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THE ECOLOGICAL IMPACT OF NECTAR-ROBBING BEES AND POLLINATING HUMMINGBIRDS ON A TROPICAL SHRUB¹

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Abstract. The consequences of nectar robbing by highly social bees were studied at 71 patches of the forest-edge shrub, *Pavonia dasypetala* (Malvaceae) at two tropical moist forest habitats in central Panama. Groups of *Trigona* (*Trigona ferricauda* (Apidae: Meliponinae) arrived at flowers in early morning; each bee dominated a single flower that it perforated to rob nectar (Fig. 1). Robbers in each patch aggressively defended their feeding sites from the sole pollinator of the plant, the Hermit Hummingbird *Phaethornis superciliosus* (Trochilidae: Phaethorninae). Less visitation by hummingbirds and reduced seed production resulted from nectar robbing. Flower number in patches was not associated with visitation per flower by pollinators, but patches having the most flowers were entered more often by *P. superciliosus*. In contrast, thieving *P. longuemareus* and robbing *T. ferricauda* showed no patch preference related to total flower number. Seed production per flower was not related to the total number of flowers presented in patches at one time. The average proportion of robbed flowers through the entire flowering episode of *P. dasypetala* was 36% among 66 patches at one site and 35% among 5 patches at a second site. Reduced seed production was not caused directly by robber damage to flowers, but indirectly through successful deterrence of birds via joint attacks by bees on and near the flower visited by a hummingbird. Further, although fewer seeds were produced by robbed flowers overall, robbed and unrobbed flowers in patches that were heavily robbed did not differ in seed production. Thus robbing primarily influenced reproductive success at the level of the flower patch. *P. dasypetala* was self-pollinating, yet unrobbed flowers that were not bagged produced 67% more seeds than those not visited by *P. superciliosus*. Persistent robbing by *Trigona* may result in selective advantage for autogamous or apomictic *P. dasypetala*.

Key words: aggressive interference; apomixis; autogamy; competition; floral larceny; nectar robbing; *Pavonia*; *Phaethornis*; *Trigona*; tropical plant-pollinator communities.

INTRODUCTION

Plants that offer food to pollinators may also attract animals that collect nectar and pollen without pollinating. Sustained interaction between such animals and flowers presumably leads to floral adaptations such as long, narrow nectar channels or other barriers to nonpollinators (Faegri and van der Pijl 1976, Opler 1981). However, completely effective barriers against robbers, organisms that enter the flower by piercing or biting, are uncommon (Inouye 1981, Opler 1981). Bee robbers of flowering plants abound in the tropics, but only three genera are known to rob flowers (Janzen 1975, Barrows 1976, Roubik 1979a, Eickwort and Ginsberg 1980, McDade and Kinsman 1980, Inouye 1981, Opler 1981). One of these genera, *Trigona* (Apidae: Meliponinae, tribe Trigonini) visits a wide range of flowers (Heithaus 1979a, b, Roubik 1979a, b) and is able to recruit nest mates, often arriving at flower patches in large numbers (Johnson and Hubbell 1975, Hubbell and Johnson 1978, Roubik 1980). Few meliponines are robbers; only 2 of 12 neotropical subgenera of *Trigona* (Wille 1979) damage flowers. Their ecological role as robbers helps clarify the se-

lective pressures that may broadly influence plant evolution in the tropics.

Interactions between robbing *Trigona* and pollinating hummingbirds have been quantified by McDade and Kinsman (1980). The present study further explores interactions of these taxa and their impact on seed production. The forest edge shrub *Pavonia dasypetala* (Malvaceae) was studied in central Panama. Its sole pollinator was the Hermit Hummingbird *Phaethornis superciliosus* (Trochilidae: Phaethorninae). A second hummingbird, *Phaethornis longuemareus*, was a nectar thief at *Pavonia*; it inserted the beak between epicalyx bracteoles and extracted nectar without damaging the flower. (See Inouye 1980 for discussion of differences between thieves and robbers.) This species seldom thieved from *Pavonia*, but the highly social bee *Trigona* (*Trigona ferricauda*) was an abundant and persistent nectar robber. *T. ferricauda* removed plant tissue from the epicalyx and calyx to reach the nectary, leaving a circular hole (Fig. 1). Like other members of its subgenus, this bee has toothed mandibles, may aggressively interfere with the activity of other foragers, and uses a pheromone to recruit nest mates to a resource (Michener 1974, Hubbell and Johnson 1978, Roubik 1980). Colonies of *T. ferricauda* consist of a few thousand workers and occupy cavities in the nest of the arboreal termite, *Nasutitermes corniger* (Roubik, *in press*). Study of *T.*

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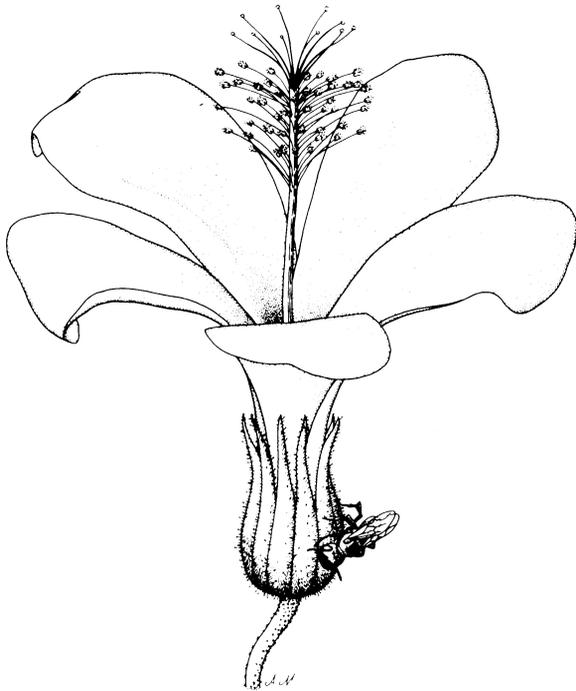


FIG. 1. A worker of *Trigona* (*Trigona*) *ferricauda* (Meliponinae) robbing nectar through a hole it has made in *Pavonia dasypetala* (Malvaceae).

ferricauda offers insight on the impact of an aggressive nectar robber and its role in the reproductive biology of a tropical plant.

METHODS AND BACKGROUND

Study plant and localities

The study was conducted primarily on a 2.5-km transect of tropical moist forest, within 40-yr-old forest edge bordering "Pipeline Road," beginning 14 km north of Gamboa within Parque Nacional Soberania, Panama. A second stand of plants was studied at the edge of a forest stream near Cerro Jefe, Panama Province, approximately 25 km east of the Pipeline Road site. Forest abutting both study transects is relatively mature and undisturbed.

Pavonia dasypetala is found at forest edges from Venezuela to Costa Rica (Croat 1978). This shrub or small tree reaches 5 m height. In Panama, flowering began in November during the late wet season and continued until early January (Croat 1978, D. W. Roubik, *personal observation*). Like all members of its genus, *P. dasypetala* has five locules, each of which may produce one seed (Robyns 1965). Ten stigmas are exerted beyond the anthers (Fig. 1). However, in some plants stigmas contact the anthers. Furthermore, the position of the pistil changes during the day: at anthesis the styles may be erect, but by late morning they may curve downward and contact anthers.

Flowers of *P. dasypetala* lasted for a single day.

The large pink flowers are covered at their base by an epicalyx of unfused bracteoles (Fig. 1). The epicalyx remains attached to the pedicel after the corolla is shed and encloses developing seeds. Seeds matured and dropped to the ground within 30 d of pollination. Ovules swelled rapidly after pollination, reaching roughly five times the diameter of unfertilized ovules within a week. Abortion of pollinated ovules rarely, if ever, occurred.

At Pipeline Road, 245 flowering plants were studied along a 2.5-km transect. Plants were grouped in 98 patches containing 1–12 individuals. Patch size varied from approximately 2–12 m in length and 2–4 m in width, with a mean interpatch distance of 24.5 m (range 6–110 m). Plants within a patch may be closely related, but vegetative propagation appeared absent.

Forager behavior

Flower visitors were observed during the time of their maximum activity, 0700 to 1100 local time, at 14 patches of *P. dasypetala* near Pipeline Road for 4 d each. From 24 November to 10 December 1979, I recorded the number and species of visitors at flowers and their behavior. Each patch was watched for 5–8 15-min periods, at near 15-min intervals. Observations at a patch were made during 2 successive d, followed by a 10-d interval, then repeated for 2 more d. The number of flowers visited by each hummingbird entering a patch was recorded. Each day the number of flowers, the number perforated by bees, and total bees in each patch were counted.

The amount of nectar consumed by robbing bees was determined by capturing individuals feeding at flowers and squeezing the abdomen with the fingers, directly collecting all the nectar contained in their crop from the mouthparts with a 10- μ L microcapillary tube.

Seed, flower, and nectar production

Seed production within patches at the Pipeline Road site was determined by harvesting over 90% of capsules from all plants in 66 patches after most flowering had terminated. At the Cerro Jefe site, capsules were collected in a similar manner from 5 patches. Ovules that were green and not expanded were not scored in the census because they may have been fertilized. However, ovules that were brown and shrunken were scored as unfertilized. Patches scored at Pipeline Road included the 14 patches that were observed for flower visitors.

Pollinators were excluded from 200 flowers on 36 plants in 28 patches at the Pipeline Road site. A bag was placed over buds and tied at the base of the panicle; seed set was then determined at least 1 wk after flowering.

During the mapping of patches at Pipeline Road, the total number of panicles in a patch was counted. Panicle number remained constant through the flowering episode. To obtain an estimate of total flowers pre-

sented at one time in a patch based on panicle number, the number of open flowers was counted on 312 panicles in 25 patches.

Standing nectar crop was determined for 168 open flowers in 10 flower patches on Pipeline Road. Measurements were made between 1000 and 1230 on 5 d after floral visitation by hummingbirds had essentially ceased. Nectar was taken directly from the nectary and the base of the corolla with a 10 μ L microcapillary tube. Corollas were removed for nectar extraction because the microcapillary tube could not be inserted through the narrow nectar channels. Dissolved sugar content in floral nectar as well as that extracted from bees (see above) was determined with a hand-held refractometer (Atago Company, Tokyo, Japan), which is calibrated as gram sucrose equivalent/100 g solute.

RESULTS

Interactions among pollinators and robbers

During 87 h observation the hummingbird *P. superciliosus* visited 7004 flowers during 456 foraging bouts in patches. *T. ferricauda* robbed flowers in each observation patch and usually fed individually at flowers. Bees attacked *P. superciliosus* on 529 occasions. In general, a bee robbing a flower approached by a hummingbird, and those on adjacent flowers, left the epicalyx and flew rapidly at the bird, possibly attempting to bite. When contacted by bees, the hummingbird flew immediately to another portion of the patch but seldom abandoned it. Hummingbirds often appeared to extract nectar successfully from a flower before being driven away by aggressive bees. In no instance did birds chase or attack bees.

The presence of robbing *T. ferricauda* markedly affected the number of flower visits by *P. superciliosus*. Heavily robbed patches (\bar{x} = 70% of flowers robbed, range 32–94%, n = 14) received 0.9 visits \cdot flower $^{-1}$ \cdot h $^{-1}$ during days of observation. Those patches with few robbed flowers (\bar{x} = 9%, range 0–23%, n = 10) received an average of 1.8 visits \cdot flower $^{-1}$ \cdot h $^{-1}$ on observation days. Statistical differences in these visitation patterns were significant at P < .001 (rank-sums test). The subset of visitation data for this analysis was taken only from patches that received substantial visitation from both *T. ferricauda* and *P. superciliosus* throughout the day. Although bees and birds visited all patches, the number of birds visiting some of them was quite low. For instance, two flower patches contained up to 45 robbing bees, the maximum seen in any patch, and they received almost no visits from hummingbirds. The total number of flowers in the above patches does not help explain the patch preferences of robbers. Total flowers in heavily and slightly robbed patches did not differ (\bar{x} = 121 and 101, respectively; P = .09, rank-sums test). However, the choice of patches by *P. superciliosus* was apparently influenced by the number of open flowers. As seen in

TABLE 1. Test of independence between total foraging bouts (entries into a patch) per observation day by *Phaethornis superciliosus* and flower number in patches of *Pavonia dasypetala*. Categories were divided about their average values.

Number of flowers in patch	Number of foraging bouts by <i>Phaethornis superciliosus</i>	
	≤ 11	> 11
	Number of observation days on which indicated number of foraging bouts were seen	
<85	17	5
≥ 85	9	15
	$\chi^2 = 7.388, P = .007, df = 1.$	

Table 1, the number of foraging bouts was not independent of flower number (P = .007, χ^2 test).

Trigona ferricauda was the only species that perforated flowers, and foragers from one colony apparently dominated each patch. Evidence for the latter was seen when one group of approximately 25 bees arrived at a patch where other bees foraged. When the second group arrived, a series of threat displays was initiated. Pairs of bees faced each other while in flight and rose into the air above flowers. This ritualized threat behavior between aggressive *Trigona* from different colonies has previously been reported by Johnson and Hubbell (1975) and Roubik (1980). Foragers landed on unopened flowers and deposited a substance with the mouthparts that attracted other bees, which subsequently landed on the bud and briefly searched. After a period of 1 h, one group of bees departed from the patch. Only once was intraspecific aggression observed, suggesting that flower patches are normally partitioned among colonies. Individual bees arrived at flowers at dawn and spent up to 30 min making a hole 2–4 mm in diameter in the epicalyx and calyx. Bees visited patches throughout the morning and, although hummingbird visitation declined in the afternoon, some bees continued to feed at flowers.

Two small *Trigona*, *T. (Trigona) buyssoni* and *T. (Plebeia) franki* were secondary robbers, exploiting perforations made by *T. ferricauda*. Three additional species, *T. (Trigona) corvina*, *T. (Trigona) silvestriana* and *T. (Trigona) fulviventris* were occasional secondary robbers, but *silvestriana* also extensively damaged flowers by removing large segments of the corolla, pistils and stamens. However, each of these species was present in few patches and in numbers of <5.

Robbing bees did not greatly deplete floral nectar during a single visit to flowers, and their rate of feeding and turnover at flowers was low. One bee fed on a flower consistently during 15-min observations at flower patches. Nectar quality in bees matched that of the flowers, having a mean sugar content of 18.54%,

TABLE 2. Chi-square analyses of patch preference based on number of flowering *Pavonia dasypetala*, as reflected in total foraging bouts, for *Phaethornis superciliosus* and *P. longuemareus*.

Number of flowers in patch	Number of foraging bouts	
	<i>P. longuemareus</i>	<i>P. superciliosus</i>
<85	21	141
≥85	13	315
	$\chi^2 = 1.882,$ $P = .170, df = 1.$	$\chi^2 = 66.394,$ $P < .001, df = 1.$

SD = 4.04% ($n = 156$). While the average amount of nectar in foraging *T. ferricauda* was 2.0 μL ($n = 21$) and an unusually distended forager had consumed 3.7 μL of nectar, the maximum standing crop of nectar in an open and unrobbed flower was 35 μL . The average amount of nectar in 108 flowers that were not robbed by *Trigona*, but may have been visited by hummingbirds, was 8.87 μL , range 0–35 μL . A random sample of 60 robbed flowers held an average of 3.15 μL nectar, range 0–15 μL . Given the large variability in standing nectar crop in unrobbed flowers, differences between robbed and unrobbed flowers might have been due to sample bias and differential visitation by hummingbirds. However, the figures indicate that nectar production exceeded that which could be removed by bees in less than several visits. The relatively long time spent at a flower with a completed perforation implies that the bees were slow to extract nectar.

The foraging behavior of thieving *P. longuemareus* and pollinating *P. superciliosus* was broadly similar but differed in relation to flower number in patches. Total foraging bouts observed for both species are given in Table 2. Foraging bouts of *P. longuemareus* were independent of flower number, but *P. superciliosus* more often visited patches with many flowers ($P = .17$ and $P < .001$, respectively; χ^2 test; see also Table 1). Foragers of both species chased arriving congeners from patches. A total of 48 such pursuits was seen. *P. longuemareus* made 424 visits to flowers during 34 foraging bouts. On a per patch basis, it visited an average of 12.8 flowers, compared to an average of 15.4 (7004/456) flowers visited by *P. superciliosus*. The total flowers in patches visited by *P. superciliosus* was, on the average, 99 (SD = 55, range 23–232), and the average number of flowers in patches visited by *P. longuemareus* was 105 (SD = 70, range 27–232).

Impact on seed production

Since a perforated epicalyx remained on the pedicel several weeks, nectar robbing by *T. ferricauda* was evident on *P. dasypetala* long after it occurred. After most flowering had ended, from 58 to 1469 capsules ($\bar{x} = 486$) were collected from each of 66 patches on Pipeline Road. Seed production clearly was not independent of the proportion of robbed flowers in patches

TABLE 3. Test of independence between nectar robbing by *Trigona ferricauda* and potential seed set in 66 patches of *Pavonia dasypetala*.

Percentage of total flowers robbed*	Percentage of potential seed produced	
	≤55	>55
	Number of patches in which the indicated percentages of seed were produced	
≤36	14	19
>36	25	8
	$\chi^2 = 7.584, P = .006, df = 1.$	

* Mean was used to divide category.

($P = .006$, Table 3). Although the combined data from all patches show that robbed flowers produced fewer seeds than unrobbed flowers ($P < .001$, Table 4) robbed and unrobbed flowers within heavily robbed patches ($\bar{x} = 70\%$ robbed) did not differ in average seed set ($P > .6$, Table 5). Thus diminished seed production was not caused directly by damage to robbed flowers but by the effect of robbers on hummingbird visitation in the entire patch.

The degree of robbing by *T. ferricauda* was comparable at the Pipeline Road and Cerro Jefe sites. At Cerro Jefe, where an average of 375 capsules was collected from each of five patches, the proportion of robbed flowers was from 4–82%, $\bar{x} = 35\%$. On Pipeline Road, the average proportion of robbed flowers in patches was 36%, range 2–97%.

An a posteriori test of foraging choice by pollinators and robbers was made by comparing panicle number in patches to the proportion of robbed flowers and total seed set in 66 patches on Pipeline Road. Panicle number did not change during the flowering period of *Pavonia*, and the number of open flowers in patches generally corresponded 1:1 with the number of panicles. This is suggested from census data from 25 patches in which 245 panicles held one open flower, 67 held two and 19 held three. If panicle number corresponded to the number of open flowers in patches, then there was no association between flower number and seed production, or flower number and the proportion of total flowers robbed ($P > .55$, χ^2 test, Table 6). Although indirect, this analysis gives the same result as the previous analysis of bee visitation. Combined with information given in Tables 1 and 2, these data show that patch visitation by *P. superciliosus* increased with total floral display, but the number of pollinations per flower did not.

Bagged *P. dasypetala* produced seeds, but an average of one-third fewer seeds were produced compared to unbagged flowers. At the Pipeline Road site the average seed set of 200 unrobbed, bagged flowers was 1.55. Among 2008 unbagged, unrobbed flowers, most on the same plants as the bagged flowers, aver-

TABLE 4. Contingency table test of independence between nectar robbing by *Trigona ferricauda* and seed production per capsule in 66 patches of *Pavonia dasypetala*.

Damage by robbers	Number of seeds per capsule						\bar{x}	SD
	0	1	2	3	4	5		
	Number of capsules with indicated numbers of seeds							
Present	4912	1263	1099	1346	2318	3588	2.39	2.06
Absent	4287	1064	1057	1905	3589	5234	2.88	2.00

$\chi^2 = 496.57, P < .001, df = 5.$

age seed set was 2.54. Differences in seed production were pronounced among bagged and open flowers producing five or no seeds ($P < .001, \chi^2$ test), yet comparable proportions of bagged and open flowers produced one to four seeds ($P > .9, DF = 3, \chi^2$, see Table 7).

P. superciliosus is strongly implicated as the pollinator; it visited at least several flowers in a patch and, although interpatch movement of individuals was not monitored, birds regularly moved from one patch to another. Further, when entering flowers this species contacted both anthers and stigmas. Self-pollination may be slightly enhanced by hummingbird visitation, but in most cases a bird visited a flower only once during a foraging bout and probed only once at a flower. The birds entered the corolla parallel to the nectar channel, and stigmas were contacted before anthers. Outcrossing undoubtedly occurred, but the amount of pollen received from a flower's own anthers or those of flowers on the same plant, compared to that of other plants, cannot be deduced from these data.

DISCUSSION

Barriers to nectar robbers include the epicalyx bracteoles of *P. dasypetala* and the thick tissue surrounding its narrow nectar channels. In addition, the calyx protects the nectary. Similar structural traits have been noted in a variety of bird-pollinated plants, implying that robbing by insects, as well as competition with the pollinators, is reduced (Proctor and Yeo 1973, Stiles 1978, Bond and Brown 1979, Faegri and van der Pijl 1976, Inouye 1981). The brief life span of individual flowers conceivably enhances these defenses. Considerable expenditure of time and energy was necessary for *T. ferricauda* to harvest nectar from *Pavonia*. The profitability from robbing is reduced if the flower lasts a single day, since no additional investment by robbers would be required if flowers produced

TABLE 5. ANOVA of average seed set per flower among robbed vs. unrobbed flowers of *Pavonia dasypetala* in heavily robbed patches.

Source of variation	df	SS	MS	F	P
Between flower classes	1	.144	.144	.21	.65
Within flower class	21	14.122	.672		

nectar for longer periods. Similarly, the relatively low sugar content of floral nectar offered by species not pollinated by bees (Ordetx 1952, Proctor and Yeo 1973, Baker 1978, Pyke 1980) is a plausible deterrent to relatively small foragers that can carry and use only a small amount of food at one time. Furthermore, small solitary bees, none of which has stores of carbohydrate within the nest, are not known to rob nectar, as do *Trigona* of comparable size. Although *P. dasypetala* cannot prevent robbing by *T. ferricauda* it seems significant that other common *Trigona* that rob nectar and pollen did not attempt to rob or dominate this flower species. In the Pipeline Road area, nectar and pollen robbers include *T. p. pallens*, *T. silvestriana*, *T. fuscipennis*, *T. fulviventris*, *T. corvina*, and *T. cupira* (D. W. Roubik, personal observation). *T. ferricauda* may deter some of these species, that might otherwise cause an even greater reduction in seed production. However, the plants clearly sustained a quantitative reproductive loss due to aggressive interference of *T. ferricauda* with *P. superciliosus*. An alternative hypothesis that nectar robbers or aggressive foragers may enhance outcrossing by increasing resource patchiness and/or forcing pollinators to travel more frequently between flowers (Frankie 1975, Heinrich 1975, Carpenter 1976, Roubik 1979a) would be attractive under very restricted conditions (see McDade and Kinsman 1980). In the present study, data are lacking to confirm that diminished reproductive output would be offset by increased seed or seedling

TABLE 6. Contingency table tests of independence between total flowers per patch and nectar robbing by *Trigona ferricauda* and the percentage of potential seed produced in 66 patches of *Pavonia dasypetala*. An average of 32 panicles per patch was counted in 98 patches.

Number of panicles per patch	Percentage of flowers robbed		Percentage of potential seed produced	
	≤50	>50	≤50	>50
	Number of patches in which indicated percentages were recorded			
≤32	19	14	13	20
>32	19	14	10	21

$\chi^2 = 0, P = 1.0, df = 1$ $\chi^2 = 0.353, P = .552, df = 1$

TABLE 7. Comparison of seed set in bagged flowers and in unbagged, unrobbed flowers of *Pavonia dasypetala*.

Visitation by pollinators	Number of seeds per capsule						
	0	1	2	3	4	5	0-5
	Numbers of capsules with indicated numbers of seeds						
Presumed (unbagged flowers)	632	184	143	175	299	575	2008
Absent (bagged flowers)	106	16	17	14	20	27	200
χ^2*	29.44	00.295	00.533	00.675	3.21	15.99	44.882
df	1	1	1	1	1	1	5
P	<.001	.587	.465	.411	.073	<.001	<.001

* Expected values for row two (bagged flowers) were derived from the observed proportions in row one (unbagged flowers).

success. Moreover, since adaptations against robbing are evident, it strains credulity to suggest that plants respond differentially to an array of robbers, some of which may interact mutualistically. Such mutualism may be incidental, but is almost certainly not co-evolved. Available information on food plants used by *P. superciliosus* shows that all 22 species visited in lowland wet forest of Costa Rica present flowers that last a single day, although the plants produce flowers for an extended period (Stiles and Wolf 1979, McDade and Kinsman 1980). *Quassia amara* (Simaroubaceae) is a notable exception (D. W. Roubik, *personal observation*), but Stiles (1978) shows that most species visited by hermit hummingbirds in Central America present flowers that last 1 d. I suggest that this phenomenon may be attributed in part to the selective advantage of deterring robbing *Trigona* by minimizing the reward made available to them.

Both autogamy and apomixis are advantageous to colonizing plants (Faegri and van der Pijl 1976, Solbrig 1979). In addition, when floral larceny is intense, autogamy and apomixis each reduce its negative impact. Controlled pollinations of *P. dasypetala* are necessary to show whether apomixis occurs. However, the large proportion of flowers setting no seed in bagged inflorescences, and low proportion setting five (Table 7) suggest apomixis is unlikely. That flowers transfer pollen to their own stigmas implicates autogamy. Movement of stigmas to contact anthers in some plants underscores the need to study self-pollination as a device to ensure some seed set in the absence of pollinators.

Combined aggressive interference from many relatively small bees permitted successful group defense of *P. dasypetala* against larger, unaggressive hummingbirds (see also Carpenter 1979). Robbing *Trigona* of the subgenus *Trigona* often arrive at resources in large numbers and recruit nest mates (Johnson and Hubbell 1975, Hubbell and Johnson 1978, Roubik 1980, 1981). *Phaethornis superciliosus* is the largest hermit hummingbird in Panama (Ridgely 1976). Since a group of *T. ferricauda* (<7 mm length) effectively deterred *P. superciliosus* from flowers, it is likely that aggressive *Trigona* of similar size deter many other pollinators. Robbing *Trigona* may present a reproduc-

tive hazard to many species of flowering plants throughout the tropics (see Hubbell and Johnson 1977, Michener 1979). The evolution of reproductive structures, flowering dynamics and perhaps the breeding systems of these species could well be influenced by the foraging habits of *Trigona*.

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