Pollen-Feeding Fly Alters Floral Phenotypic Gender in Centropogon solanifolius (Campanulaceae)

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Pollen-Feeding Fly Alters Floral Phenotypic Gender in *Centropogon solanifolius* (Campanulaceae)[1]

Key words: dichogamy; Drosophilidae; florivory; protandry; Zygothrica.

IN SOME HERMAPHRODITIC PLANTS, sexual functions are temporally separated within the same flower, such that individual flowers can be described as male-phase or female-phase on a given day. The "phenotypic gender" of these dichogamous plants can be calculated for each day of flowering as the proportion of open flowers in the female phase, and provides an estimate of potential reproductive success through male and female function (Lloyd 1980, Devlin & Stephenson 1987). Studies of protandrous species in the Campanulaceae have demonstrated that natural or artificial pollen removal significantly reduces the length of the initial male (staminate) phase, and hastens the onset of the subsequent female (pistillate) phase (Devlin & Stephenson 1984, Richardson & Stephenson 1989, Koptur *et al.* 1990). Through comparisons of control and manipulated flowers, I established that daily pollen removal significantly shortened the duration of the male phase in flowers of *Centropogon solanifolius* Benth. (Campanulaceae) growing in Monteverde, Costa Rica (Fig. 1a). In these populations, however, I also found a very different cause for this phenomenon: fly larvae living inside the anther tubes of many unopened flowers eat the developing pollen and in so doing eliminate or significantly shorten the flowers' male phase (Fig. 1b).

Here I report on the extent of larval infestation and its effects on floral phenotypic gender, as well as on the proportion of female-phase flowers in *C. solanifolius* populations in Monteverde. I also discuss the identity and life history of the fly.

Centropogon is a genus of mostly Andean herbs, shrubs, and vines with brightly colored, hummingbird-pollinated flowers (Standley 1938, Stein 1992). *Centropogon solanifolius* is common in mountain forests of central Costa Rica (Standley 1938). In *C. solanifolius,* as in other lobelioids, the style is enclosed in a tube formed by the fusion of the filaments and anthers. The anthers shed pollen into the distal portion of the tube, and pollen is released through a ventral valve. At the end of the male phase, the style lengthens until it is exserted from the anther tube. After full extension, the stigmatic lobes reflex back and are then receptive to pollen (Devlin & Stephenson 1984).

The fly larva is *Zygothrica neolinea* (Grimaldi 1987) (Drosophilidae). *Zygothrica neolinea* is a recently described species that belongs to a group of flies known largely from their massive mixed-species aggregations at patches of fungi in the forest (Grimaldi 1987). There they gather by the thousands to fight, feed on fungal spores, and mate; some species oviposit in the fungi, while others lay their eggs in flowers. Bulky or fleshy flowers in ten families seem to be the predominant hosts for flower-breeding *Zygothrica* (Grimaldi 1987). Almost nothing is known, however, about the hosts in which particular species breed (Grimaldi 1987). In some cases the relationship between host flower species and drosophilid fly is very specific, with only one floral host for a given species of fly; in others, the association is more general (Pipkin *et al.* 1966). The relationship between *C. solanifolius* and *Z. neolinea* does not seem to be species-specific: adults now known to be *Z. neolinea* have been reared from *Passiflora* (Passifloraceae) and *Aphelandra* (Acanthaceae) flowers (Pipkin *et al.* 1966, Grimaldi 1987), and larvae of other fly genera have been found in other *Centropogon* species (Brncic 1983).

Through observation, dissection, and rearing, I determined details of the life history of *Z. neolinea* within *C. solanifolius* flowers. Female flies lay single oblong eggs through the corolla onto the surface of the anther tube, or, in some cases, onto the inside of the corolla, when the flower is still a small bud. A tiny droplet of latex on the outside of a bud can reveal the location of a recent oviposition (Fig. 2). The newly hatched larva, just over one mm long, burrows into the anther tube and eats pollen as the bud grows. Larval dissections revealed guts full of pale yellow pollen (M. Weiss, pers. obs.). The larva grows within the anther tube and does not seem to damage the stigma, ovary, or other floral tissue. After approximately three weeks, and usually just prior to anthesis, the larva, now about five or six mm long, leaves the anther tube. It crawls down the inside of the corolla, making an exit hole just above the

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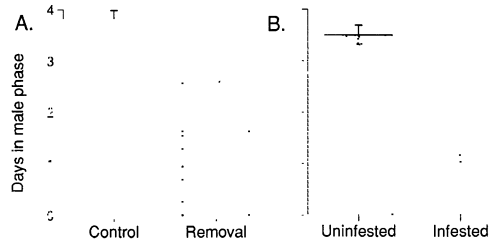

FIGURE 1. (a) "Control" flowers ($N = 11$), from which pollen was not artificially removed, remain in the male phase significantly longer than do "Removal" flowers ($N = 5$), from which pollen was removed once daily. Unpaired t-test, 14 df, $t = -3.023$, 2-tail $P < 0.01$. Bars represent one standard error. Sample sizes are small due to extensive larval infestation of study populations. (b) Uninfested flowers ($N = 16$) remain in the male phase significantly longer than do infested flowers ($N = 36$). Unpaired t-test, 49 df, $t = 8.178$, 2-tail $P < 0.0001$.

constriction at the base of the flower (Fig. 2). Presumably, the insect pupates in the soil; adult flies emerge from pupae after 17–20 days.

Dissection of infested buds and flowers revealed a clear relationship between larval size and host size: small larvae were found only in small buds, while larger larvae inhabited larger buds and flowers (Fig. 3). I never found very small (~one mm long) larvae inside buds more than 30 mm long, suggesting that female flies selectively oviposit in young buds. Buds containing newly deposited eggs (located beneath fresh latex droplets) ranged from 7 to 18 mm in length (mean 13.5 ± 1.2 SE. $N = 11$). Figure 3 also shows the size of the anther tube relative to bud and flower size. By the time the bud is 15 mm long, the anther tube has reached its full length of approximately 7 mm, and pollen is already formed. Thus a larva hatching out in a relatively small bud will have access to a full complement of pollen. Anthesis occurs when the flower is about 50 mm long.

The distribution of larvae within buds differs significantly from the random pattern expected for a Poisson distribution ($\chi^2 = 11.68$, 2 df, $P < 0.005$). In a sample of 82 buds and flowers, 41 contained no larvae, 39 contained 1, and only 2 contained 2 larvae. These results suggest that females may somehow detect the presence of an egg or larva inside a bud, and thus avoid ovipositing in already infested host flowers.

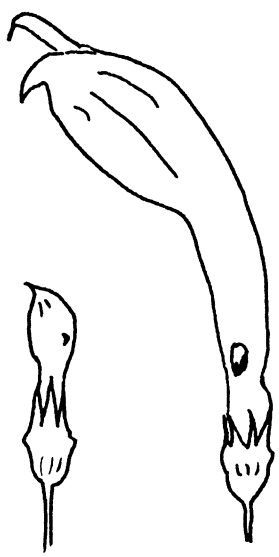

FIGURE 2. *Centropogon solanifolius* bud with latex droplet over site of recent oviposition (left); male-phase flower with larval exit hole above the calyx lobes (right). The exit hole could be mistaken for a hole made by a nectar-robber.

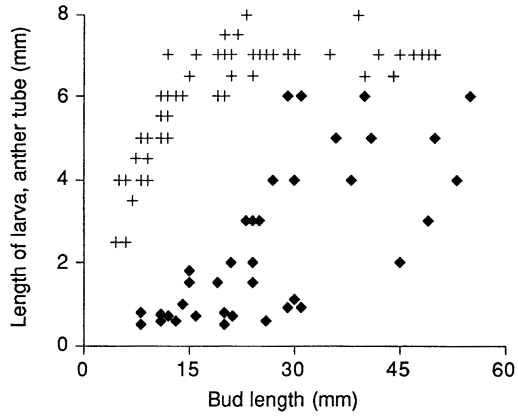

FIGURE 3. Size distribution of *Z. neolinea* larvae within *C. solanifolius* buds and flowers. Black diamonds represent larvae; crosses represent anther tubes. Very small larvae (~1 mm) are found only in buds less than 30 mm long. Larvae grow as the flower develops and leave the flower when they are 5 or 6 mm long. Anthesis occurs when the bud is approximately 50 mm long. The anther tubes reach their full size (~7 mm) by the time the bud is 15 mm long.

Larval infestation of *C. solanifolius* seems to be intense and widespread at Monteverde. In 1987, larvae infested 71 percent (44/62) of the flowers in my study population. In 1988, 50 percent of the flowers and 87.5 percent of the plants were infested in a sample of 82 flowers and buds on 16 plants; I also found evidence of infestation (larvae, frass, or exit holes) in 74 percent of a different population of 19 marked plants.

Both larval and artificial pollen removal significantly reduce the duration of the male phase in *C. solanifolius* flowers (Fig. 1). Thus it seems that the removal of pollen itself, rather than the presence of a larva within the anther tube, results in the reduction of the male phase. Presumably pollen removal by hummingbirds also reduces the length of the male phase in *C. solanifolius* flowers, as it has been shown to do in *Lobelia cardinalis* flowers (Devlin & Stephenson 1985).

Larval-mediated changes in floral phenotypic gender may yield changes in the proportion of male- and female-phase flowers at the population level. I tagged 119 buds and flowers on 19 plants growing along the road to La Ventana in the Monteverde Cloud Forest Reserve in February 1988 to determine the proportion of female-phase flowers in the population. Each day for 21 days, the phenotypic gender and infestation status of every flower was noted. Flowers were accessible to pollinators, and I did not manipulate them in any way. They were considered to be in the male phase if the anther tube protruded from the end of the open corolla, and in the female phase if the stigma was visible at the end of the anther tube.

Within my census population, on average, 6 male-phase and 14 female-phase flowers were open on a given day. The male phase lasted a mean of 1.78 days ± 0.20 SE (N = 46 flowers), while the female phase lasted 3.89 days ± 0.25, (N = 41 flowers). The mean daily proportion of flowers in the female phase over 21 days was 0.72 ± 0.03 SE.

Due to high levels of larval infestation, I could not directly measure the relative frequencies of male- and female-phase flowers in an uninfested population at Monteverde. In related species in Costa Rica and elsewhere that showed no evidence of larval infestation, however, the male phase is longer than the female phase, and more male-phase flowers are open at a given time. In another Costa Rican species, *Centropogon granulosus,* the male phase was estimated to last 5.4 days, and the female phase 3.0 days; population censuses yielded proportions female of 0.38 and 0.44 (L. A. McDade, pers. comm.). In *Lobelia cardinalis* the male phase lasts about 5.5 days and the female phase lasts about 2.8 days (Devlin & Stephenson 1985).

Larval infestation may have important fitness consequences for *C. solanifolius,* at both the individual and population level. Larval pollen removal shortens the duration of the male phase and hastens the onset of the female phase, so that at any one time relatively fewer flowers will be available to donate

pollen. In addition, while pollen removed by hummingbirds has the potential to reach an appropriate stigma, pollen consumed by larvae is entirely unavailable for pollination. Thus larval infestation reduces both the time that pollen is available and the overall amount of pollen in the system.

These preliminary studies of *Z. neolinea* larvae in *C. solanifolius* flowers raise a number of interesting questions. How, for example, does the bias towards female-phase flowers affect patterns of male and female fitness? How patchy is larval infestation across space and time? How does the female fly locate her host flowers, and once there, how does she know if a bud already contains an egg?

In comparison with plant-pollinator interactions, the relationships between flowers and their insect herbivores, parasites, and robbers have received relatively little attention (but see McDade & Kinsman 1980, Colwell 1995, Paciorek *et al.* 1995). While these systems may not be visually obvious, they can nonetheless have important direct and indirect consequences for plant fitness, as suggested by this study.

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