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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Hummingbird foraging behavior favors increased stature in *Wigandia caracasana* (Hydrophyllaceae)

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Abstract: Some herbaceous plants in high altitude tropical areas grow much taller than related species in other ecosystems, a phenomenon that has been referred to as gigantism. Lief (1996) found that insect pollinators were more likely to visit high *Senecio oesterdianus* inflorescences than low ones, suggesting that increased height is a product of sexual selection to increase pollination success. To further test the sexual selection hypothesis, we carried out experimental and observational studies of hummingbird visits to *Wigandia caracasana*, an unusually large member of the Hydrophyllaceae. As predicted by the sexual selection hypothesis, hummingbirds visited high inflorescences more often than lower ones. This was especially pronounced when we experimentally increased inflorescence height, but hummingbirds also visited more flowers in the top portion than the low portion of an unmanipulated shrub. Volcano hummingbirds are attracted to higher inflorescences; this behavioral tendency may favor unusually tall growth forms via a process of sexual selection.

Key Words: flowering height, Selaphorus flammula, *volcano hummingbird*

Introduction

Numerous herbaceous plants in high altitude tropical forests of Costa Rica grow much larger than related species in other ecosystems. Examples include *Bocconia frutescens* (Papaveraceae), *Circium subcoriaceum* (Compositae), *Myrrhydendron donnel-smithii* (Umbelliferae) and *Wigandia caracasana* (Hydrophyllaceae). The fact that these unusually large species come from several different plant families implies that large plant stature has independently evolved on numerous occasions in this environment. This suggests that some feature of the environment may produce selection for large plant size (gigantism *sensu*, Lief et al. 1996 and Brown et al. 2000). One hypothesis is that the typically cool temperatures greatly limit the activity of insect pollinators and causes the reproduction of many plants to be limited by pollination. This then leads to strong competition among plants for pollination services. Lief et al. (1996) hypothesized that this selects for tall plants because insect visitors are more likely to visit inflorescences that are displayed above the surrounding vegetation. This hypothesis was supported with experimental manipulations of inflorescence height in *Senecio oerstedianus* that influenced visitation rates from bees (Lief et al. 1996). This suggests a system of sexual selection such as those that produce moose antlers, peacock tail feathers, etc.

However, there are other hypotheses that could explain the recurrent evolution of gigantism in high altitude tropical plant communities. For example, several of the gigantic species have wind dispersed seeds, and height may be an adaptation to aid in seed dispersal (Brown et al. 2000). When released from a greater height, wind dispersed seeds are likely to travel greater horizontal distances, and seeds that land further from their parent plants could have a higher probability of survival.

In this study, we tested whether the sexual selection hypothesis may also hold for *Wigandia caracasana*, a very large member of the Hydrophyllaceae that grows over 6 m tall and has light purple inflorescences that are visited extensively by hummingbirds. The sexual selection mechanism might not hold for this plant because hummingbird visitation is presumably not limited by air temperature and sunlight. Furthermore, hummingbirds may or may not behave similar to bees. The

sexual selection hypothesis predicts that hummingbird visitation will increase with increasing height of an inflorescence. We tested this by monitoring hummingbird visitation patterns in natural inflorescences that varied in height and with experimental inflorescences in which we manipulated the height.

Methods

On 27 - 28 January 2002, we observed hummingbird visitations to flowers of *W. caracasana* in Cerro de la Muerte, Costa Rica. All data were collected in two fields about 500 m northeast of the Cuerici Biological Reserve.

Natural Observations

We observed 6 different shrubs, ranging 3 - 6 m tall, for 11 separate 20 - min periods. Five shrubs were observed only once, but one particularly active shrub was observed for six periods. Observations were conducted between 08:00 and 16:30, excluding time during which it was raining. We divided the flowering zone of each shrub into upper and lower halves with equal numbers of inflorescences. During each period, we recorded number of hummingbird visitations to the shrub and numbers of high and low flowers visited per visitation. We measured the average height of low and high flowers on each experimental shrub (mean ± SD = 4.6 ± 0.7 m vs. 6.2 ± 0.4 m respectively).

Experimental Set-up

We experimentally manipulated flowers to test for effects of flower height on visitations. We severed natural inflorescences, attached them to a bamboo pole either at 1.7 m (a typical height for *W. caracasana* vegetation) or at 3.0 m. Both inflorescences contained approximately 20 - 25 flowers of comparable appearance and developmental stage. We planted the pole in a sunny area frequented by hummingbirds with vegetation approximately the same height as the lower inflorescence. We observed the pole from a distance of 10 m for 20 min periods and recorded the number of hummingbird visitations to each inflorescence, as well as the number of flowers per inflorescence that were visited by each hummingbird. We repeated this trial a total of 7 times from 0800 to 1630 in seven different locations. For 12 of these observation bouts, we also recorded the duration of visitation.

We compared the number of high versus low flowers that were probed per hummingbird visit with an ANOVA model that included height, observation bout and height x observation bout. We employed a chi-square test to compare visitations for high vs. low flowers.

Results

Natural Observations

In the ten 20 - min observational periods where natural shrubs received visitations, there were 45 hummingbird visitations to high flower inflorescences and 43 to low flower inflorescences ($\chi^2 = 0.05$, df = 1, P = 0.83). However, the mean number of flowers probed per hummingbird visit was more than twice as great for high vs. for low inflorescences: mean ± SE = 21.8 ± 3.3 vs. 9.7 ± 1.8 (Fig. 1, $F_{1,50} = 4.93$, P = 0.031). There was some variation among observation bouts in flowers probed per visit ($F_{7,50} = 2.51$, P = 0.027), but there was no interaction between height class and observation bout ($F_{7,50} = 0.27$, P = 0.96). As absolute inflorescence height increased, so did the number of flowers probed per visit (Fig. 2, $r^2 = 0.31$, df = 16, P = 0.01).

Experimental Set-up

In the experimental test, hummingbirds showed a strong preference for higher flowers. In seven 20 - min observation periods, there were 14 visits to high inflorescences and only one visit to a low inflorescence ($\chi^2 = 13.71$, P < 0.001). There was a strong positive correlation between the number of flowers probed/visit and duration of visit (Spearman Rho, r = 0.85, n = 12, P < 0.001).

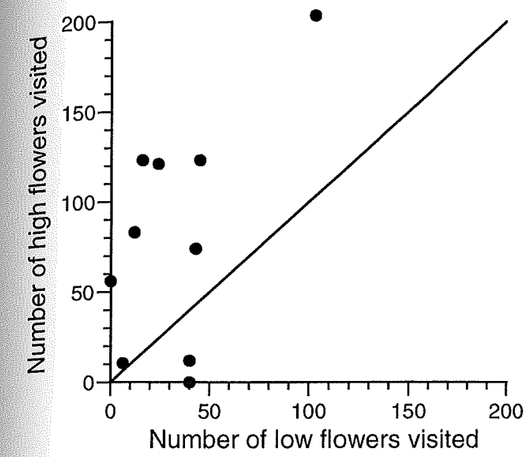

FIG. 1. Number of high and low inflorescences in unmanipulated plants that were visited by hummingbirds during each observation bout. Note that most points lie above the line of equality.

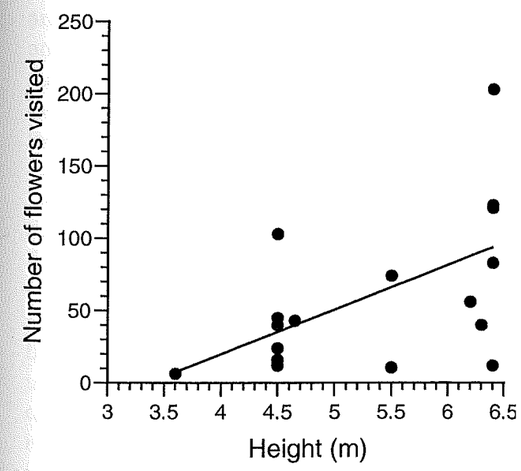

FIG. 2. Number of flowers visited on unmanipulated shrubs of *Wigandia carasana* as a function of inflorescence height.

Discussion

As predicted by the sexual selection hypothesis, hummingbird visitors to *W. caracasana* showed a clear preference for inflorescences that were displayed at a greater height than other inflorescences in the area. This was evident as a greater probability of visiting experimentally elevated inflorescences and as more flowers probed per hummingbird visit (Fig. 1, 2).

Hummingbird preference for higher flowers may be influenced by their territoriality and predator avoidance behavior. All the visitations in the experimental setting and most in the natural setting were of volcano hummingbirds, *Selasphorus flammula*. Volcano hummingbirds are territorial, and we observed males perched high on vegetation calling and scanning their territory. By preferentially visiting higher inflorescences, hummingbirds may be able to forage and maintain their territory at the same time.

It is not known whether volcano hummingbirds pollinate *W. caracasana* or just feed on the nectar, but they appear to be a good morphological match to the flowers. The small bill of the volcano hummingbird matches the flower's shallow cup shape and basal nectaries. Future studies could test this pollinator match by mist-netting birds and checking for pollen from *W. caracasana*. The sexual selection hypothesis requires that the animals preferring high flowers be pollinators and not just visitors or nectar thieves.

Hummingbird preference for higher inflorescences may be selecting for growth patterns in this very large shrub. In high altitude tropical regions, animal-pollinated plants face especially heavy competition for visitation, so those able to increase their pollinator visits should have higher fitness. This study adds to other evidence (Lief et al. 1996) that behavioral preferences of pollinators generate sexual selection for increased plant structure in the high altitude ecosystems of Costa Rica. It does not, however, discount the possible role of other explanations such as strong selection for seed dispersal (Brown et al. 2000). Indeed, sexual selection cannot possibly explain all of the tendency for large plant stature, because *Alnus acuminata*, which is wind pollinated, is one of the plants species in this area that grows unusually large compared to congeneric relatives.

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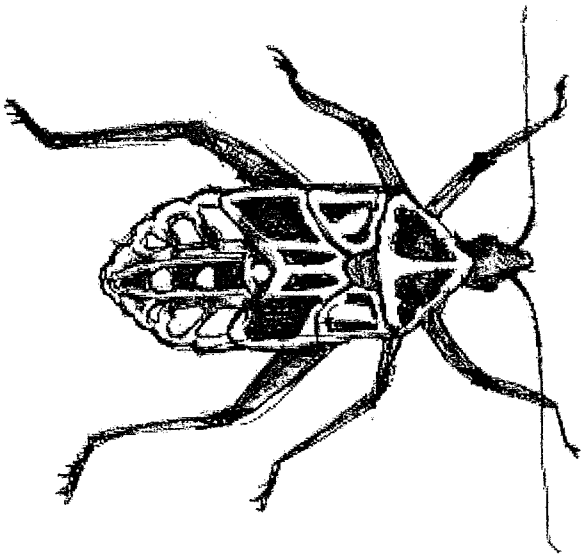
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