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POLLINATION ENERGETICS AND FORAGING STRATEGIES

IN A METROSIDEROS-HONEYCREEPER ASSOCIATION

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ABSTRACT

Evidence suggests that birds, specifically certain nectar-eating species of Drepanididae, are necessary for proper pollination, outcrossing, and high levels of seed set in Metrosideros collina on the island of Hawaii. Selection pressures acting upon the honeycreeper-M. collina association in the Keauhou Ranch forests on Mauna Loa fluctuate through the year. At the peak of the M. collina blooming season in late spring, nectar is relatively abundant to the honeycreepers, which means that the most important pollinators are potentially limiting to M. collina. Resultant intraspecific competition has selected for high rates of nectar secretion to attract pollinators; a ceiling in the population has been placed on these rates by the fact that seed set declines at very high flow rates, apparently because of decreased outcrossing due to pollinator sedentariness in such trees. At other times of the year when M. collina flowers are less abundant, a surplus of pollinators occurs, which results in high levels of seed set but in competition for food among the nectar-eaters. Loxops virens, and also Himatione sanguinea to a lesser extent, can turn to insectivory under these circumstances and therefore need not possess a highly specialized and efficient nectar-foraging strategy, but the more nectar-dependent Vestiaria sanguinea establishes interspecifically-defended territories in M. collina and visits flowers on its territory in a timed sequence. An hierarchy of interspecific aggression seems to be aligned among the three honeycreeper species in order of degree of nectar dependency.

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INTRODUCTION

Ecologists have recently recognized the interface between the pollination ecology of plants and the energetics of the foraging strategies of their animal pollinators. Heinrich and Raven's (1972) classical article consolidated much of the descriptive knowledge about pollination, and posed hypotheses to account for the observed data. Their principle thesis assumed that pollinators are sometimes limiting to plants so that outcrossing species compete for pollinators. This selects for rich rewards in nectar or pollen to attract pollinators. However, Heinrich and Raven continue, there is a counter-selection pressure that puts an upper limit to the richness of the reward. If the reward is too rich, the potential pollinator will be able to obtain all its requirements from a single plant, thus not effecting outcrossing. Thus, a plant must provide a rich enough reward to attract potential pollinators, but a poor enough one to prevent satiation and encourage them to leave after feeding. The result should be that outcrossing plants with specific types of pollinators should evolve an amount of reward finely tuned to the energetics of its major pollinator. Below that amount, successful reproduction (i.e., setting of viable seeds) should decline because of lack of attractiveness relative to other plants; above that amount, seed set also should decline because the plant is too attractive.

This is a simple and attractive hypothesis, but its basic assumption conflicts with the zoologists' frequent assumption for many animal groups, that food limits animal populations. If, for example, nectar is limiting to animals dependent on that nectar, this means that potential pollinators are relatively abundant and there should be little selection pressure for the kind of fine tuning Heinrich and Raven (1972) propose. On the contrary, limited nectar would lead to competition among the pollinators, which will select for efficiency of foraging strategies, but allow a great deal of variability in the energetic efficiency of pollination strategies of the plants. In fact, food limitation has been strongly implicated in the biologies of some nectar-dependent animals, most notably, the hummingbirds (see discussion in Stiles 1973). Nectar-eaters can increase their foraging efficiencies basically in two ways which result from the fact that nectar is a continually renewing resource and thus flowers must be allowed time between visits to accumulate nectar if a visit is to be energetically rewarding. Ideally, the nectar-eater needs to know where its blossoms are and to control how frequently they are visited. The best way to do this is to exclude other nectar-eaters and then forage on the flowers in a timed pattern. Such exclusion is called "feeding territoriality" (e.g. see

definition in Wolf 1970) and is highly obvious in nectar-eating hummingbirds. Another way to exert some control over flower visitation is to forage in a flock. Seed-eating finches do this in desert habitats (Cody 1971): the flock acts as if it has a memory and does not revisit an area which has been recently foraged.

The *Metrosideros collina*-honeycreeper association offered a system suitable for testing Heinrich and Raven's (1972) hypothesis and also the above ideas on foraging efficiency.

MATERIALS AND METHODS

Our study area was on the Keauhou Ranch, Kau District, Hawaii, between 1200 and 1900 m elevation. *Metrosideros collina polymorpha* (Myrtaceae) is a major native component of the forested slopes of Mauna Loa (Porter 1973, Mueller-Dombois and Fosberg 1974). The flower looks like a typically bird-pollinated flower, with bright red color and long exerted style and stamens (Grant and Grant 1968). The chances seemed good that it would be an obligate outcrosser with birds as the primary pollinators, and as such would be a good subject for testing Heinrich and Raven's (1972) ideas. We had to provide four tests:

1. Determine if *M. collina* does require outcrossing;
2. Determine if it is mainly bird pollinated;
3. if so, determine that its nectar reward is commensurate with the energy demands of the birds; and
4. determine if highest seed set does actually occur at some optimal nectar flow rate or amount of flowering.

Of 76 trees worked on for nectar secretion and/or seed set, 6 were known to be orange-flowered and 3 were yellow-flowered. Most of the remaining 67 were red-flowered, but color of flower was unknown in some trees used only for seed set. To answer the questions about   outcrossing and who is the main pollinator, we performed bagging experiments both high and low in the trees. High inflorescences were reached either via a 10 m extensible ladder or by assistants using telephone pole climbing equipment and a sling for support while working. Maximum height reached in this manner was 15 m. We chose blossoms in the bud stage, counted the buds in an inflorescence and marked the inflorescence with a green numbered band. Then we bagged the buds either with a fine-mesh net to exclude all pollinators and determine selfing, or with chickenwire cages to exclude birds but allow in insects, the other possible major pollinator group. We left control buds open to both birds

and insects. Comparison of controls with chickenwire-bagged buds provided information on the relative amounts of pollination by birds and insects. We returned several months after bagging and counted the number of mature seed capsules in the marked inflorescences to compare with the original number of buds, which gave the percent seed set on a capsule basis. Techniques are described in more detail in Carpenter and MacMillen (1973).

We netted birds with mist nets hung from telescoping poles extensible to 10 m. We measured the relative amounts of M. collina pollen on the heads of recently captured birds by pressing the feathers with a 2 x 3 cm piece of Scotch tape and applying the tape to a microscope slide (technique communicated to MacMillen by Carolyn Corn). The pollen could be accurately identified microscopically and categorized into absent, light, or heavy. Comparing the loads on different species of honeycreepers helped determine which species was or were the main pollinators among the birds. We concentrated our work on the Amakihi (Loxops virens), Apapane (Himatione sanguinea), and Iiwi (Vestiaria coccinea)--all members of the Drepanididae.

The energy provided by M. collina nectar was determined by excluding all nectar-feeders from open blossoms and at known intervals sampling nectar volumetrically and by concentration to get absolute amount of sugar secreted per flower per hour and translating this into calories (techniques in Carpenter and MacMillen 1973).

RESULTS AND DISCUSSION

M. collina

There was little selfing in the red flowers--17% (N=25, S.D.=15). However, selfing was high in the yellow flowers--53% (N=3, S.D.=20). This was statistically significant (two-tailed t-test) with p < .001. The results with the yellow flowers are important since they show that selfing can occur within the bags without pollinating agents, but does not occur in the red-flowered trees. We noticed that pollen accumulates within the nylon bags and is spread around the florets of an inflorescence perhaps by rubbing action of the leaves, twigs, and the bag itself. Thus, the red-flowered trees apparently not only require pollinators, but they also must be outcrossed if they are to set seed at levels comparable to the selfing seed set in the yellow trees.

Yellow-flowered trees were omitted from the remaining analysis. Flowers open to birds as well as to insects set significantly more than flowers open only to insects (one-tailed paired t-test, N=22, p < .005); on the average, they set 2.7 times more.

The distribution of M. collina pollen loads on the three bird species were as follows:

	absent	light	heavy
Amakihi (N=27)	4%	85%	11%
Apapane (N=39)	0%	13%	87%
Iiwi (N=14)	0%	29%	71%

The Apapane and Iiwi are therefore the most capable of pollinating M. collina. The Iiwi seems to carry slightly lighter pollen loads than the Apapane, perhaps because its longer bill results in less effective contact with the anthers.

The concentration of M. collina nectar is extremely variable from tree to tree and from day to day, and therefore the presentation of such data in terms of calories produced per unit time is the only way to express secretion rates consistently. On the average, M. collina secreted 0.52 calories per floret per hour. This is comparable to the rates found in other bird-pollinated plant species, and is higher than those bee, fly, and ant pollinated flowers that have been measured (e.g. Hickman 1974; see Heinrich and Raven 1972, Percival 1965). Thus, M. collina nectar production is commensurate with the higher energy demand of birds, and is evidence supporting Heinrich and Raven's ideas.

It is puzzling that a plant apparently geared for bird-pollination has not evolved tubular corrolas to prevent nectar thievery by insects. Evolution of tubular corrolas is within the genetic capacity of Myrtaceae because one taxonomic group within the family (Genus Darwinia) possesses them (Bryan Barlow, pers. comm.). One possible explanation is that M. collina may exist in an unpredictable pollinator environment, which should select for maintenance of a relatively generalized pollination strategy (see Levin 1968). This would be true if honeycreeper populations experience large fluctuations over the years (given relatively constant flower availability) so that the plants cannot always depend upon them for pollination. Seed set in the chickenwire cages averaged 39%, or about double the amount of selfing, so insects alone can effect some pollination. Furthermore, even in times of

bird availability, the amount of outcrossing effected by birds actually might be increased by the taking of nectar by insects, forcing the birds to include more trees in their foraging ranges. This kind of interaction has been found in red clover, in which seed set effected by long-tongued legitimate insect pollinators increases in the presence of short-tongued nectar thieves which pierce the corollas and do not effect outcrossing (cited in Heinrich and Raven 1972).

The most critical test of Heinrich and Raven's (1972) hypothesis was to show that there is some optimal degree of nectar availability that results in greatest seed set, and that seed set declines when nectar is more or less available than the optimum. For this, we have two independent tests.

First, Figure 1 shows the seed set values in 13 trees from which we also obtained nectar secretion rates. The regression of 11 of these trees yields a slope that is significantly different from 0 at the .02 level and a correlation significant at about .03. It shows that seed set is lower in trees with high nectar flows. The other two trees were the only ones available with low secretion rates, but these indicate that seed set falls off rapidly below a rate of 0.40 cals/floret/ hr. The optimum flow rate is about 0.45. This corresponds very well with the mean value of flow rate for our population sample of 38 trees (0.52). Thus, flow rates and seed set in individual trees support Heinrich and Raven's hypothesis.

The other supportive evidence comes from differences in seed set at different flowering intensities. Apparently the peak of the 1974 blooming season occurred about in April, as one of our assistants reported that all of our experimental trees selected in January were in heavy/bloom. When we arrived in early July blooming percentages varied between 20 and 50%, depending on elevation, and continued to decline through August and September. Average seed set was significantly (one-tailed t-test, p < .025) lower in the trees that bloomed in the peak period than later when fewer trees were blooming and the number of blossoms per tree were lower.

Since there was no statistical difference in nectar flow rate in different seasons (.2 < p < .3), the difference in seed set was attributed to greater nectar avail-ability in April because of large numbers of blossoms per tree.

Thus, higher nectar availability--either due to high flow rates or to large numbers of blossoms within a tree results in lower seed set. We also have some evidence that at very low flow rates, seed set declines. There is ample evidence for this aspect of the hypothesis from other pollination studies (see Percival 1965), but our data offer to our knowledge the first supportive evidence that selec-tion pressures act to prevent plants from being too attractive as well as to make them attractive in the first place. This also supports, therefore, Heinrich and Raven's assumption that pollinators may be limiting to plants.
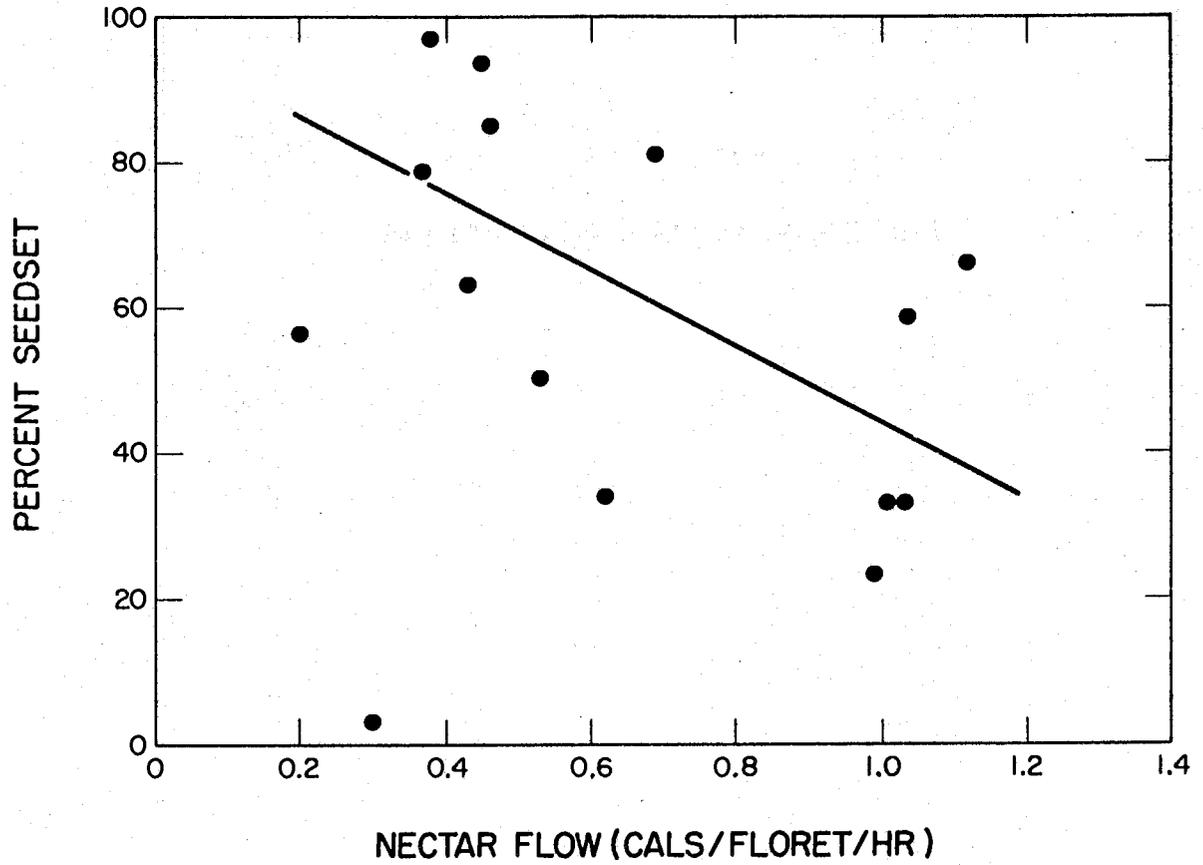
FIG. 1. Effect of nectar flow on seed set (N = 13 trees, r = .61, p < .05).

The birds

This however does not mean that nectar is not limiting to the birds, as the blooming percentages showed that nectar availability varies through time. In flowers commencing their bloom in July 1974, seed set was higher than in those in bloom in April 1974 because pollinators could not afford to limit their visits to one or a few trees during the sparser bloom in July. Thus, nectar was probably limiting to the birds then, although it probably had not been earlier during the peak of blooming. This was supported by the fact that very small amounts of nectar were left over in unbagged open flowers in summer of 1974, whereas nectar was often left over in large amounts during the summer of 1973, a much more intense bloom. We expected therefore some selection to exist for efficiency of honeycreeper foraging strategies, and looked for feeding territoriality and/or flocking strategies in the three species.

Bill shapes are often considered indicative of the degree of specialization of a species (Darwin 1859). By this criterion, the Amakihi is more generalized than the Apapane, which in turn is more generalized than the Iiwi. The Amakihi showed no specialized foraging strategy for nectar--it did not defend feeding territories, nor did it forage within the trees in a flock. It spent much time hunting insects in non-blooming trees, but would take nectar when it could get it, which was primarily when it was not chased by the other two species.

The Apapane spent relatively more time on flowers. It was not strictly territorial but would chase Amakihis from its immediate vicinity, eventually moving on to another area to forage. A single area was not defended, yet this is necessary if aggression is to increase greatly nectar availability to the aggressor. Given the high rates of nectar flow in $M.$ collina, however, even this degree of aggression should increase nectar availability slightly to the Apapane.

Apapane also did not forage in flocks. However, it tends to forage high in the trees in morning and late afternoon, using intermediate levels in the interim (see Carpenter and MacMillen 1973; we have more data of these kinds as yet not fully analyzed). Thus, it is in contact with untapped blossoms early in the morning after a night of accumulation, in midday, and then again in late afternoon when it is stocking up for a night's roosting. Thus, its pattern of foraging for nectar is more efficient and with a greater degree of control than it would be if it foraged randomly with respect to time and the location of blossoms and of other nectarivores.

The Iiwi was the only species that defended feeding territories. It excluded not only other Iiwis from its area but also Amakihis and Apapanes. We have constructed and tested a cost-benefit model of territoriality for the Iiwi (Carpenter and MacMillen, in review) that shows that these birds are intensely territorial, but only when it pays energetically. Furthermore, we have evidence that a territorial Iiwi visits its flowers in a pattern, allowing for nectar replenishment: we watched a single branch of flowers on a territory and timed the owner's visits to that branch. The visits were spaced 31 min apart (S.D. = ± 5 min) for seven consecutive visits.

The Iiwi's strategy is by far the most efficient for nectar gathering of the three species studied and enables the birds to obtain their energy from only one or two trees. We measured seed set on an Iiwi territory that was comprised of a single M. collina. With a t-test that compares a single specimen against the sample of seed set values the Iiwi tree set less capsules than the average (one-tailed test, p < .01). Thus, if the Iiwi were the only honeycreeper in the area, we would expect selection for lower nectar flow rates in M. collina to force the Iiwis to include several trees in their territories thus resulting in outcrossing. However, the Iiwi is the rarest of the three species (S. Conant, pers. comm.). The commonest species is the Apapane (S. Conant, pers. comm.), which, judging by pollen loads, is also the most important pollinator of M. collina.

CONCLUSION

During part of the blooming season nectar is abundant relative to the honeycreeper population size--then seed set is low, and competition for pollinators selects for high nectar rewards--but not too high. During other parts of the blooming season nectar is limited relative to the numbers of honeycreepers, seed set is high, and the birds compete for the nectar. This in turn selects for efficiency of foraging strategy, the degree of which may depend upon the degree of nectar dependency of the honeycreeper species. Thus the Metrosideros collina-honeycreeper association in Hawaii represents a finely tuned system, one in which the major producer member of the community regulates its energy reward, thereby reaping reproductive benefits, while concomitantly promoting energetic efficiency in and providing much of the energy needs for its pollinator-consumer.

ACKNOWLEDGMENTS

NOTE

Measurements on nectar flow in Sophora chrysophylla indicated low rates compared to ohia: 0.09 cal per flower per hour (N = 19 flowers). This possibly could be interpreted in terms of pollination 1) by insects, which have lower energy requirements, or 2) by 'I'iwi, which, when territorial, would effect only selfing if flow rates were higher. Sophora nectar had a low sucrose concentration (mean = 16.4%, S.D. = 1.2%, N = 3 flowers), which is more characteristic of bird flowers than of insect flowers (Percival 1965).

Data on nectar flow and seed set as functions of elevation, size of tree, stage of flower, and flower color will be presented in a subsequent report, as will the details of methodology. A discussion comparing the generalized pollination strategy of ohia with strategies in mainland communities, and proposing ecological segregation in the major tree species in the Mauna Loa forests on the basis of pollination strategies and blooming seasons will also be presented later.

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