nectar-foraging insects, we classified individual visits as either (1) exclusively to male-phase flowers or (2) including at least some female-phase flowers, either exclusively or in addition to male-phase flowers. Visits of the first type were significantly more common in pollen-foraging insects (Fig. 5; G -test of independence, $P < 0.01$, $n = 114$).

Discussion

The characteristics of *Besseyia bullii* are contrary to the pollination syndrome first identified by Darwin. *B. bullii* has acropetal (bottom up) floral development in a vertical inflorescence, and there is a weak tendency for insect floral visitors to move from lower to higher flowers. Despite this, individual flowers are protogynous, not protandrous as in Darwin's syndrome. This set of characteristics would seem to promote self-pollination of *B. bullii*. However, two factors could counteract the expected high rate of deposition of self-pollen: the variability of insect behavior on inflorescences and the relatively large proportion of solo-female flowers.

The tendency for insects to move from the bottom up was only weakly supported by our observations on

B. bullii. This result contrasts with other studies that have shown a very strong tendency for pollinators to arrive at the bottom of vertical inflorescences and to move upward (e.g., Pyke 1978, 1979; Waddington and Heinrich 1979; Best and Bierzychudek 1982). However, these studies were carried out on nectar-foraging bees, (mostly *Bombus*) and in many cases the bees were following a gradient of nectar rewards. Alternative explanations of why insects forage upwards are provided in Corbet et al. (1981) and Lloyd and Webb (1986).

Since insects visiting *B. bullii* were often foraging for pollen, it is not surprising that they would have a strong preference for male-phase flowers. Pellmyr (1985) found that pollen-foraging bees arrive at the part of the vertical inflorescence of *Cimicifuga arizonica* (Ranunculaceae) that has the most available pollen, often at middle or upper positions. Pollen-collecting bees and flies that visit the gynodioecious shrub *Hebe stricta* (Scrophulariaceae) strongly prefer plants with hermaphrodite flowers over plants with only female flowers (Delph and Lively 1992). In contrast, pollen-foraging bumblebees (*Bombus* spp.) forage from the bottom up on the vertical inflorescences of *Lupinus polyphyllus* (Fabaceae) despite the fact that more pollen is available in upper flowers (Haynes and Mesler 1984). However, the anthers of *L. polyphyllus* are hidden within the flower and insects may not be able visually to detect the variation among flowers.

As a class, nectar-foraging visitors to *B. bullii* were more likely to contact stigmas (Fig. 5) and therefore might be more effective pollinators. Wilson and Thomson (1991) found that some visitors (including a species of *Dialictus*) to *Impatiens capensis* were efficient at pollen removal but not pollen deposition on stigmas. Similarly, *Dialictus* and other mainly pollen-foraging bees may be inefficient pollinators of *B. bullii* relative to nectar-foraging species.

Though insects spent most of their time on male-phase flowers in *B. bullii*, it is the visits to female-phase flowers that determine whether outcrossing will occur. There were 85 insect observations where female-phase flowers were visited: 22.4% of these observations included no visits to male-phase flowers, and 30.6% included visits to male-phase flowers only after female-phase flowers were visited. Thus over half of the visits to female-phase flowers were *not* preceded by a visit to a male-phase flower on the same inflorescence, and potentially could have resulted in deposition of non-self pollen.

Even if many of the upper flowers in the inflorescence were self-pollinated, a substantial proportion (38% on average) of the lower flowers (solo females) are receptive before any anthers have dehisced on the inflorescence. Solo females clearly have a high potential for outcrossing, though they could be selfed if they remain unpollinated and receptive until their anthers open. Solo females also could be self-pollinated if there

were other pollen-producing inflorescences on the same plant. A survey of the study population in 1992 found that 36.5% ($n = 156$) of *B. bullii* rosettes have multiple inflorescences.

Given these options for outcrossing, it is not clear to us whether the outcrossing rate in a hypothetical protandrous *B. bullii* would necessarily be greater than at present. The “solo females” of a protandrous inflorescence would be produced at the end of the flowering period, but since pollen is rarely completely removed from anthers (Harder 1990; Young and Stanton 1990; Stanton et al. 1992), self-pollination within the flower would still be possible (Faegri and van der Pijl 1979). As a result, the “solo females” of a protandrous inflorescence could have a higher selfing rate than the truly solo females of a protogynous inflorescence. Whether a protandrous *B. bullii* would in fact have a higher outcrossing rate depends on whether the potentially increased selfing in “solo females” is offset by potentially decreased selfing in the other flowers.

Interestingly, the bottom of the inflorescence that contained the solo-female flowers was also characterized by low fruit set. Average fruit set in the lower third of the inflorescence was less than half that in the middle and top (Table 1). There was not a single fruit produced in the bottom section of 4 out of 16 plants counted; all other positions always had at least 12% fruit set. One hypothesis to explain this lack of fruit set is pollen limitation. Visitation to solo females is presumably less frequent because of the insects' strong preference for male-phase flowers, and the general synchrony of inflorescence development in the population means that solo females tend to be receptive when relatively few inflorescences are producing pollen (Fig. 3). Whether these factors will in fact result in pollen limitation depends on whether the stigmas of solo-female flowers remain receptive when the flowers enter male phase. We are currently investigating the duration of stigma receptivity. If fruit production in solo females is pollen-limited, it suggests that the presumed advantage of high outcrossing rates in solo females may be partially offset by the risk of failing to produce a fruit.

We have made no field observations on other *Besseyia* species, but we suspect that the occurrence of both protogyny and acropetalous maturation is widespread in the genus. On herbarium sheets at the Missouri Botanical Gardens, several *Besseyia* species from North America clearly showed a band of female-phase flowers above a band of male-phase flowers (as in Fig. 1); the pattern seemed particularly clear in *B. rubra* and *B. ritteriana* (see Hufford 1993 for a recent taxonomic treatment of *Besseyia*). The combination of protogyny and acropetalous development may occur also in the closely related genera *Synthyris*, *Wulfenia*, and *Picrorhiza* (Hufford 1992, personal communication). Some more

distantly related members of the tribe Veroniceae (19 genera including *Besseyia*; see Hong 1984) do not seem to have the same pattern as *Besseyia*. For instance, many *Hebe* species are either protandrous or are not dichogamous (L. F. Delph, personal communication) and *Veronicastrum virginicum* is either slightly protandrous or not dichogamous (personal observation). Whatever the evolutionary cause of *B. bullii*'s flowering behavior, it appears to have originated within this tribe in the ancestor of a clade of several genera.

Beyond close relatives of *Besseyia*, the only well-documented case of a contradiction to Darwin's syndrome of which we are aware occurs in the genus *Pedicularis* (Scrophulariaceae, tribe Euphrasieae). Williams and Batzli (1982) investigated five species of *Pedicularis* in Alaska, and found that all are protogynous, have acropetalous development, and are pollinated by bees (*Bombus* and *Megabombus* spp.). Some of the *Pedicularis* species have few flowers per inflorescence and therefore might not be considered vertical inflorescences, but *P. kanei* averages 28 flowers per shoot and appears vertical (Williams and Batzli 1982). Faegri and van der Pijl (1979) discuss other protogynous species of *Pedicularis* that may have vertical inflorescences. It would be particularly useful to investigate the proportion of solo females and the pattern of insect movements in these species.

In conclusion, we have found that *B. bullii* is one of the very few bee-pollinated species known to have vertical inflorescences, acropetalous floral maturation, and protogyny. This arrangement produces the unexpected placement of newly receptive stigmas above dehiscing anthers, and seemingly could lead to high selfing rates in this self-compatible species. Substantial outcrossing is still possible, however, because of the foraging behavior of the pollinators and the presence of solo-female flowers at the base of the inflorescence. Many of the well-studied species that fit Darwin's syndrome are pollinated by nectar-foraging *Bombus*. As emphasized by Ginsberg (1985), generalizations based on *Apis mellifera* and *Bombus* species may not apply to the large majority of other bees. Other exceptions to Darwin's syndrome may be found in plants pollinated by smaller bees and flies that are foraging for pollen.

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References

- Bawa KS, Beach JH (1981) Evolution of sexual systems in flowering plants. *Ann Mo Bot Gard* 68: 254–274

- Bertin RI (1993) Incidence of monoecy and dichogamy in relation to self-fertilization in angiosperms. *Am J Bot* 80: 557–560
- Bertin RI, Newman CM (1993) Dichogamy in angiosperms. *Bot Rev* 59: 112–152
- Best LS, Bierzychudek P (1982) Pollinator foraging on foxglove (*Digitalis purpurea*): a test of a new model. *Evolution* 36: 70–79
- Coffin B, Pfannmuller L (1988) Minnesota's endangered flora and fauna. University of Minnesota Press, Minneapolis, Minn
- Corbet SA, Cuthill I, Fallows M, Harrison T, Hartley G (1981) Why do nectar-foraging bees and wasps work upwards on inflorescences? *Oecologia* 51: 79–83
- Curtis JT (1959) The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wis
- Darwin C (1877) The various contrivances by which orchids are fertilised by insects, reprint of 2nd edn. University of Chicago Press, Chicago, Ill
- Delph LF, Lively CM (1992) Pollinator visitation, floral display, and nectar production of the sexual morphs of a gynodioecious shrub. *Oikos* 63: 161–170
- Faegri K, Pijl L van der (1979) The principles of pollination ecology, 3rd edn. Pergamon Press, Oxford
- Ginsberg HS (1985) Foraging movements of *Halictus ligatus* (Hymenoptera: Halictidae) and *Ceratina calcarata* (Hymenoptera: Anthophoridae) on *Chrysanthemum leucanthemum* and *Erigeron annuus* (Asteraceae). *J Kans Entomol Soc* 58: 19–26
- Harder LD (1990) Pollen removal by bumble bees and its implication for pollen dispersal. *Ecology* 71: 1110–1125
- Haynes JM, Mesler M (1984) Pollen foraging by bumblebees: foraging patterns and efficiency on *Lupinus polyphyllus*. *Oecologia* 61: 249–253
- Holmgren NH (1986) Scrophulariaceae. In: Great Plains Flora Association, Flora of the Great Plains. University Press of Kansas, Lawrence, Kan, pp 751–797
- Hong D-Y (1984) Taxonomy and evolution of the Veroniceae (Scrophulariaceae) with special reference to palynology. *Opera Bot* 75: 1–60
- Hufford L (1992) Floral structure of *Besseyia* and *Synthyris* (Scrophulariaceae). *Int J Plant Sci* 153: 217–229
- Hufford L (1993) A phylogenetic analysis of *Besseyia* (Scrophulariaceae). *Int J Plant Sci* 154: 350–360
- Lloyd DG, Webb CJ (1986) The avoidance of interference between the presentation of pollen and stigmas in angiosperms. I. Dichogamy. *NZ J Bot* 24: 135–162
- Lloyd DG, Yates JMA (1982) Intrasexual selection and the segregation of pollen and stigmas in hermaphroditic plants, exemplified by *Wahlenbergia albomarginata* (Campanulaceae). *Evolution* 903–913
- Mitchell TB (1960) Bees of the eastern United States, vol I. *Tech Bull Agric Exp Stn (NC)* 141
- Moure JS, Hurd PD Jr (1987) An annotated catalog of the halictid bees of the Western Hemisphere (Hymenoptera: Halictidae). Smithsonian Institution Press, Washington, DC
- Pellmyr O (1985) Pollination ecology of *Cimicifuga arizonica* (Ranunculaceae). *Bot Gaz* 146: 404–412
- Pyke GH (1978) Optimal foraging in bumblebees and coevolution with their plants. *Oecologia* 36: 281–293
- Pyke GH (1979) Optimal foraging in bumblebees: rule of movement between flowers within inflorescences. *Anim Behav* 27: 1167–1181
- Stanton ML, Ashman T-L, Galloway LF, Young HJ (1992) Estimating male fitness of plants in natural populations. In: Wyatt R (ed) Ecology and evolution of plant reproduction. Chapman and Hall, New York, pp 62–90
- Waddington KD, Heinrich B (1979) The foraging movements of bumblebees on vertical "inflorescences": an experimental analysis. *J Comp Physiol [A]* 134: 113–117
- Williams JB, Batzli GO (1982) Pollination and dispersion of five species of lousewort (*Pedicularis*) near Atkasook, Alaska U.S.A. *Arct Alp Res* 14: 59–74
- Wilson P, Thomson JD (1991) Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. *Ecology* 72: 1503–1507
- Wyatt R (1983) Pollinator-plant interactions and the evolution of breeding systems. In: Real L (ed) Pollination biology. Academic Press, Orlando, Fla, pp 51–95
- Young HJ, Stanton ML (1990) Influences of floral variation on pollen removal and seed production in wild radish. *Ecology* 71: 536–547