Patterns of diel nectar production in flowers pollinated by hummingbirds versus insects

Erik R. Schoen, Lindsay V. Reynolds, Erin L. Kinney and Matthew T. Burke

Abstract: Many tropical angiosperms attract pollinators with a nectar reward. To maximize pollinator visits while minimizing costs, plants should coordinate their nectar production with the activity patterns of their pollinators. However, pollinator activity may not correspond to the high temperature and light levels at midday that are most physiologically conducive to metabolic processes. We tested whether diel patterns in nectar production are determined by pollinator feeding times or physiological constraints, measuring nectar production in two herbaceous flowering species, one insect-pollinated (*Hemichaetum fruticosa*), and one hummingbird-pollinated (*Bomarea costaricensis*). Nectar production varied across the day for both species. *B. costaricensis* nectar production peaked in the morning and late afternoon while *H. fruticosa* peaked in the morning. The pattern in *B. costaricensis* seems to match humming bird activity while the pattern in *H. fruticosa* seems suited to an insect pollinator that would visit during midday. Despite potential physiological constraints, these plant species have apparently responded to selective pressure to match the timing of nectar production with the activity rhythms of their pollinators.

Key Words: Bomarea costaricensis, Hemichaena fruticosa, *mutualism, nectar production patterns, pollination*

Introduction

The fitness of many angiosperms depends on their ability to lure pollinators with the colors, shapes, smells and nectar rewards of their flowers (Barth 1991, p. VII). Hummingbirds, insects and bats are all important pollinators in the tropics, and many flowering plants compete for their visitation (Kricher 1997, p. 263). These three groups of pollinators have different diurnal behavior patterns and are active at different times of the day. For example, the volcano hummingbird (*Selasphorous flammula*) has two peaks in foraging activity, one in the morning and another in late afternoon (Chen et al. 1997). Also, nectar production in a hummingbird pollinated flower, *Bomarea costaricensis* (Amarylidaceae), was highest during the midday hours, suggesting that flowers may prepare for afternoon peaks in pollinator activity (Frank et al. 2000).

We evaluated two hypotheses about nectar production in *B. costaricensis* and an apparently insect pollinated flower, *Hemichaena fruticosa* (Scrophulariaceae). The timing of nectar production may be determined by (1) pollinator feeding patterns or (2) physiological constraints on the plant. The pollinator hypothesis predicts that nectar production should be highest prior to peak visitation times. If volcano hummingbird activity is typical of *B. costaricensis* pollinators, this plant should produce the most nectar in early morning and at midday to prepare for peak foraging activity. Assuming that insect pollinators in a cool environment are most active at midday, we would predict *H. fruticosa* should produce the most nectar in late morning prior to visitation. If, instead, nectar production is limited by affects of temperature and sunlight on photosynthesis and catabolism, then both species should produce the most nectar at midday.

Methods

We sampled nectar production on 26 - 27 January 2002 at Cerro de la Muerte, San Jose Province, Costa Rica, 1 km east along the main trail from the Cuerici Biological Station.

The weather on both days was 18 – 24°C, and cloudy with light, intermittent rain and a few sun breaks.

We haphazardly selected 10 individuals each of *Bomerea costaricensis* and *Hemichaena fruticosa* along the lower part of the main trail. At sundown we covered one inflorescence on each plant with cheesecloth to prevent their nectar from being consumed. At 05:30 the next day, we haphazardly chose two flowers from each inflorescence and emptied them of nectar using capillary tubes. We then sampled nectar from these flowers at 07:30, 11:00, 13:00, 15:30, 17:30, 20:30 and the following morning at 07:30. We measured the nectar in each flower by inserting a 5 µL graduated capillary tube into its nectaries. We kept each inflorescence covered with cheesecloth between samples to prevent their nectar from being consumed by pollinators.

For each sampling interval, we calculated the amount of nectar produced per hour and used ANOVA to test for patterns attributable to species, time and individual plants.

We also observed individual *B. costaricensis* and *H. fruticosa* plants during 15 min intervals, identifying the number and type of visitors to flowers of each species. On 26 and 27 January, we monitored a total of 11 plants of each species, 4 from 06:30 to 07:00 and 7 from 13:00 to 16:30.

Results

There was significant diurnal variation in nectar production for both *B. costaricensis* and *H. fruiticosa* (Fig. 1, Table 1). Nectar production of *B. costaricensis* was highest in the morning, decreased throughout the day, had a smaller peak in late afternoon and decreased into the night. Average *H. fruiticosa* nectar production was also highest in the morning, decreased throughout the day and increased slightly into the night. However, there was a significant interaction between time and species (Table 1). The late afternoon peak in nectar production of *B. costaricensis* was comparable to the morning peak, while afternoon nectar production by *H. fruiticosa* remained far below morning production (Fig. 1). Average nectar production by *H. fruiticosa* was significantly greater (~2-fold) than that of *B. costaricensis* (main effect of species in Table 1). There was significant variation among plants within species (Table 1), but individual plants did not deviate from the characteristic temporal pattern of production for that species.

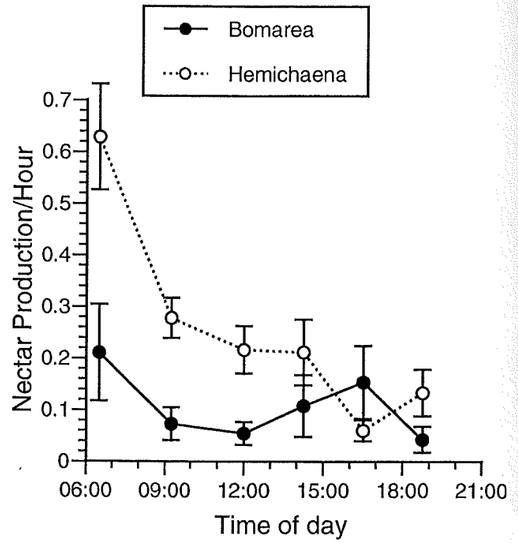

FIG. 1. Average nectar production per hour (± SE) for each time period.

TABLE 1. ANOVA results testing for patterns in nectar production with respect to plant species, time of day, and individual plants. Plant was treated as a random effect nested within species.

Source	df	MS	F	P
Species	1	2.27	14.37	0.002
Time	5	0.53	9.27	<0.0001
Species x Time	5	0.17	3.06	0.014
Plant (Species)	17	0.16	2.79	0.001
Time x Plant (Species)	85	0.06	1.12	0.289
Error	110	0.05	--	--

We observed gray-tailed mountain gems, fiery-throated hummingbirds, and magnificent hummingbirds visiting *B. costaricensis*. A total of 4 individual hummingbirds visited 4 focal plants of *B. costaricensis* between 13:00 and 16:30 on 26 January, and 7 visited 7 focal plants during the same time interval on 27 January. There were no visits to our focal plants of *B. costaricensis* during the early morning, although hummingbirds were active elsewhere at that time. We observed no insects visiting *B. costaricensis*. The only visitor to *H. fruiticosa* flowers in 24.5 plant-hours of observation was a single bee during the mid-afternoon. Many insects of other plant species on both days, and were most visited nearby flowers active at midday.

Discussion

The plants we sampled appear to coordinate their nectar production to match the feeding behaviors of their pollinators. *B. costaricensis* produced the most nectar in the morning and in the evening (Fig. 1), the most active feeding times of volcano hummingbirds (Chen et al. 1997). Similarly, *H. fruiticosa* nectar production may peak in the morning in preparation for the mid-day peak activity of insect pollinators. The slight increase in *H. fruiticosa* nectar production after dark may indicate preparation for a night pollinator such as a moth or possibly preparation for the next morning.

We assumed that *H. fruiticosa* is insect-pollinated based on its yellow color and trumpet shape (Barth 1991, pp. 20 - 2, 144 - 5). The large size of the *H. fruiticosa* flower and the high position of the stamen and anther seem well adapted for small bees like the one we observed visiting a flower. The apparent lack of attractiveness to diurnal insect pollinators suggests either that *H. fruiticosa* is pollinated by moths or that the weather (cool and cloudy on the day of sampling) discouraged some insects during our observations. Interestingly, we found a different nectar production pattern for *B. costaricensis* than Frank et al. (2000). They sampled at two time intervals and found *B. costaricensis* nectar production was lowest in the morning and peaked at midday. We found the opposite pattern across those two times. Our methods differed slightly in that we sampled from the same flowers on each inflorescence and Frank et al. sampled from different flowers at each sample time. Difference in sampling method, day-to-day or possibly inter-annual variation in nectar production may explain this discrepancy in nectar production patterns. Because we sampled both species simultaneously, day-to-day variation should not affect our comparison between species. However, interannual variation may be a factor since this region received more than usual amounts of precipitation during the month preceding our study.

Flowers of both species appeared to have a short life span, probably no longer than 2 - 4 days. It is possible that repeated sampling of flowers exceeded their capacity to replace nectar, or that our sampling damaged the nectaries and inhibited later nectar production. However, it seems unlikely that any such spurious effects were large because nectar production in both species tended to increase late in the day.

Neither *B. costaricensis* nor *H. fruiticosa* showed the predicted symptoms of physiological constraints. We assumed that the high light intensity and high temperatures of midday would be most conducive to nectar production. Yet, neither species had peak nectar production near midday. It appears that any physiological constraints imposed by low morning temperatures and lack of photosynthesis at night have been overcome to facilitate attracting pollinators when they are most active.

The match between diel patterns in nectar production and pollinator activity is consistent with the hypothesis that plants in the system can be pollination-limited. Other plants in the same community exhibit other surprising adaptations to attract pollinators. For example, some species improve their chances of pollinator visitation by extending their inflorescences to unusual heights (Lief et al. 1996, Butcher et al. *in this volume*). Further studies of pollination ecology at Cuerici are likely to reveal additional features of plant morphology and physiology that are the product of selection for increased pollination success.

Acknowledgements

Special thanks go to Matt Fagan for hours of field assistance and especially for seeing the only bee to visit a *H. fruiticosa* plant.

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