Pollination Ecology and Effect of Nectar Removal in *Macleania bullata* (Ericaceae)[1]

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ABSTRACT

The floral syndrome of *Macleania bullata* Yeo (Ericaceae) reflects its adaptation to hummingbird pollination. Its flowers, however, are subject to high levels of nectar robbing. I examined the floral visitor assemblage of *M. bullata* in a tropical montane wet forest in southwestern Colombia, focusing on the behavior of the visitors. I also tested for the presence of nocturnal pollination and the effects of nectar removal on new nectar production. The principal floral visitors were the nectar robbing hummingbirds *Ocreatus underwoodii* (19.1% of visits) and *Chlorostilbon mellisugus* (18.9%). Only two species of long-billed hummingbirds visited the flowers of *M. bullata* as "legitimate" pollinators: *Coeligena torquata* (14.7% of visits) and *Doryfera ludoviciae* (14.3%). The remaining visits constituted nectar robbing by bees, butterflies, and other species of hummingbirds. Nocturnal pollination took place, although fruit set levels were 2.4 times higher when only diurnal pollination was allowed as opposed to exclusively nocturnal pollination. Nectar robbers removed floral nectar without pollinating the flower. Treatments of experimental nectar removal were carried out to examine if flowers synthesize more nectar after nectar removal. Nectar removal increased the total volume of nectar produced by each flower without affecting sugar concentration. Thus, nectar robbing can impose a high cost to the plants by forcing them to replace lost nectar.

RESUMEN

El síndrome floral de *Macleania bullata* Yeo (Ericaceae) refleja su adaptación a la polinización por colibríes. Sin embargo, las flores están sometidas a un continuo robo de néctar. Examiné el conjunto de visitantes florales de *M. bullata* en un bosque pluvial montano tropical localizado en el suroeste de Colombia, haciendo especial hincapie en el comportamiento de los visitantes durante sus visitas florales. Además, evalué la aportación que los posibles polinizadores nocturnos hacen a la producción de frutos, así como también el efecto que tiene la eliminación de néctar en una nueva producción de esta recompensa floral. Los principales visitantes florales fueron dos especies de colibríes robadores de néctar: *Ocreatus underwoodii* y *Chlorostilbon mellisugus* (19.1 y 18.9% de las visitas observadas respectivamente). Unicamente dos especies de colibries de pico largo visitaron las flores de *M. bullata* comportándose como polinizadores "legítimos": *Coeligena torquata* (14.7% de las visitas) y *Doryfera ludoviciae* (14.3%). El resto de las visitas observadas correspondieron a diferentes especies de colibríes, abejas y mariposas robadores de néctar. Aparentemente *M. bullata* recibe la visita de polinizadores nocturnos, aunque el nivel de fructificación obtenido en las flores a las que se permitió unicamente el acceso de visitantes diurnos fue 2.4 veces superior al registrado en aquellas flores a las que se permitió unicamente el acceso de visitantes nocturnos. Los robadores de néctar extraén el néctar sin realizar polinización. Con el fin de verificar si las flores son capaces de sintetizar más néctar cuando éste es extraido, se realizaron experimentos de extracción de néctar. Los resultados mostraron que al eliminar néctar de las flores, éstas vuelven a producir más, incrementando el volumen total de néctar producido por una flor, sin afectar por ello a la concentración de azúcar. Así, desde el punto de vista energético, el robo de néctar puede suponer un alto costo para las plantas, puesto que se ven obligadas a producir cantidades adicionales cuando éste es eliminado.

Key words: Colombia; diurnal pollination; hummingbird pollination; Macleania bullata; *nectar robbing; nocturnal pollination.*

INTERACTIONS BETWEEN HUMMINGBIRDS AND PLANTS IN THE NEOTROPICS are said to involve two distinct kinds of interactions: short hummingbird-pollinated flowers (corolla lengths <25 mm) receiving "legitimate" visits almost exclusively from hummingbirds with correspondingly short bills (<25 mm

total culmen length), and long flowers (corolla lengths (≥30 mm) receiving visits primarily from hummingbirds with correspondingly long bills (>28 mm total culmen length; Feinsinger & Colwell 1978, Stiles 1981, Feinsinger 1983). This simple dichotomy, however, ignores floral visitors that are not adapted to these floral morphologies but who obtain nectar by piercing floral tissues without contacting the anthers and stigma (Feinsinger *et al.* 1987). As a consequence of nectar robbing, plants might be expected to secrete more nectar than oth-

erwise required to maintain attractiveness to legit-imate pollinators that transfer pollen effectively. In this sense, Roubik *et al.* (1985) showed that on a population of *Quassia amara* (Simaroubaceae) that did not receive nectar-robbing visits, nectar pro-duction was lower than in populations with a high incidence of nectar robbing. Thus, a plant's re-sponse to nectar robbing might be to synthesize more nectar after nectar is removed by robbers. New nectar production, however, might impose a high cost to the plant (Southwick 1984, Pyke 1991). Pyke (1991) reported that nectar removal increased the net quantity of sugar secreted by *Blandfordia nobilis,* but also entailed a cost to the plant; seed production was significantly lower than on plants from which no nectar was removed (Southwick 1984). In those studies that examined the effect of nectar removal on production rates (Raw 1953; Feinsinger 1978; McDade & Kinsman 1980; Plowright 1981; Pleasants 1983; Gill 1988; Pyke 1991; Cocucci *et al.* 1992; Galetto & Ber-nardello 1992, 1993; Bernardello *et al.* 1994; Ga-letto *et al.* 1994; Guitián *et al.* 1995), the patterns of response were diverse. Considering the costs to the plant imposed by nectar robbing, Haber and Frankie (1982) suggested that the pressure repre-sented by diurnal nectar robbers could result in evolutionary shifts from diurnal to nocturnal pol-lination.

In spite of the potential importance of nectar robbery in natural populations of hummingbird-pollinated plants, detailed information on the be-havior of floral visitors has been largely ignored. In other work on the floral biology and breeding sys-tem of *M. bullata* (Ericaceae), I have shown that its flowers are typical of those pollinated by long-billed hummingbirds; however, although floral size and morphology greatly limit visitor access, the flowers under natural conditions are subject to fre-quent nectar robbing (74.9% of 1000 flowers re-corded). I also found that robbed flowers set fewer fruits than non-robbed flowers (8.2 vs. 28.7% of fruit set, respectively; Navarro, pers. obs.). The goals of the current study were to: (1) study the visitor assemblage of *M. bullata* in a tropical mon-tane wet forest in southwestern Colombia, with an evaluation of visitor behavior and the frequency of nectar robbers; (2) examine if nocturnal pollination exists; and (3) evaluate the response of flowers to nectar removal. The last experiment was carried out to evaluate the assumption that continuous pres-ence of nectar robbers removing nectar without pollinating imposes an energetic cost to the flowers if they synthesize more nectar following removal.

STUDY SITE.—The study was carried out in the Re-serva Natural La Planada, near the village of Ri-caurte (1°10′N, 77°58′W; Departamento de Na-riño, Colombia). The reserve is located on the western flank of the Andes and comprises 3200 ha of montane wet forest (bmh-PM sensu Holdridge 1996) at altitudes of 1200 to 2100 m. Mean an-nual precipitation is 4375 mm (Carlos Valderrama, pers. comm.) and annual mean temperature ranges between 12 and 23°C.

PLANT NATURAL HISTORY.—*Macleania bullata* Yeo. (Ericaceae) is an epiphyte, which in the study area, typically forms part of the fringe community around mature forest. It has several flowering peaks during the year. Flowers are hermaphroditic with a fleshy, orange–red, tubular corolla *ca* 42-mm long. The style is slightly exerted and the short anthers are beneath the style. The small diameter of the corolla tube denies access to the nectar by avian visitors with bill diameters > 5 mm. Also, the co-rolla's length does not permit "legitimate" visits by animals having bills ≤ 35 mm. Flower life is four days. Anther dehiscence occurs during the first two days, and 100 percent of stigmas are receptive from the third day onward. Results from other studies in the same population and year showed that fruit production following pollinator exclusion was zero. Fruit set following xenogamous pollen transfer ($\bar{x}$ ± SD = 36.8 ± 2.8%) was significantly higher than both population control (11.8 ± 4.3%) and autogamous pollen transfer (6.3 ± 4.0%). Supple-mentary hand-pollination on open flowers did not significantly increase fruit set over control plants (15.4 ± 5.5%) but was significantly lower than that from xenogamous pollen transfer (L. Navarro, pers. obs.). The fruit, a translucent white berry when mature, probably is eaten by frugivorous birds. Voucher specimens of *M. bullata* from the study site were deposited at the herbarium of the Universidad de Pasto in Departamento de Nariño, Colombia.

METHODS

Direct observations of flower visitors were made in an area no larger than 14 m² that could be ob-served easily from *ca* 4 m away. Surveyed plants belonged to the fringe community around mature forest and were < 3-m high. The number of flow-ers in this area ranged between 400 and 700 during surveillance sessions. Visits were tallied during a se-ries of 30-min surveillance sessions at different times of day and totaled 36 h. For each visit, I

recorded the species of flower visitor and counted the number of flowers probed per branch. I also recorded the type of visit (nectar extraction or primary nectar robbery when the visitor made a hole in the corolla tube, and secondary nectar robbery when the visitor took advantage of a previously made hole).

The amount of nectar available to visitors was measured on randomly selected flowers with capillary micropipettes at the time of the visitor censuses (just before each surveillance session and after the last time interval: 0600, 0800, 1000, 1200, 1400, 1600, and 1800 h; $N = 20$ different flowers/time interval). Sugar concentration in the nectar was determined with a portable refractometer; the amount of sugar (mg/flower) was then calculated according to Prys-Jones and Corbet (1987).

To evaluate the relative importance of pollination at different times of day, I used four plants, bagging all flowers on two branches of each plant (one branch for each treatment) as follows: (1) nocturnal exclusion: flowers exposed to visitors from dawn to dusk (0600–1800), but bagged at night ($N = 98$ flowers); and (2) diurnal exclusion: flowers exposed from dusk to dawn, but bagged during the day ($N = 115$ flowers).

Fruit set for each treatment was recorded two months later and compared to that obtained in the control population (11.8 ± 4.3%) during the same year. The control population was obtained from flowers of branches on the same plants in which nocturnal/diurnal exclusion experiments were carried out. These flowers were opened to pollinators (L. Navarro, pers. obs.).

To investigate if nectar removal induces nectar secretion, I marked 48 flowers of 12 different plants with indelible ink and bagged them with mosquito netting. Flowers that lasted four days were subjected to one of four treatments: (A) removal of nectar four times during the flowers' life span (once a day after anthesis); (B) removal of nectar three times (once a day after the first day); (C) nectar removal two times (once a day after the second day); and (D) nectar removal only on the last day. Nectar was extracted without removing the flower from the plant and always at ca 0900 h. To do so, I made a hole in the base of each corolla tube with a jackknife and extracted the nectar. Thus, I avoided contacting the anthers and stigma with the capillary micropipette. Care was taken to avoid damage to nectaries. The mean amounts of sugar produced by flowers of each group were compared by analysis of variance (ANOVA).

DATA ANALYSIS.—Number of flowers visited by vis-itors on each foraging visit, standing crop of nectar at different times of day, or the effect of nectar removal on further secretion for each of four treatments were compared using ANOVA. Percentage data were subjected to an arcsine transformation prior to ANOVA. Comparison of fruit set levels from the nocturnal and diurnal exclusion experiment and control was achieved using the Friedman one-way ANOVA with an a posteriori contrast.

RESULTS

POLLINATION ECOLOGY.—Of the 556 visits recorded (Table 1), 29.0 percent were "normal" nectar extraction visits, 29.3 percent were visits by primary nectar robbers, and the rest (41.7%) were visits by secondary nectar robbers. Thus, the percentage of the number of flowers visited "legitimately" by hummingbirds to those visited by robbers was 0.41. The legitimate visits were all made by two long-billed hummingbirds, *Coeligena torquata* and *Doryfera ludoviciae*. Between these two species, *D. ludoviciae* visited more flowers per branch than *C. torquata* ($F_{1,159} = 26.2$; $P < 0.0001$). The principal species of primary nectar robber was the hummingbird *Chlorostilbon mellisugus*. The main species of secondary nectar robbers were the hummingbird *Ocreatus underwoodii*, the hymenopteran *Trigona* sp., and the lepidopteran *Pronophila orcus*. Robbery occurred both before (especially by *Diglossa cyanea*) and after anthesis. None of the robbers appeared to contact the sexual organs of the plant during the process of nectar robbery, although *D. cyanea* tended to shake branches heavily while piercing the flower. Primary nectar robbers pierced the corolla tubes near the base to extract nectar, leaving a conspicuous slit in the floral tissues. Usually, nectar robbing does not involve reproductive tissue damage. Only two percent of robbed flowers showed a damaged style ($N = 356$ robbed flowers); however, it is important to note that stamens can be touched by robbers and cause the release of some pollen.

The relative frequencies of visits by the eight visitors differed throughout the day (Fig. 1). Most visits occurred between 0800–1000 h (19.2 visits/h). The frequency of visits declined to 2.7 visits/h after 1400 h. The two pollinator species limited most of their activity to the morning hours, although *C. torquata* made some visits during the last hours of daylight.

STANDING NECTAR CROP.—Significant differences existed in the volume of nectar available at different

TABLE 1.   *Visitors to* Macleania bullata *in the study area. Number of floral visits and mean number of flowers visited by branch for each of the three foraging modes (P = nectar extraction + pollination; R1 = nectar robber making holes in corolla tubes; R2 = nectar robber using hole made by primary robber). Numbers in brackets show the percentage of total visits.*

Species	Type of visits	No. of visits (%)	No. of flowers visited/branch
Order Hymenoptera			
Trigona sp.	R2	66 (11.8)	1.5 ± 0.8
Order Lepidoptera			
Family Satyridae			
Pronophila orcus	R2	60 (10.8)	1.5 ± 0.8
Order Aves			
Family Trochilidae			
Ocreatus underwoodii	R2	106 (19.1)	2.1 ± 1.2
Doryfera ludoviciae	P	79 (14.2)	3.0 ± 1.7
Coeligena torquata	P	82 (14.7)	1.9 ± 1.5
Chlorostilbon mellisugus	R1	105 (18.9)	1.9 ± 1.5
Aglaiocercus coelestis	R1	40 (7.2)	1.8 ± 1.0
Family Thraupidae			
Diglossa cyanea	R1	18 (3.2)	1.6 ± 0.7
Total		556	

times of day ($F_{6,98}$ = 42.2; P < 0.0001), with greater availability during the early morning (Fig. 2). The volume of nectar available to visitors decreased to values near zero after 1600 h.

DIURNAL VERSUS NOCTURNAL POLLINATION.—Experiments showed that nocturnal pollination exists (Fig. 3), although flowers exposed to diurnal visitors set significantly more fruits than those exposed only to nocturnal visitors. Fruit set was 2.4 times higher in diurnally exposed flowers than in nocturnally exposed flowers. When I compared the results of diurnal and nocturnal bagging experiments with controls in this population (data from Navarro, pers. obs.), the results showed significant differences between two treatments and controls (χ^2 = 6.5; P < 0.05). However, although controls set more fruits than nocturnally exposed flowers, the differences were not significant. Also, flowers exposed only to diurnal pollinators did not set significantly more fruits than controls (Fig. 3). On the other hand, none of the flowers exposed only to nocturnal pollination had signs of nectar robbery.

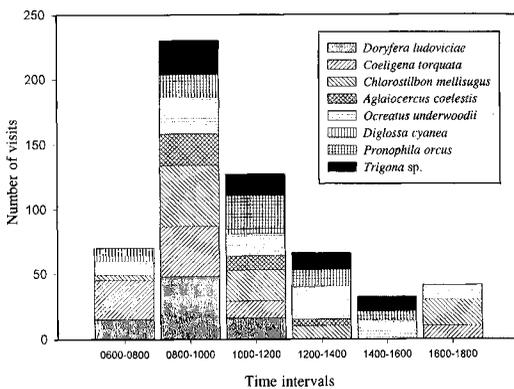EFFECTS OF NECTAR REMOVAL.—Removal of nectar

FIGURE 1.   Diurnal variation in relative frequency of visitors to flowers of *Macleania bullata*.
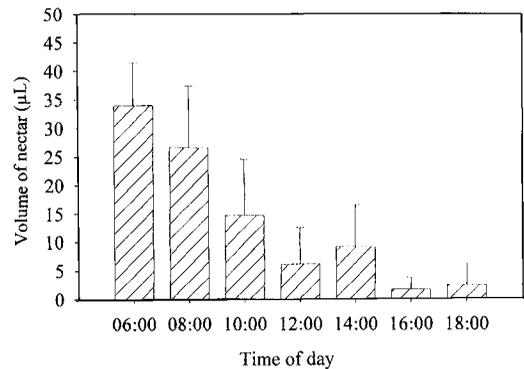

FIGURE 2.   Diurnal variation in nectar volume available to visitors of *Macleania bullata* (N = 20 different flowers per time interval).
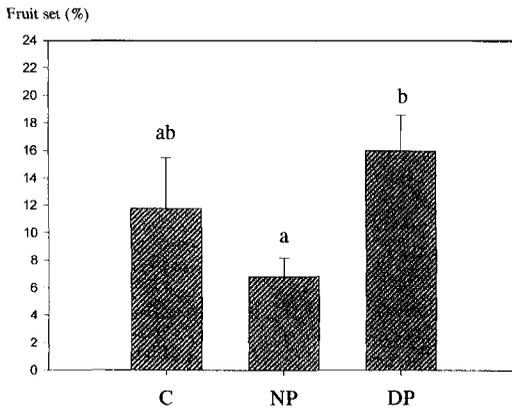
Fruit set (%)

FIGURE 3. Fruit set levels from the pollinator exclusion experiment and control plants (C = control plants; NP = nocturnal pollination; DP = diurnal pollination). Bars with the same letter do not differ significantly (multiple comparisons test).

increased the total volume of nectar produced (Table 2) and did not affect sugar concentration (Table 3). Flowers with nectar removed four times (treatment A) produced about 47 percent more nectar than controls (treatment D), and flowers with nectar removed three times (treatment B) produced about 28 percent more than controls. The nectar volume produced by flowers subjected to treatment C was similar to that of controls. The total mass of sugar secreted during a flower's life span also increased significantly with nectar removal ($F_{3,44}$ = 7.6, P = 0.0003). The total mass of sugar produced was greater in group A than in group B, and greater in group B than in group C. The total mass of sugar produced by flowers of group C was slightly lower than that produced by flowers of group D (Fig. 4).

DISCUSSION

The results obtained for *M. bullata* support the hypothesis that flowers with long tubular corollas are pollinated by long-billed hummingbirds (Baker & Baker 1983), but also show that this type of

flower suffers a high incidence of visits from nectar robbers. Observations showed that the hummingbirds *D. ludoviciae* and *C. torquata* are the exclusive "legitimate" pollinators at the study site, but other species of short-billed hummingbirds, as well as passerine birds, bees, and butterflies visited the flowers of *M. bullata* "illegitimately." Taking into account that legitimate pollinator species showed the highest activity early in the morning, flowers receive pollen at that time while nectar robbing also will take place later in the day.

The short-billed hummingbirds *C. mellisugus* and *A. coelestis* pierce the corolla tubes near the base to extract nectar, leaving a conspicuous slit in the floral tissues. Similar "primary nectar robbery" by short-billed hummingbirds frequently have been recorded for other Neotropical flowers (Colwell 1973, McDade & Kinsman 1980, Willmer & Corbet 1981, Feinsinger *et al.* 1987, Ornelas 1994). The behavior of *D. cyanea*, which robs nectar by piercing the corolla tube, has been described in other plant species and is considered typical of birds in this genus (Colwell *et al.* 1974, Phelps & de Schauensee 1978, Graves 1982, Arizmendi *et al.* 1996). Similarly, the behavior of bees in the genus *Trigona* which take nectar from existing holes, has been reported in other species of flowers with long corollas (Willmer & Corbet 1981).

Nectar robbing is a common phenomenon in bird-pollinated flowers (McDade & Kinsman 1980, Willmer & Corbet 1981, Graves 1982, Roubik *et al.* 1985, Feinsinger *et al.* 1987, Carpenter *et al.* 1993, Powers & Conley 1994, Arizmendi *et al.* 1996, Bittrich & Amaral 1996). Nevertheless, the effect on a flower's reproductive success is not well known. Arizmendi *et al.* (1996), comparing the pollination efficiency of *Diglossa baritula,* a nectar robber of *Salvia mexicana* and *Fuchsia microphylla,* to that of five species of hummingbirds, showed that this flower-piercer did not affect fruit set levels. The number of seeds produced by flowers visited only by this nectar robber, however, was similar to or lower than that of flowers visited by the least efficient pollinator. A number of other studies have

TABLE 2. *Nectar volume (µL; x̄ ± SD) measured in flowers subjected to different removal schedules throughout flowering (see text). NE = not extracted.*

	N	1st day	2nd day	3rd day	4th day
Group A	12	12.9 ± 6.1	29.3 ± 9.6	17.3 ± 7.0	5.6 ± 5.2
Group B	12	NE	32.3 ± 9.3	17.7 ± 6.2	6.8 ± 8.1
Group C	12	NE	NE	29.3 ± 3.9	11.9 ± 6.5
Group D	12	NE	NE	NE	44.4 ± 4.0

TABLE 3.   *Sugar concentration of nectar ($\bar{x} \pm SD$) measured in flowers subjected to different removal schedules throughout flowering (see text). NE = not extracted.*

	N	1st day	2nd day	3rd day	4th day
Group A	12	19.4 ± 1.7	16.8 ± 2.2	17.4 ± 2.3	16.5 ± 3.7
Group B	12	NE	16.8 ± 1.9	17.4 ± 1.2	17.1 ± 1.6
Group C	12	NE	NE	18.4 ± 1.1	19.1 ± 0.9
Group D	12	NE	NE	NE	18.4 ± 0.9

revealed that nectar robbers may enhance reproductive success if their bodies come into contact with anthers and stigmas during the robbery (Macior 1966, Koeman-Kwak 1973, Waser 1979, Graves 1982, Higashi *et al.* 1988, Navarro *et al.* 1993, Scott *et al.* 1993). In *M. bullata,* however, neither the primary nor the secondary nectar robbers contact the plant's sexual organs. Other studies have shown or have suggested a positive effect of nectar robbers, because a consequence of illegal nectar removal is that the nectar variability among flowers is increased to promote a greater number of flower visitations by legitimate pollinators (Heinrich & Raven 1972, Soberón & Martínez del Río 1985, Cushman & Beattie 1991) or greater foraging distances (Zimmerman & Cook 1985). In *M. bullata,* that positive effect of nectar robbing is dubious because nectar variability among flowers is relatively low when legitimate pollinator visits occur, since they have the highest activity early in the morning (Fig. 2). In addition, flowers tend to produce additional nectar when it is removed.

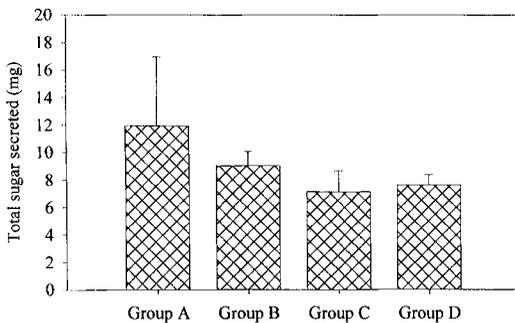In contrast to positive effects, there is some ev-

FIGURE 4.   Total mass of sugar produced by flowers of different treatments with group A corresponding to flowers that had nectar removed four times during their lifespan (once a day after anthesis). Flowers of group B had nectar removed three times (once a day after the first day of life). Flowers of group C had nectar removed twice (once a day after the second day of life). Flowers of group D had nectar removed only on the last day. Bars indicate means with standard deviations.

idence of negative impacts that affect plants which are robbed. These negative impacts can be a consequence of: (1) the reproductive tissue damage produced during nectar robbing; (2) the decrease in floral attraction to legitimate pollinators; and/or (3) the energetic cost of nectar resynthesis. Apparently, nectar robbing in *M. bullata* does not cause relevant reproductive tissue damage, which can reduce seed set in other plants (Galen 1983). Floral attraction to legitimate pollinators can decrease as a consequence of nectar drops in robbed flowers; however, the results obtained showed that flowers that were emptied following experimental nectar robbing, synthesized more nectar with the same quality as the original.

Complementary results in *M. bullata* (Navarro, pers. obs.) were that: (1) both bagged and hand-pollinated flowers produced significantly more fruits than flowers that were opened and pollen supplemented. (Note that this last set of flowers was opened to all visitors and consequently submitted to nectar removal.); and (2) analysis of robbed flowers versus non-robbed flowers showed that the fruit set level on non-robbed flowers was higher and was not a consequence of pollen limitation. This suggests that increased fruit set levels in bagged or non-robbed flowers could be a consequence of energetic savings due to reduced nectar production. Pyke (1991) reported that nectar removal increases the net quantity of sugar secreted by *Blandfordia nobilis*; thus, the energetic cost of this new secretion could lead to reduced fruit set, seed size, and/or seed number.

On an evolutionary time scale, if nectar robbing has a negative effect on the plant species, the costs represented by diurnal nectar robbers could result in shifts from diurnal to nocturnal pollination (Haber & Frankie 1982). In fact, none of the nocturnally exposed flowers in this experiment were robbed. Alternatively, the availability of diurnal and nocturnal pollination suggests the possibility of donating and receiving pollen 24 hours a day, thereby increasing reproductive success in pollen limited species (Jennersten 1988). This does

not seem to be the case in *M. bullata,* since supplemental pollination showed that the study population was not pollen limited (Navarro, pers. obs.). The results of the nocturnal/diurnal exclusion experiments indicate that fruit production with only diurnal pollination is 2.4 times greater than when only nocturnal pollination is allowed. This suggests that pollination of *M. bullata* in the study area is largely diurnal, although diurnal bagging did not significantly reduce fruit set level relative to controls. Thus, it is not clear whether or not the presence of nocturnal pollination in *M. bullata* is a consequence of functional changes in the reproductive mechanism of the plant species due to the high cost of diurnal nectar robbing (Haber & Frankie 1982).

Clearly, the flowers of *M. bullata* provide food for many types of visitors, most of these removing the nectar by robbery without effecting pollen

transfer. As a consequence of nectar robbing, flowers produce more nectar. This additional nectar secretion entails an energetic cost that can lead to a reduction in fruit set. Nevertheless, the real consequences of nectar robbing on plant fitness in *M. bullata* need to be studied further.

ACKNOWLEDGMENTS

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