POLLINATION ECOLOGY OF *CASTILLEJA* IN MOUNT RAINIER NATIONAL PARK[1]

W. JAMES DUFFIELD

Department of Botany, University of Michigan, Ann Arbor, Michigan 48104

ABSTRACT

The pollination ecology of four species of *Castilleja* was studied in the Berkeley Park-Yakima Park area of Mt. Rainier National Park, Washington, from 2 July to 13 August 1970. One species, *C. cryptantha*, was found to be self-pollinating, while the other three, *C. miniata*, *C. oreopola*, and *C. rupicola*, are primarily hummingbird-pollinated. Bumblebees were observed to forage on *Castilleja oreopola* for nectar, but a cinematographic record showed them to be too small to be effective in pollination of these plants.

INTRODUCTION

The earliest work on pollination in *Castilleja* was that of Warming (1890), which discussed autogamy and heterostyly in *C. pallida*. Robertson (1891) was the first to describe hummingbird pollination in this genus as a method of outcrossing for *C. coccinea*. Merritt (1897) observed pollen transfer by hummingbirds for *C. affinis* and speculated that thrips might play a role in effecting self-pollination. Clements and Long (1923) gave detailed observations on the behavior of some Halictid bees and hummingbirds foraging on both normal and experimentally mutilated flowers of *C. miniata*. Pennell (1935), in his monograph of the eastern Scrophulariaceae, suggested that the red-bracted species of this genus were usually pollinated by hummingbirds, while closely related yellow-bracted species might have arisen through continual self-pollination. Pennell also felt that the yellow-bracted *C. sessiliflora* would prove to be pollinated by butterflies; Crosswhite and Crosswhite (1970), however, report that this species is pollinated by queens of *Bombus fervidus*. In their work with hummingbirds and hummingbird flowers, Grant and Grant (1966, 1967a, 1967b, 1968) have made a number of observations of hummingbirds foraging on red-bracted species of *Castilleja* and propose that this is the usual method of pollination for members of the genus. A summary of all known pollen vectors for *Castilleja* as recorded in the literature is given in Table 1. The present study reports observations on the pollination of four species of *Castilleja* in Mount Rainier National Park: *C. cryptantha*, *C. miniata*, *C. oreopola*, and *C. rupicola*.

METHODS AND MATERIALS

Between 2 July and 13 August 1970, a total of 220 man-hours was spent observing insect and hummingbird foragers on the four species of *Castilleja* abundant in the Berkeley Park area of Mount Rainier National Park. These areas of the park are in Pierce County, Washington, and include an altitudinal range of from 6300 to 7200 ft. The species studied and their altitudinal ranges were: *Castilleja miniata*—abundant up to 6500 ft, *C. rupicola*—abundant above 6500 ft, and *C. oreopola* and *C. cryptantha*—both abundant throughout the study area. Identification of all plant species in the area was made using Jones' (1938) treatment of the flora. Voucher specimens of all the *Castilleja* species have been deposited in the Willard Sherman Turrell Herbarium of Miami University, Oxford, Ohio.

Records were kept of all foragers to the plants under observation and any special behavior patterns were noted. Twenty-two insect foragers were taken on *Castilleja oreopola* and identified to species. Extracorbicular pollen on forager bodies and corbicular pollen loads were mounted in glycerine jelly tinted with fast

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TABLE 1

Pollen vectors in the genus Castilleja.

Red-bracted species	Vector	Authority
C. affinis	Unidentified hummingbirds	Merritt, 1897
C. applegatei	Unidentified hummingbirds	Grant and Grant, 1968
C. breweri	*Stellula calliope*	Grant and Grant, 1966
C. coccinea	*Trochilus colubris*	Robertson, 1891; 1928
C. foliolosa	Unidentified hummingbirds	Grant and Grant, 1968
C. irasuensis	*Selasphorus flammula*	Kalin and Gregg[1]
C. linariaefolia	*Stellula calliope* and *Selasphorus rufus*	Grant and Grant, 1966
C. martinii	Unidentified hummingbird	Grant and Grant, 1968
C. miniata	*Selasphorus platycerus*, *Halictus pulzenus*, and *Sphecodes* sp.	Clements and Long, 1923
	Stellula calliope and *Selasphorus rufus*	Grant and Grant, 1966; 1968
C. oreopola	*Selasphorus rufus*	Duffield
C. payneae	*Stellula calliope*	Grant and Grant, 1967a
C. patriotica	Unidentified hummingbirds	Grant & Grant, 1968
C. rupicola	*Selasphorus rufus*	Duffield
C. stenantha	Unidentified hummingbirds	Grant and Grant, 1968
PALE-BRACTED SPECIES		
C. cryptantha	Autogamous	Duffield
C. occidentalis	*Bombus* sp.	L. W. Macior (pers. comm., July, 1970)
C. pallida	Autogamous	Warming, 1890
C. sessiliflora	*Bombus fervidus* (queens)	Crosswhite and Crosswhite, 1970
C. sulphurea	*Bombus* sp.	L. W. Macior (pers. comm., July, 1970)

[1]Unpublished mimeographed paper by M. Kalin and K. Gregg on "Hummingbird behavior and pollination studies in *Castilleja irasuensis*," based on trip with the Organization for Tropical Studies in 1968.

green. The pollen constituents were identified to genus by comparison with a reference collection of pollen from flowers collected in the area. Tongue lengths of the insects were obtained from the combined mentum and glossa length of dissected material mounted in glycerine jelly.

Plants of each species with immature flowers were caged with 18-x-14-mesh screen to exclude pollinators. After flowering, the number of fruit capsules per inflorescence of caged and nearby uncaged control plants was compared. Reflectance spectrophotometric readings were taken for the showy bracts of representatives of each of the four species. These readings were plotted on trichromatic coefficient computing forms for illuminant C and then transferred to a Maxwell color-mixture diagram. A cinematographic record was made of one of the insects while it was foraging on a population of *Castilleja oreopola*.

As a final part of this study, thirty plants of *Castilleja oreopola* were selected at random from a population observed to be frequented by hummingbirds. These plants were then mutilated, by variously removing the bracts, calyces, and corollas, to observe the effects of a change in the floral structure on the behavior of the foragers.

OBSERVATIONS

On the basis of the number of individual foragers effecting pollination (table 2) · hummingbird pollination is the most prevalent condition found in this genus. Three quarters of the references in the literature on pollination of *Castilleja* are

for hummingbird pollinators (Table 1). The method by which pollen transfer is effected by the hummingbirds is much the same for all the red-bracted species. When the hummingbird inserts its beak into the corolla, probing for nectar, pollen is brushed over the forehead of the bird as the upper lip of the corolla is spread apart exposing the anthers. As the hummingbird probes the next flower, its pollen-covered forehead contacts the stigma, thus effecting cross-pollination. The hummingbirds and bumblebees with almost equal frequency. A cinematographic plant population on which they were foraging, and to use these perches as bases from which to make their foraging trips.

No foragers were observed to visit *Castilleja cryptantha*, a small yellow-bracted species, even though it was frequently found growing with or near *C. oreopola* and *C. rupicola*. Dissecting 25 flowers of this species revealed that the stigma usually

TABLE 2

Observations of foragers on Castilleja. *Beak-length data for the hummingbirds are based on measurement of 25 specimens from the Natural History Museum of the University of Puget Sound. Identification of the bumblebees is based on Stephen (1957); voucher specimens are preserved in the Insect Division, Natural History Museum, University of Michigan, Ann Arbor, Michigan.*

Species	Total man-hours observed	Foragers	Average beak or tongue length of foragers
C. miniate Dougl.	49	11 *Selasphorus rufus*	17.4 mm
C. cryptantha Pennell and G. N. Jones	47	None	———
C. rupicola Piper	40	19 *Selasphorus rufus*	17.4 mm
C. oreopola Greenm.	70	18 *Selasphorus rufus*	17.4 mm
		19 *Bombus flavifrons dimidiatus*	12.8 mm
		2 *B. bifarius nearcticus*	10.5 mm
		1 *B. melanopygus*	11.0 mm

extended only to a level at or only slightly beyond the anthers and never beyond the corolla which, in turn, never exceeded the calyx. This floral structure and the high percentage of fruit capsules formed on caged plants (Table 3) indicate that this plant may not require a pollinating agent.

Field observations on *Castilleja oreopola* showed this species to be visited by hummingbirds and bumblebees with almost equal frequency. A cinematographic record of one of the bumblebees foraging on a population of *C. oreopola* revealed that, although the bumblebee was being contacted by the anthers, it was not large enough to contact the stigma while it was foraging for nectar. Observations on flowers which had been mutilated gave evidence that the hummingbirds were

TABLE 3

Floral dimensions and fertility in Castilleja.

Species	Corolla length	Corolla tube length	Fruit set		No. inflorescences observed
			caged	control	
C. miniata	31.4 mm	16.6 mm	0%	80%	24
C. cryptantha	13.4 mm	10.4 mm	89%	91%	26
C. rupicola	29.5 mm	10.9 mm	1.6%	54%	28
C. oreopola	24.4 mm	15.3 mm	3.9%	83%	28

accustomed to probing all flowers in the population as possible nectar sources, and they showed no hesitation in doing so.

DISCUSSION

The data from this study, together with the relative lack of insect-pollination records for *Castilleja* in the literature, show that the red-bracted species are primarily hummingbird-pollinated. They also confirm previous reports (Grant and Grant, 1966, 1968; Clements and Long, 1923) of hummingbird pollination for *C. miniata*. Although hummingbirds visited both *C. miniata* and *C. rupicola*, with more hummingbirds visiting the latter species, the latter showed a lower percentage of fruit capsules formed per inflorescence. Because *C. rupicola* is found above timberline, the lower number of capsules may be correlated with a lack of perching places for the hummingbird to return to between foraging flights. The lack of foragers on *C. cryptantha*, the shorter, more enclosed stigma, and the high percentage of fruit capsules set by the caged plants seem to suggest that this species is autogamous.

Analysis of corbicular pollen loads and extra-corbicular pollen on the insects foraging on *Castilleja oreopola* indicates that they were foraging on nearby lupines (*Lupinus subalpinus*) and bluebells (*Mertensia laevigata*) for pollen and on *Castilleja* for nectar. *Castilleja* pollen was found on the vertex and frons of the bumblebees, but not in the pollen loads. Reflectance spectrophotometer readings show that, although *C. oreopola* is a bright magenta color, it was reflecting a substantial amount in the blue region of the spectrum. This suggests that the bumblebees were reacting to the reflected blue light, while the hummingbirds were being attracted by the bright magenta color of the inflorescences.

With pollination records for only about one-tenth of the species in this large genus, it is difficult to postulate any distinct pattern of evolution of pollinating systems. However, it does appear highly probable that most of the red-bracted species will prove to be hummingbird-pollinated. This is not surprising in light of the fact that all bright-red colors are known to attract hummingbirds. Unfortunately, the pollination ecology of too few of the yellow-bracted species is known to allow sufficient room for speculation as to whether or not bumblebee pollination or autogamy will prove to be the usual method of ensuring pollination. Once the relationships of the different species in this genus are better understood, the evolutionary importance of the pollinating systems will also be better understood.

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