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FLOWER-BREEDING SPECIES OF HAWAIIAN DROSOPHILIDS IN AN EARLY STAGE OF SYMPATRY

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Abstract. We report here population densities of 2 drosophilid species that were found to be breeding in blossoms of the morning glory, *Ipomoea acuminata*. Scaptomyza (Exalloscaptomyza) caliginosa is a species endemic to the island of Hawaii, while Drosophila (Phloridosa) floricola is a recent introduction into the Hawaiian Archipelago. Estimates of population densities as well as descriptions of reproductive strategies in both species will provide bases for future studies of resource competition between these flower-breeding species.

Where 2 or more species utilize a common resource, evolutionary theory suggests that natural selection favors either a change in the way the organisms obtain the resource (character displacement) or the eventual extinction of one or more of the sympatric populations (competitive exclusion) (MacArthur 1972). Unfortunately, it is difficult to assess the role of interspecific competition if there is uncertainty about the recent evolutionary histories of the present-day populations (Grant 1972).

During September–November 1980 we conducted a field study of an endemic flower-breeding drosophilid, *Scaptomyza* (*Exalloscaptomyza*) caliginosa Hardy, in Hawaii Volcanoes National Park on Hawaii Island in the Hawaiian Archipelago. This species lives and breeds only in open morning glory blossoms (*Ipomoea acuminata*) (Hardy 1965, 1966; Ibara 1976). We also discovered a second flower-breeding drosophilid, *Drosophila* (*Phloridosa*) floricola Sturtevant, breeding in sympatry with *S. caliginosa*. This exotic species was not present in any samples collected from the same area by Ibara (1976). In this note we report estimates of population densities within morning glory blossoms and aspects of reproductive biology and population dynamics of both species of drosophilids. This will document estimates of population parameters at an early stage of sympatry and provide the basis for future investigations of competitive interaction between the 2 species.

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Table 1. Mean densities of adults and eggs of *S. caliginosa* and *D. floricola* per morning glory blossom. Values in parentheses are 1 standard deviation; n = no. blossoms per sample.*

	S. caliginosa				D. floricola			
	♀ per blossom	ੋਂ per blossom	Eggs per blossom	RE**	♀ per blossom	ර per blossom	Eggs per blossom	RE**
Sun-lit blossoms $n =$	2.56 (3.27) 243	1.58 (2.17) 243	1.03 (1.14) 300	0.45	0.12 (0.41) 243	0.07 (0.38) 243	0.18 (0.21) 300	1.50
Covered blossoms $n =$	0.77 (1.22) 243	1.13 (1.72) 243	1.29 (1.16) 300	1.65	0.08 (0.32) 243	0.05 (0.26) 243	0.38 (0.34) 300	4.75
Shrub blossoms $n =$	3.12 (4.04) 162	3.02 (3.03) 162	2.11 (1.23) 200	0.68	0.05 (0.24) 162	0.06 (0.26) 162	0.16 (0.09)	3.20

^{*}Montague (1982) used square-root transformed counts per blossom in ANOVA to show that females, males and eggs of both species had significant variation in mean densities per blossom among all 3 classes of blossoms.

METHODS AND MATERIALS

The study was carried out in Bird Park (Kipuka Puaulu) near the Kilauea Crater in Hawaii Volcanoes National Park. Bird Park is a mixed forest-savannah area of roughly 35 km² and situated 1200 m above sea level on the SE slopes of the volcanic peak Mauna Loa (Steiner 1979). Morning glory vines cover extensive areas of the open fields, and on any given day tens of thousands of fresh morning glories bloom in Bird Park. Since these blossoms remain open only for a single day, adult flies must disperse each morning to fresh blossoms in order to mate and lay eggs. The larvae develop within decaying blossoms.

During September–November 1980, blossoms from 3 different spatial situations were sampled: (1) sun-lit blossoms exposed to direct sunlight most of the day; (2) covered blossoms found beneath vines, leaves or layers of grass; and (3) shrub blossoms found along vertically growing vines, mostly at the forest canopy edges. Adults of both species were collected in plastic bags that were quickly enclosed around the blossoms. These were collected over a 9-day sampling period (17–19.IX.1980, 30.IX–2.X.1980, and 2–4.XI.1980). A total of 648 blossoms were collected at 1200 h, which is assumed to be the period of peak adult activity.

A second sample (800 blossoms) was collected at 1700 h over a 10-day sampling period (20–29.X.1980). These were collected to estimate the numbers of eggs per blossom. Each blossom was cut open and examined under a stereomicroscope at the Hawaii Field Research Center, Hawaii Volcanoes National Park.

The eggs of the 2 species cannot be morphologically distinguished. In order to estimate the proportion of total eggs of each species per blossom, a third sample (440 blossoms) was collected at 1700 h (120 blossoms collected on 9.IX.1980, 160 blossoms collected on 23.IX.1980, and 120 blossoms collected on 5.XI.1980). Each blossom in

^{**} RE = reproductive effort = no. eggs per \mathcal{P} per blossom.

TABLE 2. Comparative reproductive morphologies for S. caliginosa and D. floricola females. Means
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followed by 1 standard deviation in parentheses; $n = \text{no.}$ females per sample.
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	Thorax length (mm)	No. ovarioles	Egg length (mm)	Egg width (mm)	
S. caliginosa $(n = 20)$	0.98 (0.07)	2.0 (0)	0.80 (0.06)	0.28 (0.03)	
D. floricola $(n = 6)$	1.05 (0.10)	13.5 (1.97)	0.63 (0.10)	0.26 (0.15)	

this sample was individually stored in a perforated plastic bag containing 1 gram of sterile sand. As adults emerged they were identified and counted to estimate the proportions of reared imagoes per blossom of each species (assuming equal larval survivorship). Each total egg count per blossom from the second sample (800 blossoms) was then multiplied by these proportions to determine the mean egg densities per blossom for each species.

Adult females of both species were collected in the field and dissected at the Research Center (after Kambysellis & Heed 1971); thorax length, ovariole number, and length and width of the largest mature egg were recorded for each female.

RESULTS AND DISCUSSION

The densities of adults and eggs per blossom for both species are shown in Table 1. The results of the female dissections are shown in Table 2.

S. caliginosa, an endemic Hawaiian species, is probably descended from 1 of several founder species from the Old World hirtodrosophila radiation (Throckmorton 1975). The exotic D. floricola appears to be descended from the New World virilis-repleta radiation (Throckmorton 1975). Sturtevant (1942) found D. floricola adults in blossoms of Datura, Ipomoea and Cucurbita spp. from California. Less is known about its distribution in the New World tropics, although Wheeler (1982) reported it present in Mexico and Colombia.

D. floricola was first detected in the Hawaiian Archipelago by Dr Hampton L. Carson on Mt Tantalus, Oahu, in 1963. Since then, it has been found on the islands of Kauai, Maui, and Kahoolawe, as well as on Hawaii. It has apparently been successful in establishing populations in a relatively short period of time.

Adults of both species occupied sun-lit blossoms in higher densities than covered blossoms, while females of both species apparently preferred to oviposit in covered blossoms (Table 1). It is possible that covered blossoms are less susceptible to desiccation stress and are thus more suitable larval substrates than are sun-lit blossoms. On the other hand, density-dependent factors may also be responsible for the increased female reproductive effort in covered blossoms. Montague (1982) observed populations of *S. caliginosa* in *I. acuminata* blossoms that were caged within screened boxes. He found that over the course of a day, females in the absence of males had

significantly higher reproductive effort than did females in the presence of males. Montague (1982) suggested that male courtship and mating behavior distracts females and serves to inhibit oviposition within blossoms containing several or more males. Since the mean male density per blossom was lowest in covered blossoms, female reproductive effort should have been increased there (Table 1).

Although females of both species are similar in size, *D. floricola* females have more ovarioles (indicating higher potential fecundity) and smaller eggs than *S. caliginosa* (Table 2). This is consistent with the general inverse relationship between egg size and number in drosophilids (Kambysellis & Heed 1971, Atkinson 1979, Montague et al. 1981). The difference in biotic potential between the 2 species makes it possible for *D. floricola* to increase in relative density over future generations. However, Kambysellis & Heed (1971) and Montague et al. (1981) suggested that the large-egg/small-clutch strategy of the flower-breeding *Scaptomyza* species evolved in response to severe larval competition within decaying blossoms. The comparatively high biotic potential of *D. floricola* in morning glories might be balanced by nutritional stress and decreased larval survivorship resulting from competition with larger, more precocious *S. caliginosa* larvae.

In November 1980, we also found *D. floricola* adults and eggs within squash blossoms (*Cucurbita pepo*) growing on the eastern edge of Bird Park. There were roughly 50–100 adults and 50–100 eggs per squash blossom. *D. floricola* was also found in squash blossoms from gardens around Volcano Village (less than 10 km from Bird Park). However, no *S. caliginosa* adults or eggs were found in any squash blossoms. Perhaps this minimal resource overlap will allow the 2 species to coexist in Bird Park. Squash blossoms might be preferred by *D. floricola*, and it is probable that this species was introduced to the archipelago by way of rotting squash plants.

In summary, the estimates reported here represent population densities of competing species in an early stage of sympatry. This situation provides a unique opportunity for the future study of resource competition between these distantly-related flower-breeders.

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