

Technical Report No. 76
PLANT-POLLINATOR INTERACTIONS IN HAWAII:
POLLINATION ENERGETICS OF
METROSIDEROS COLLINA (MYRTACEAE)

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ISLAND ECOSYSTEMS IRP
U. S. International Biological Program

April 1976

ABSTRACT

The most abundant tree species in much of the undisturbed Hawaiian forests was the subject of a two year study on plant-pollinator interaction and energetics. The purposes of the study were 1) to determine the roles of insects and of some endemic Hawaiian birds in the pollination of the tree, Metrosideros collina, 2) to test the hypothesis that maximal outbreeding and seed set occur at intermediate levels of nectar availability, 3) to understand the adaptive significance of profuse flowering in this species, and 4) to compare the pollination ecology of this species and the degree of specialization in the plant-pollinator community with those of similar mainland systems.

Endemic Hawaiian birds (Drepanididae) are essential for high levels of fruit set and outbreeding in M. collina. Fruit set was much higher in red-flowered individuals when birds were allowed to use inflorescences than when only insects used them. This is apparently caused by partial self-incompatibility, such that maximal fruit set occurs only with outbreeding, the primary agents of which are the birds. The predominant flower color in the population, the dimensions of floral parts, and copious nectar secretion adapt this species to bird pollination. However, insects effect moderate amounts of pollination and fruit set. The open flower and the color- and scent-variability within the population may be adaptations for insect pollination in the event that bird pollination fails. The population seems to have differentiated along an elevational gradient, with adaptations for bird pollination increasing proportionally with elevation. The generalization of the pollination strategy is on both an individual and populational basis, and enables M. collina to be the good colonizer that successional patterns and its own geographical distribution show it to be.

Red-flowered individuals are partially self-compatible, but yellow-flowered individuals are totally self-compatible. The yellow-flowered morph may be evolving autogamy. At this stage its breeding system is intermediate between autogamy and outbreeding, with geitonogamy being encouraged due to 1) increased attractiveness to insects relative to the high energy birds by means of color and scent cues, and 2) increased nectar flow which satiates pollinators. Furthermore, yellow-flowered individuals have a floral structure that facilitates transferal of pollen to stigmas in the same inflorescence by means of small size pollinators, or even without the aid of a pollinator. A model is derived that predicts the selective results of various degrees of pollinator

limitation on nectar productivity.

Bird numbers are more constant relative to nectar availability than would be expected by random sorting, although temporary deficits and surpluses of these pollinators occur: their inability to respond instantly to changes in the intensity of bloom introduces lags into the system, and these have important consequences for pollination, outbreeding, and gene flow. During some times of the year pollinators are limiting to M. collina, and intraspecific competition occurs. Maximal fruit set and outbreeding do occur at intermediate nectar availabilities. Interspecific competition between species of trees for pollinators is a potential selective force that may explain the character displacement and staggering of flowering seasons of several tree species in the Hawaiian forests. Comparison with a similar but more diverse forest community in New Zealand and with mainland tropical forests suggests that the length of flowering season per tree species is inversely related to the number of tree species competing for pollinators.

Profuse flowering in M. collina results in lowered fruit set per inflorescence because of decreased outbreeding, but the total number of fruits set per tree is probably high because of partial self-compatibility in most individuals. Thus, the M. collina system does not help explain profuse flowering in mainland tropical species that are totally self-incompatible.

In comparison with mainland communities, the degree of specialization in the plant-pollinator relationship seems to be less in Hawaiian forests, although more information is needed on the Hawaiian lobelias and Sophora chrysophylla before such a statement should be made with any certainty.

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INTRODUCTION

Probably the most abundant and widespread of the native forest trees on the island of Hawaii is the ohia, *Metrosideros collina* (Myrtaceae), which grows from sea level to 2600 m under several climatic regimes (Porter 1973, Mueller-Dombois 1975). This species colonizes new lava flows rapidly (Eggler 1971, Smathers and Mueller-Dombois 1974), yet persists as one of the most abundant trees in later stages of succession on mature soils as well, where it can grow to 40 m tall (Baldwin 1953). As the major component of vast areas of forest and woodland, it necessarily must play an important role in the lives of much of the Hawaiian flora and fauna and in energy flow through the Hawaiian ecosystems. I chose to study a portion of this role, namely, the interrelationships between ohia and the organisms that take its nectar. Because comparable mainland systems are highly diverse with many specialized species (e.g. Ricklefs 1973), it would seem likely that specialized coevolved relationships should be common among the various plant-animal interactions on mainlands. For example, one would expect that many mainland plants should be obligately pollinated by specific groups of pollinators. Many instances of tightly bonded relationships do occur in the mainland tropics (Colwell 1973; Heinrich 1975) and deserts (see Baker and Hurd 1968 for examples). In contrast with mainlands, islands have low plant and pollinator species diversity (e.g. MacArthur and Wilson 1967) and island species seem to be generalized (see MacArthur 1972 for examples). I hope to determine the degree of dependency of ohia on certain animals for pollination, and that of the animals on the tree as an energy source, and to compare these interdependencies with those of reciprocally-evolved (Baker and Hurd 1968) associations in mainland communities. This paper concentrates on the pollination ecology and energetics of ohia and will be followed by a paper on the energetics and foraging strategies of its associated birds.

Plants adapted for outbreeding effected by specific groups of pollinators should produce an energy reward rich enough to attract those pollinators but scant enough to force them to include more than one individual plant in their foraging ranges (Heinrich and Raven 1972). It is well known that each plant species produces a characteristic kind and amount of nectar reward (Percival 1961, 1965) and that the richness correlates in general with the type of pollinator, "fly-flowers" producing little, "bee-flowers" more, and "bird-flowers" still more (Faegri and van der Pijl 1971). But whether the richness

is finely tuned to maximize outbreeding by minimizing sedentariness in the pollinators has not been studied. Trees in the tropics often flower profusely as individuals (Janzen 1967, Richards 1950), and this would seem to be an anomalous situation (Heinrich 1975) that would increase selfing by geitonogamy--that is, by pollination of another flower on the same individual plant--at the expense of outbreeding, or even result in poor seed set in those species that are self-incompatible. Ohia is capable of profuse flowering, and thus offers an opportunity not only to test the idea of a ceiling on richness of nectar reward, but also to investigate the anomaly of profuse flowering. The purpose in this paper, then, is two-fold: to determine the degree of specialization in the pollination system of ohia, and to test recent ideas about optimization of nectar flow in outbreeding plants.

MATERIALS AND METHODS

Ten study sites were situated along an elevational gradient on the southeastern slopes of the volcano Mauna Loa (Kau District, Hawaii) between 1200 and 1850 m. Three sites were located in ohia scrub forest with native shrubs on thin ash and soil over pahoehoe lava (Mueller-Dombois and Fosberg 1974; also see Baldwin 1953) between 1200 and 1230 m elevation near Kipuka Puaulu in Volcanoes National Park. The remaining seven sites were in fairly continuous Metrosideros-Acacia koa forest beginning at 1200 m in Kipuka Puaulu and continuing up through the Keauhou Ranch to Keawewai at 1850 m (site elevations: 1200 m, 1290 m, 1350 m, 1560 m, 1700 m, and two sites at 1850 m). The forests of the Ranch have been disturbed somewhat by logging which has cleared narrow strips and patches of land, now grassland grazed by cattle. The land separating these strips contains relatively undisturbed forest with rich complements of native fauna and flora. I found the Ranch especially favorable for work because the cleared strips facilitated transportation between sites and provided vantage points for intensive observation of the trees and their associated animals, such observation being extremely difficult in completely closed forest. In Kipuka Puaulu the forest is mature and diverse, with trees up to 40 m tall. The six higher sites were in less mature forest in which ohia was by far the most abundant species of tree and rarely grew above 25 or 30 m tall. Our study sites were situated intermediately between wet montane rain forest characteristic of the Kilauea Forest Reserve and the

deleted, as the values were abnormally low.

The rate of nectar secretion was hypothesized to be related to any or a combination of the following factors: the intrinsic factors of flower color, height of inflorescence in tree, and size (age) of tree, and the extrinsic factors of elevation on the mountain and of season. Each of these factors had to be studied independently of the others, requiring a large sample size (216 inflorescences in 37 trees). Preliminary work (Carpenter and MacMillen 1973) had suggested that height of inflorescence in tree might affect nectar flow. The data from December 1973 and summer 1974 indicated that elevation likely also affected secretion rates. Thus, to test the effect of height and to describe the effect of elevation, secretion rates from red inflorescences sampled within the essentially homogeneous and continuous strip of forest from 1290 to 1850 m and at heights from 0.6 to 14.5 m in the trees, were analyzed by weighted multiple regression assuming a parabolic effect of elevation and linear effect of height in tree. Four trees occurred in the scrub forest at elevations less than 1290 m and were not included in the regression because soil type and vegetation structure were both different from those in the forest and had an obvious effect on secretion rate. The effect of season was tested by a t-test on summer (July-September 1974) and winter (December 1973) rates in red-flowered trees at the 1350 m site where the data were most comprehensive. Rates in orange- and yellow-flowered trees at 1350 m were compared with the rate for red-flowered trees at that elevation predicted from the regression equation. The rates in large (> 12 m) and small (< 9 m) red-flowered trees at the 1350 m site were compared with a t-test. Sample sizes and tests are summarized in Tables 1 and 2, presented in the order in which the tests were conducted.

In collecting data, the assistants and I attempted always to select inflorescences that looked fresh and whose florets were just opening or had been open not more than one or two days. Unfortunately the bloom at the time of the most intensive data collecting (summer 1974) was sparse and I could not perform neatly symmetrical experiments with equal sample sizes in each treatment. Blossoms of the appropriate age that were reachable in any given tree were variable in abundance so that in some cases replicated experiments within trees were not possible. I tried to compensate for this by increasing the number of trees in the sample.

TABLE 1. Weighted multiple regression analyses.

Dependent variable	Independent variables	Sample sizes (N_t/N_i)
Rate of nectar secretion over 24 hr periods in red- flowered trees (cals/floret/hr)	Elevation and height of flower in tree; Scrub vs forest Red- vs yellow- and orange- flowered trees	25/75 4/6 (scrub), 25/75 (forest) 3/5 (non-red), 25/75 (red)
A seed set (on capsule basis)	Elevation, height of flower in tree	28/105
B seed set (on capsule basis)	Elevation, height of flower in tree	25/82
C seed set (on capsule basis)	Elevation, height of flower in tree	29/149

TABLE 2. Single variable analyses.

Sample population or Experimental treatment	Sample sizes N_t/N_1	test	Variables measured
Florets sampled 1, 2, 3, or 4 times per day for one to five days at 1350 m elevation	4/10	--	Dependent: Cals. nectar secreted per floret per hr Independent: No. samples per day, hrs and days since floret opened
Winter red flowers <u>vs.</u> Summer red flowers at 1350 m	11/26	t-test	Dependent: Cals. nectar secreted per floret per hr over a 24 hr period Independent: Season
Large (old) <u>vs.</u> small (young) red-flowered trees at 1350 m	13/29	t-test	Dependent: Cals. nectar secreted per floret per hr over a 24 hr period Independent: Size category of tree
Selfing seed set effected by artificial pollination <u>vs.</u> selfing seed set effected by A bags in red-flowered trees at 1350 m	3/6	Paired t-test	Dependent: Percentage capsule set Independent: Selfing treatment type
A <u>vs.</u> B seed set (percents). B <u>vs.</u> C seed set (percents). All elevations and flower colors included.	25/82 25/82(B) 94(C)	Paired t-tests	Dependent: Percentage capsule set Independent: Bagging treatment (A or B) or control (C)
A seed set in red flowers <u>vs.</u> A seed set in yellow flowers. All elevations included.	28/105	t-test	Dependent: Percentage selfing set Independent: Flower color

TABLE 2 Continued.

Sample population or Experimental treatment	Sample sizes N_t/N_i	test	Variables measured
Seed set effected by insects at peak of bloom <u>vs.</u> that effected at decline of bloom.	23/82	t-test	Dependent: Percentage capsule set in B bags, corrected to 1500 m elevation (refer to Table 1) Independent: Date of bloom--April 1974 or Summer 1974
Seed set effected by birds plus insects at peak of bloom <u>vs.</u> that effected at decline of bloom.	25/92	t-test	Dependent: Percentage capsule set in C bags, corrected to 3.7 m height in tree (refer to Table 1) Independent: Date of bloom--April 1974 or Summer 1974
Seed set in trees of different characteristic nectar secretion rates.	13/16	regression	Dependent: Percentage capsule set in B and in C bags, corrected to 1500 m elevation for B treatment, and to 3.7 m height in tree for C treatment Independent: Mean rate of nectar secretion in each individual tree

1
6
1

Blossoms higher than 2 m above ground were sampled either from a 5 m step ladder with a 5 m central extension that gave a maximum working height of 9 m, or by climbing trees using the spikes and harness of standard pole climbing gear. Maximum height reached with climbing gear was 15 m, or well into the highest level of the forest canopy in most areas.

I attempted to estimate the relative amounts of nectar taken by insects and birds by setting up trios of bagging treatments in 19 trees at five sites. In each tree one or more inflorescences were assigned one of the following three treatments: A) bagging with the fine-mesh nylon bags to determine baseline nectar secretion ($N_t=19$, $N_i=71$); B) bagging with 0.3 x 0.5 m cylinders made of 2.5 cm mesh chickenwire positioned so that the sides of the cylinders were far enough from the enclosed inflorescences that birds could not reach them ($N_t=19$, $N_i=54$); or C) no bagging at all ($N_t=15$, $N_i=54$; four trees in December 1973 were not provided with C treatments). Each inflorescence was marked with an inconspicuous numbered plastic band placed around the twig at the base of the inflorescence, and the bags were carefully removed and replaced to allow periodic sampling. Amounts of nectar left over by insects (treatment B) could be compared to that left over by insects plus birds (treatment C), and by comparing these to the amount of nectar produced (treatment A), the totals taken by insects and by birds plus insects could be calculated by subtraction. I was unable to develop a technique that could exclude insects but not birds, and as a result the activity of birds alone could not be determined.

Seed set measurements

Similar bagging treatments were executed on inflorescences in the bud stage to determine the amounts of seed set by selfing, by insect pollination, and by bird plus insect pollination. Inflorescences in bud were selected just prior to opening, the number of buds per inflorescence was counted, each inflorescence was marked with a numbered band, and the A and B bags were established. At least one complete trio (A-B-C) of treatments was set up in each of 25 trees; unbalanced experiments in summer 1973 account for the unevenness of total tree sample sizes in the three treatments (see Tables 1 and 2). Within one month after flowering, the capsules had reached nearly maximum size, and two to three months after flowering the bags were removed and the number of swollen capsules counted and compared to the initial number of buds in each inflorescence. This

yielded percentage of seed set on a capsule basis for each inflorescence and for each treatment within a tree. A more thorough analysis would have involved counting absolute numbers of seeds produced, but this was not feasible because of the time involved to count the hundreds of seeds per capsule and examine each for presence of embryos. Because of the great variability of ohia and of the data, large numbers of trees and inflorescences for each sample were required, placing a premium on time. Seed set on a capsule basis was easily and quickly determined and a good approximation of the effect of various factors on pollination. Darwin (1876) found, in fact, that capsule count reflected seed count accurately.

If a floret is not pollinated, it usually is shed. Occasionally a floret does not develop normally, drying in a semi-closed stage and not being shed. In these instances, the dried florets were subtracted from the initial bud count. Rarely, an entire inflorescence failed to set seed--this occurred only a very few times, and in all three bagging treatments. These inflorescences were considered abnormal and were deleted, since seed set even by selfing alone was found to occur at appreciable rates. It is possible that these failures were caused by bud- and flower-destroying insects (Corn 1972a).

I compared the amount of selfing by artificial pollination with that in the undisturbed A bags by performing a paired experiment with one inflorescence per treatment in each of three red-flowered trees. Artificial pollination was effected by collecting pollen from inflorescences bagged to prevent pollen removal by insects and then placing a large smear of it on the stigmas of the florets in the experimental inflorescences on the same tree; the inflorescence was protected from natural pollination by the fine-mesh nylon bags. Artificial pollination was repeated at all stages of the life of each floret. Seed set in this inflorescence then was compared to that in an undisturbed inflorescence on the same tree bagged with an A bag in the same manner as described above.

Stage of maximum receptivity was determined in one inflorescence on each of two trees by snipping off anthers as soon as the stamens began to exert before dehiscence of any pollen. Each floret was marked, the date of the first exerting of stamens was recorded and the inflorescence was bagged. Some florets were artificially pollinated on the day of first stamen exertion (0-1 day treatment), others on the next day (1-2 day treatment), and others 3-4 days after. The terminal 0.5 cm of stigma and style was snipped off 24 hr after

pollination. After all stigmas were removed, the bag was removed.

Most of the same intrinsic and environmental factors were investigated for effects on seed set as were studied for nectar secretion: height of inflorescence in tree, flower color, elevation and season. A, B, and C treatments were performed at various tree heights and at five elevations, in 26 red- and 3 yellow-flowered trees. Weighted multiple regression analysis was carried out separately for each treatment to determine any effects of elevation or height in tree, and the effects of season and flower color were tested by a t-test. Heinrich and Raven's (1972) ideas were tested by 1) comparing seed set at the peak of bloom with that during the decline of the bloom and 2) collecting data from A, B, and C treatments for both nectar and seed set pairwise on the same trees. See Tables 1 and 2.

In sum, seed set was measured directly as a function of 1) age of floret, 2) artificial self-pollination vs. selfing within A bags, 3) insects vs. birds plus insects as pollinators, 4) flower color, 5) height of inflorescence in tree, 6) rate of nectar flow, 7) stage of blooming season, and 8) elevation.

Miscellaneous measurements

In July, August, and September 1974, the percentage of trees blooming and the intensities of bloom per tree were measured along an elevational transect with stations every 61 m (200 ft) elevational rise in July, and every 123 m (400 ft) elevational rise in August and September. I counted the number of trees fully visible within a 300 m radius of each station and recorded, using binoculars, the number of individuals falling into each of the following blooming categories: 1) 1 to 10 inflorescences, 2) 11 to 30 inflorescences, or 3) > 30 inflorescences per tree. In addition, one of the field assistants recorded less precise categories of blooming at the 1560 m station in April 1974, categorizing intensities as "heavy", "partial", or "light".

The inside diameter of the nectar cups on yellow-, orange-, and red-flowered trees was measured from five florets chosen at random from two inflorescences per tree ($N_t=6$, $N_i=12$) to determine any relationship between floral color and morphology. In a separate experiment intended to determine the relationship between floral morphology and elevation, cup diameters and style lengths were measured on one floret from each of two inflorescences chosen from each of 16 trees at the six forest elevations.

Live birds were captured by setting mist nets on telescoping poles and extending the nets 10 m into the forest canopy between blooming trees. The pollen of 104 freshly caught birds was sampled by pressing the feathers of the head with a 2 x 3 cm piece of Scotch-tape and applying the tape to a microscope slide (Corn 1972a). The pollen was compared microscopically with standards made from all major flowering plants in the study area likely to be used by honeycreepers: M. collina, Acacia koa, Sophora chrysophylla, and Myoporum sandwicense. These standards and the slides of bird-borne pollen are located in the Museum of Systematic Biology at the University of California, Irvine. Because the pollen was collected from the heads of the birds in a standardized manner, the density of ohia pollen from any one bird could be categorized on the slides to indicate relative heaviness of pollen load. Three categories were employed: absent, light, and heavy.

I extracted data on the blooming seasons of ohia and Sophora chrysophylla and information on the association between blooming intensities and honeycreeper relative abundances from Baldwin (1953); method of extraction is described in MacMillen and Carpenter (in prep.).

Statistical treatment

I assumed that the dependent variables in this study, such as nectar and seed set values, were normally distributed, and applied simple parametric analyses for most comparisons. Unless specifically stated, all t-tests performed were two-tailed.

Weighted multiple regressions were carried out to allow for the fact that the number of inflorescences sampled in each tree was not constant and that observations within a tree were correlated.

Unless otherwise stated, confidence limits for means are given at the 95% level.

RESULTS

Nectar production

A distinct day-night cycle occurred in the nectar production of ohia (Fig. 1). Nocturnal secretion was significantly lower than diurnal secretion (paired t-test, $p < .001$). Peaks of nectar flow were variable between trees and

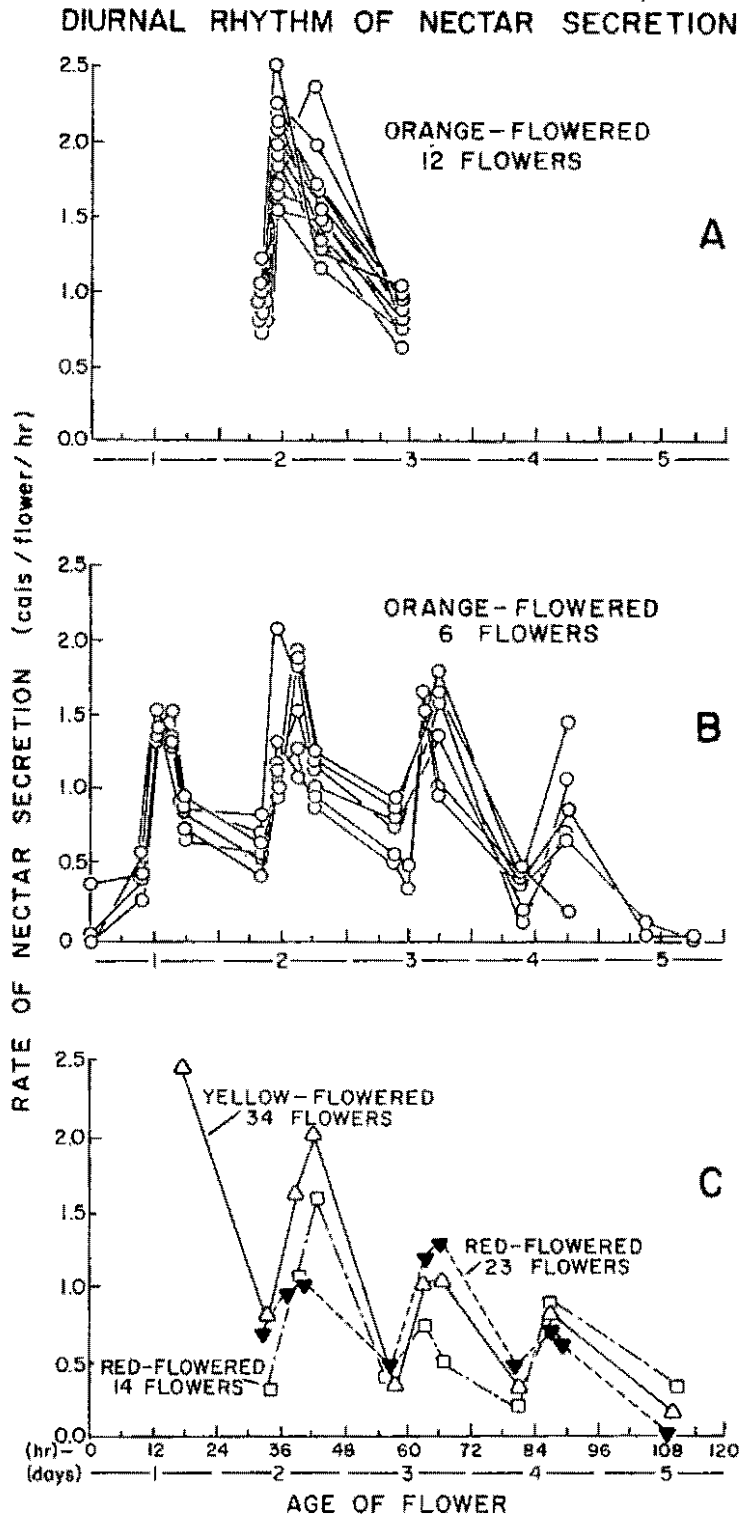


FIG. 1. Diurnal rhythm of nectar secretion in two orange, one yellow, and two red inflorescences. In A and B individual florets were measured separately, whereas in the three inflorescences in C, nectar was combined from all florets in an inflorescence. Time 0 hr was the first exertion of stamens from the bud (A,B) or buds (C).

within the same tree from day to day (Table 3), but generally occurred between noon and 1600 hr. Mean nectar flow in the entire population sample of 29 red-flowered trees ($N_t=79$) sampled for baseline nectar secretion was 0.57 cal per floret per hr averaged over a 24 hr period. Since an average of 17 producing florets occurred per inflorescence ($N_t=31$, $N_f=156$ --includes inflorescences in B and C treatments), total production in an inflorescence was about 10 cal per hr.

The rate of nectar secretion was affected by age of the flower but not by sampling regime (Fig. 2). Florets began secreting within 10 to 18 hr and reached high rates within 13 to 24 hr after first style or stamen exertion from the bud (Fig's. 1A, 1B, and 2). The 24 hr rate peaked broadly between one and three days after opening, and the rate declined after that until stamen dehiscence on days five to seven, when secretion ceased. During the last day or two of the flow, the nectar was often secreted at higher concentrations: at the peak of flow nectar was 14% sucrose within 4 hr of the time of secretion ($N_t=5$, $N_f=10$), whereas on the last day of measurable secretion the mean concentration rose to 32% ($N_t=13$, $N_f=35$). When nectar was allowed to remain unsampled for more than 4 hr, concentrations varied because of evaporation by wind and sun but averaged 21% ($N_t=20$, $N_f=92$). Weather and old age of floret sometimes interacted to produce concentrations of 50% sucrose or more.

Of the factors of elevation, height of flower in tree, size of tree, and season, only elevation affected nectar flow significantly. In red-flowered trees flow rate was related parabolically to elevation between 1290 and 1850 m, the predicted minimum rate occurring at 1580 m (Fig. 3). Weighted multiple regression analysis assuming linear effect of height in tree and quadratic effect of elevation revealed that height in tree did not contribute significantly to the regression and that the quadratic term was necessary to describe the effect of elevation. Floral dimensions were linearly related to elevation (Fig. 4), which suggests that rate of nectar secretion is independent of these facets of floral morphology. Our largest sample size was obtained at 1350 m; analysis of data at this site showed there was no difference between nectar flow rates of small (< 9 m) and large (> 12 m) red-flowered trees (t-test, $p > .9$), nor was there a significant difference between December and July-August flow rates (t-test, $.3 < p < .4$). The mean of three yellow- and orange-flowered trees at 1350 m was significantly higher than the value for red trees at that elevation

TABLE 3. Timing of peak nectar flow in four trees.

Tree no.	Day	Sampling interval containing peak	Midpoint of sampling interval
73-10 (yellow)	2	1400-1730 hr	1545
73-4	2	1400-1730	1545
	3	1100-1400	1230
73-5	2	1300-1700	1500
	3	1330-1700	1515
74-16	1	1000-1300	1130
	2	1200-1500	1330
74-16	1	0800-1000	0900
			Mean = 1400 ± 2 hr

EFFECT OF AGE AND SAMPLING RATE ON NECTAR SECRETION

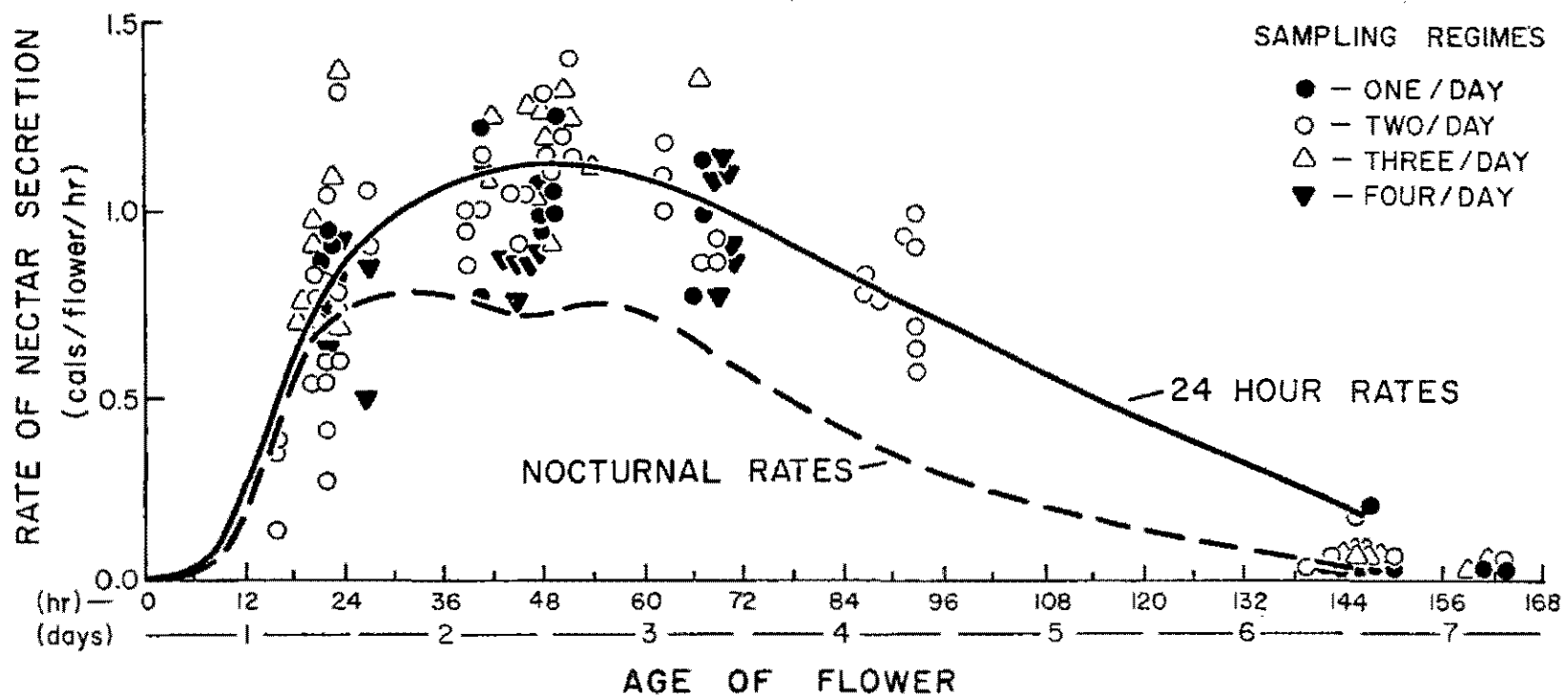


FIG. 2. Effect of age and sampling rate on nectar secretion in one inflorescence. Values plotted are the combined calories secreted over a 24 hr period regardless of number of samplings per day.

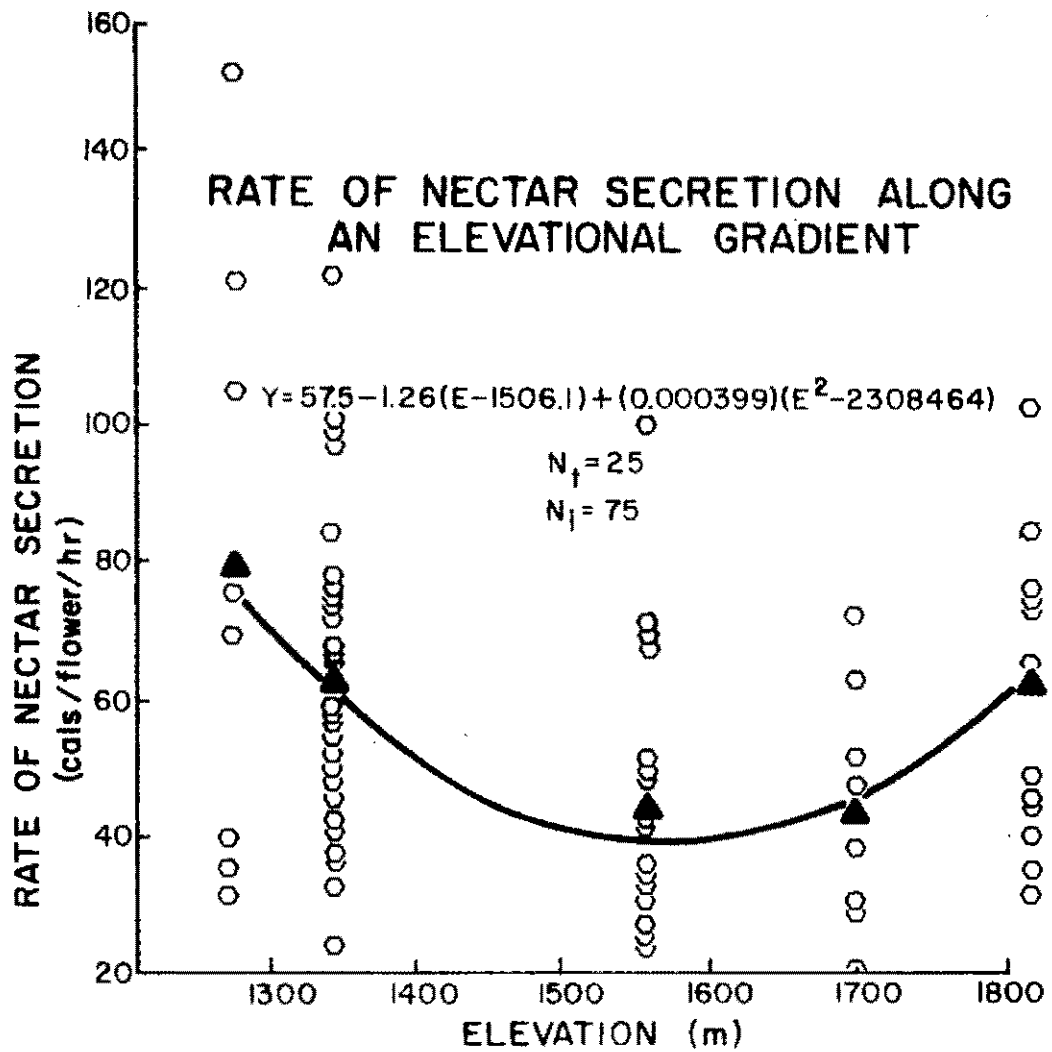


FIG. 3. Rate of nectar secretion along an elevational gradient. Each data point represents an average 24 hr value for one inflorescence. The number of inflorescences sampled per tree varied, and the closed triangles represent weighted means for each elevation. The line drawn represents the best-fit equation indicated on the graph.

FLORAL DIMENSIONS ALONG AN ELEVATIONAL GRADIENT

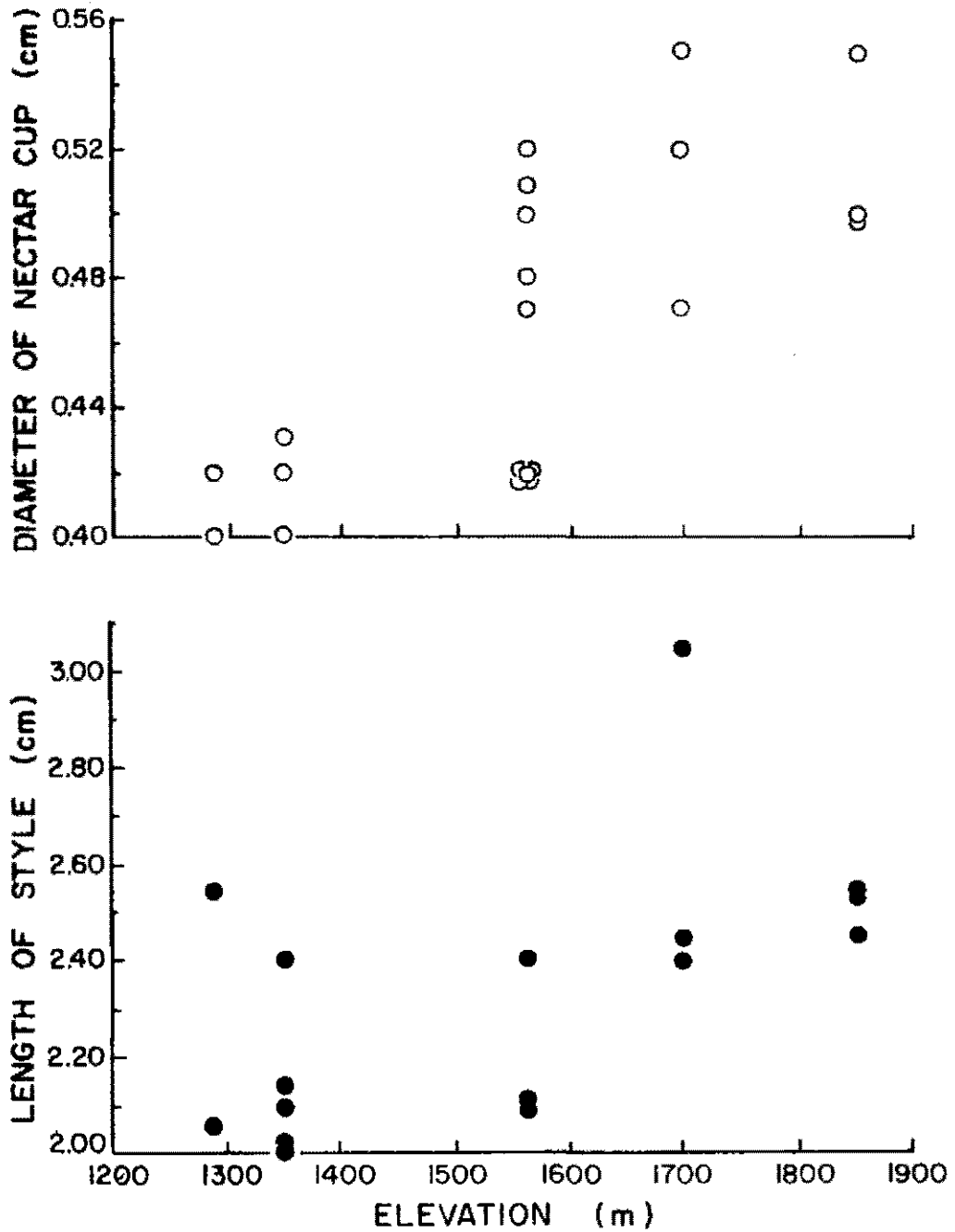


FIG. 4. Floral dimensions along an elevational gradient; top: diameter of nectar cup; bottom: length of style.

predicted from the regression (Fig. 3, $p < .05$). Finally, observed secretion rates in four trees in the scrub woodland at 1200 to 1230 m were significantly lower ($p < .01$) than the rate predicted by extrapolation.

Nectar availability and utilization

The percentage of trees blooming varied with elevation in summer 1974 (Fig. 5) in a similar manner as did nectar flow, except that upon descending from the forest at 1290 m to the scrub at 1230 m, I found that blooming usually continued to increase whereas secretion dropped markedly, as explained above. The percentage of bloom was correlated (July, $p < .01$; August, $p < .05$) with the intensity of bloom (number of inflorescences per tree) except in September when the percentage of bloom was extremely low. Thus, nectar availability varied spatially.

Nectar availability also varied temporally. In April 1974 at 1560 m the bloom was $> 50\%$ with 89% of the blooming trees being heavily in flower ($>> 30$ blossoms per tree), whereas the bloom at that elevation in the summer was less than 15% with 0% heavily in flower. Trees in heavy bloom possess hundreds of blossoms; I counted 600 in a tree in summer 1973--enough to satisfy the energy requirements of seven honeycreepers (modified from Carpenter and MacMillen 1973). Detailed information on the temporal changes in bloom in this general area is available in Baldwin (1953) and Porter (1973); data extracted from Baldwin (1953) are shown in Figure 14. Little nectar was used during the night, as large quantities accumulated and were available at dawn. The daily periodicity of nectar used differed in insects and birds. Figure 6 shows the proportion of the observations made at each hour of the day that represent large unexploited nectar quantities. Birds were able to exploit nectar rapidly after dawn (Fig. 6, line C), whereas insects when acting alone (Fig. 6, line B) did not reduce the nectar in the inflorescences to low levels (≤ 0.1 cal/floret) until afternoon. Furthermore, insects were not able to keep the nectar levels down in late afternoon while birds were. A comparison of lines B and C suggests that birds (high energy homeotherms) rapidly replenish their energy reserves at dawn after their nocturnal fast and that they stock up on energy late in the day in preparation for another fast, whereas the poikilothermic insects forage most intensely during the heat of midday.

The total amount of nectar taken during the day by insects within the

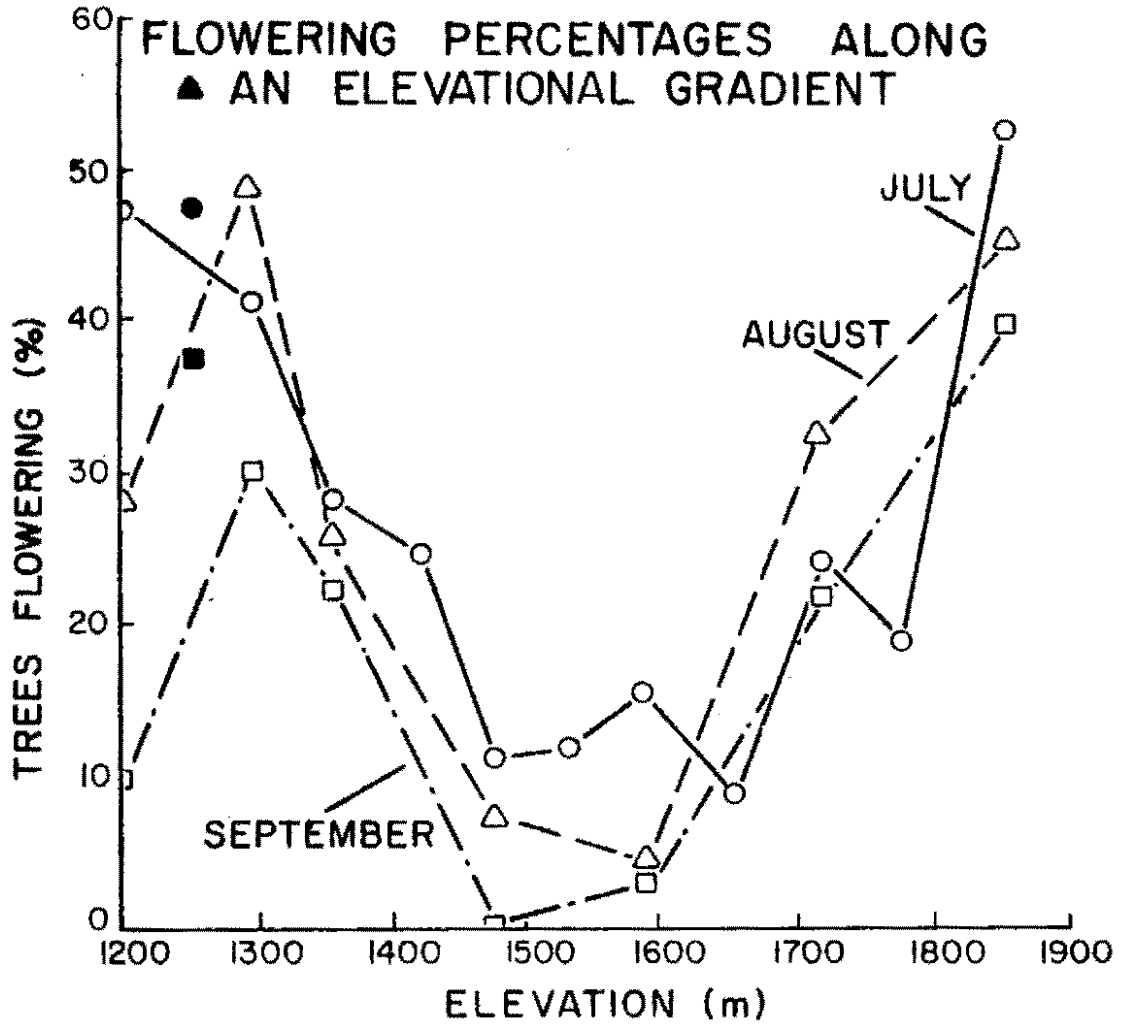


FIG. 5. Blooming percentages along an elevational gradient in July, August, and September 1974. The three closed symbols are the percentages in the scrub sites between 1200 and 1230 m in those three months.

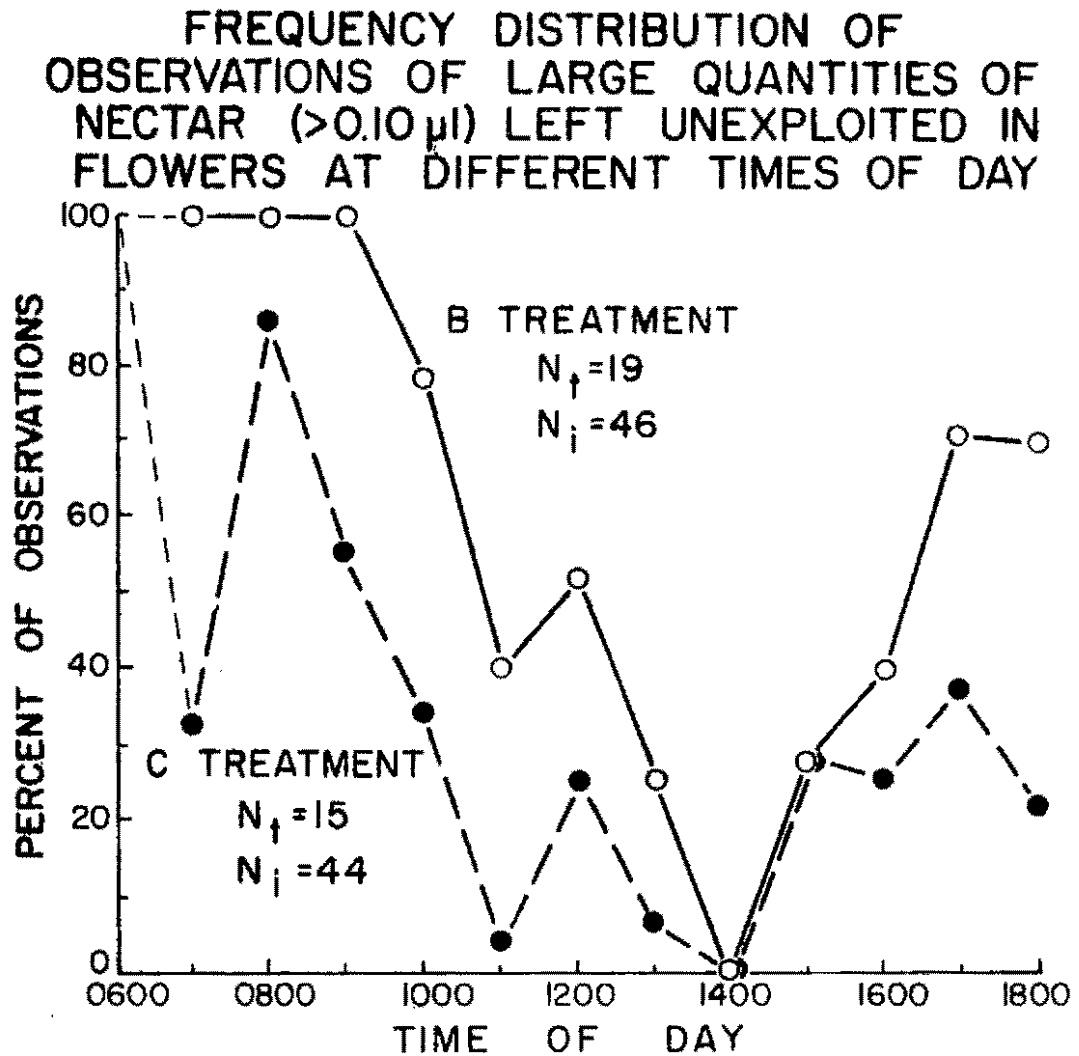


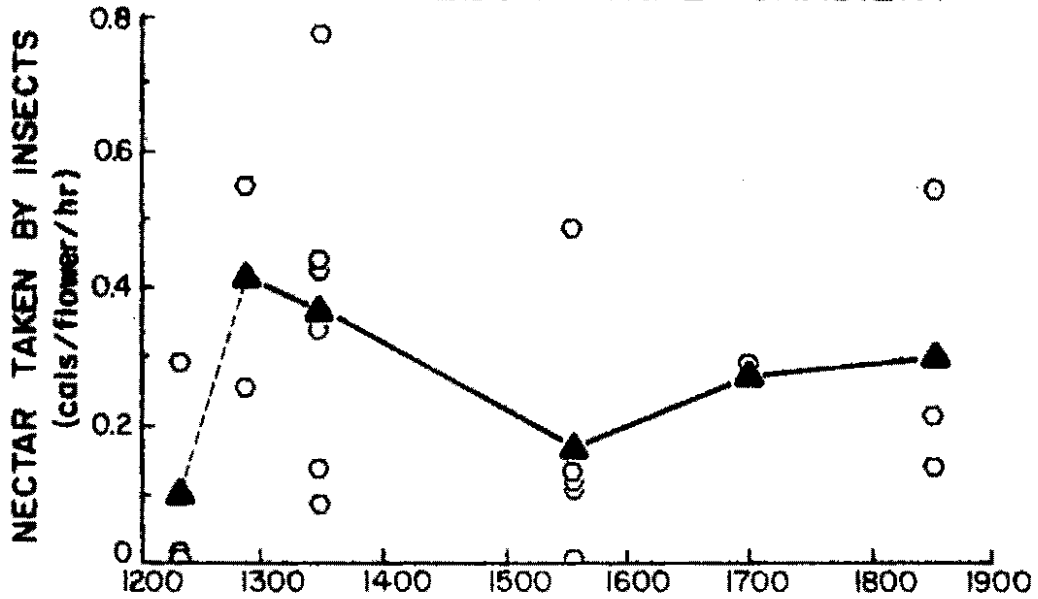
FIG. 6. Frequency distribution of observations of large quantities of nectar ($\geq 0.10 \mu\text{l}$) left unexploited in flowers at different times of day. Solid line represents insect (B) treatment, dashed line represents bird plus insect (C) treatment. A total of 113 observations were made for both B and C treatments.

forest varied parabolically with elevation (Fig. 7, top), suggesting that insect densities may have varied with elevation in the same way. This is supported by the fact that at the elevation of lowest nectar use in the forest (also the elevation of lowest nectar flow rate), the mean proportion of the nectar produced that was left unused by insects was probably about 20% (Fig. 7, bottom), so that lower nectar use at this elevation did not reflect merely less nectar available there. In contrast, there was no apparent relationship between elevation and the percentage of nectar left unused in flowers open to birds and insects both--amounts left over were universally low within the forest. In the scrub, nectar seemed not to be exploited by either birds or insects (Fig. 7) and with binoculars we could see huge accumulated quantities glistening in the nectar cups.

Pollination and seed set

For red-flowered trees the percentage seed set by selfing, A treatment, was significantly less than that set by insects, B treatment (one-sided t-test of the means of percentages, $p < .005$; one-sided t-test of the paired differences, $p < .001$). The B seed set in turn was significantly less than that set by birds plus insects, C treatment (one-sided t-test of the means of percentages, $p < .025$; one-sided t-test of the paired differences, $p < .005$). See Table 4. Thus, pollination was necessary for high levels of seed set; the results also suggest that highest seed set occurred as a result of outbreeding and that ohia may have a weak self-incompatibility system. To test this, I performed an artificial self-pollination experiment as described in Methods. I expected that selfing by repeated artificial pollination in three red trees would be higher than that in A bags in the same trees; however, it was only 2% higher, and this difference was not statistically significant (one-sided t-test, $p > .45$). Thus, both selfing situations (undisturbed A bag and artificial self-pollination) result in low seed set, and the results indicate that the partial self-incompatibility suggested by A-B-C seed sets must be, at least in part, non-mechanical. Since selfing probably requires a pollinator (C. Corn, pers. comm.), the movement of bag and enclosed twigs and leaves in the breezes must be adequate to effect selfing in the A bags, within which large quantities of sticky pollen accumulate and are spread among the enclosed inflorescences at various stages of development.

CALORIES OF NECTAR TAKEN BY INSECTS ALONG AN ELEVATIONAL GRADIENT



PROPORTION OF NECTAR PRODUCED THAT IS LEFT UNEXPLOITED ALONG AN ELEVATIONAL GRADIENT

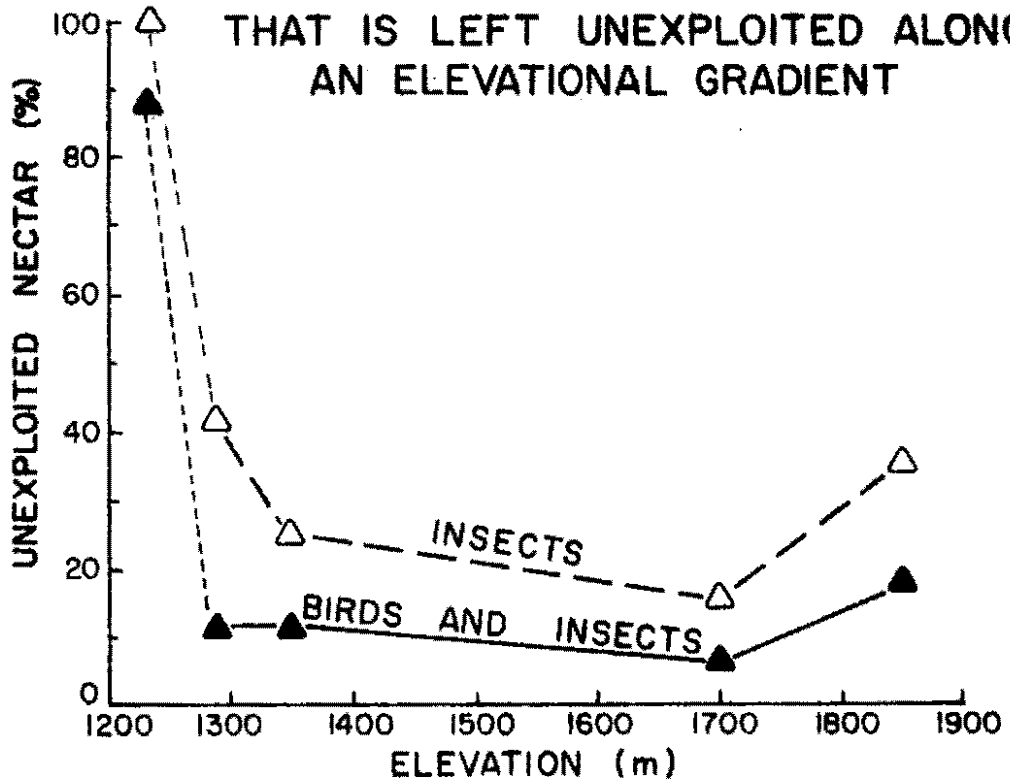


TABLE 4. A, B, and C seed sets (in %) compared.

	A	B	C
RED-FLOWERED TREES			
Mean	19.4	38.9	55.3
Standard deviation	17.6	25.7	22.5
N_t	25	22	26
N_i	97	75	143
Paired comparisons ($N_t=20$)		B=4.4xA	C=2.7xB
YELLOW-FLOWERED TREES			
Mean	53.1	56.7	60.1
Standard deviation	20.2	18.2	25.9
N_t	3	3	3
N_i	8	7	6
Paired comparisons ($N_t=3$)		B=1.3xA	C=1.1xB

Some of the self-incompatibility in the red-flowered trees may be mechanical, however. This is suggested by significantly higher selfing in yellow-flowered trees (Table 4, t-test, $p < .01$), which also had significantly smaller nectar cups (3.55 mm in yellow, 3.35 mm in orange) than did red florets (4.14 mm, t-test, $p < .001$). Smaller diameters bring stamens and anthers closer to the central stigma, facilitating pollen transfer within florets. In following up this suggestion of different floral morphologies in red and yellow inflorescences, I found a tendency (one-sided t-test, $.05 < p < .10$) for yellow inflorescences to have more florets than red ones. Yellow inflorescences gave the impression of being tightly packed with many small florets; this would decrease the distance of the anthers of one floret to the stigmas of its neighboring florets, thus morphologically facilitating between-floret selfing. Apparently, the yellow and perhaps also the orange forms have lost any genetic self-incompatibility and may be developing automatic selfing (autogamy).

In two red trees studied the stigma seemed maximally receptive one to two days after the stamens began exerting (Fig. 8). This corresponded with the peak of nectar production determined in two different trees (Fig's. 1, 2), and thus presumably with the peak of pollinator visitation. Pollen usually was shed from the moment the stamens exerted to four or five days afterwards, and some nectar was presented at these times also. The data on timing of receptivity did not agree with those of Corn (1972a); however, she worked with members of a different population than mine, and may have been dealing with a different "variety".

Comparing pairs of B and C seed set treatments within red-flowered trees showed that flowers open to birds as well as insects set 2.7 (± 1.2) times more seed than did flowers open only to insects (Table 4). However, in the three yellow-flowered trees, C seed set was only 1.1 times higher than B seed set and only 1.4 times higher even than A seed set. Thus, birds were important pollinators of the red trees, and most pollination occurred when flowers were open to both birds and insects. Birds either were not attracted to the yellow trees, or else did not effect greater seed set because the levels of selfing were so high in the yellow form. The smears made of the head feathers of nectar-eating birds produced large quantities of pollen, most of which was ohia pollen; the relative loads of ohia pollen carried by the various species on our study area during summer 1974 are shown in Table 5. The heaviest loads were

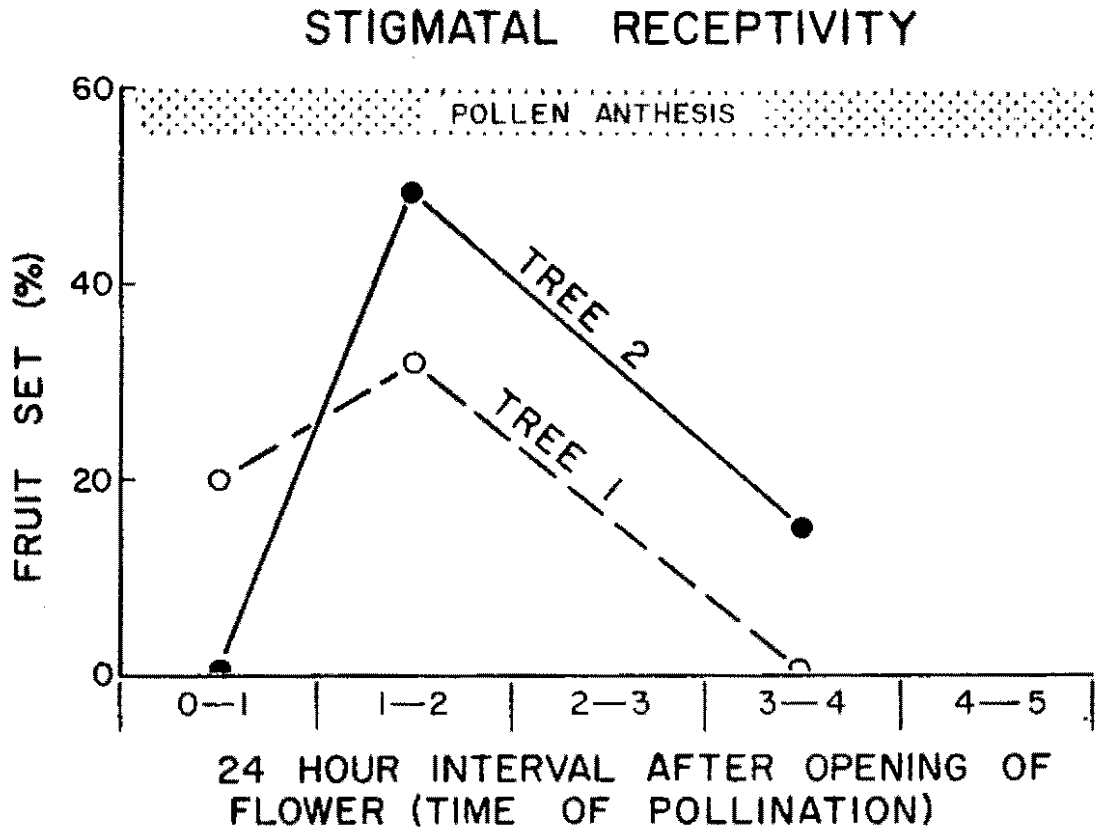


FIG. 8. Periodicity of receptivity of stigma, measured by proportion of florets setting seed. Timing of pollen dehiscence is represented by stippling.

TABLE 5. Distribution of M. collina pollen loads on 11 bird species (all birds collected between 1350 m and 1850 m on Keauhou Ranch).

	Absent	Light	Heavy
NECTAR-FEEDING SPECIES			
<u>Loxops virens</u> (N=27)	4%	85%	11%
<u>Himatione sanguinea</u> (N=39)	0	13	87
<u>Vestiaria coccinea</u> (N=14)	0	29	71
<u>Zosterops japonica</u> (N=7)	0	14	86
SPECIES USING LITTLE OR NO NECTAR*			
<u>Loxops coccinea</u> (N=1)	0	100	0
<u>Hemignathus wilsoni</u> (N=1)	100	0	0
<u>Loxops maculata</u> (N=1)	100	0	0
<u>Phaeornis obscurus</u> (N=6)	83	17	0
<u>Leiothrix lutea</u> (N=4)	50	50	0
<u>Carpodacus mexicanus</u> (N=3)	100	0	0
<u>Lonchura punctulata</u> (N=1)	100	0	0

*All records in the "Light" category except for one of the Leiothrix resulted from a single pollen grain on the slide.

carried by two honeycreepers, Apapane (Himatione sanguinea) and Iiwi (Vestiaria coccinea), and by the introduced White-eye (Zosterops japonica, family Zosteropidae).

Weighted multiple regression analysis showed that in summer 1974 seed set effected by birds plus insects (C treatment) was not dependent on elevation ($p \gg .05$), whereas seed set effected by insects alone (B treatment) tended to show a parabolic relation with elevation (Fig. 9, $p = .05$). This corresponded to the pattern of insect activity (Fig. 7, top) and suggested that seed set fell because of low pollinator activity in the B treatments at 1600 m. The analysis showed that there was no correlation of seed set and height in tree for the B treatment ($p \gg .05$) but that seed set was positively correlated with height for the C treatment ($p < .01$, Fig. 10). This pattern almost certainly reflects the pattern of foraging activity in the bird pollinators, Apapane and Iiwi occupying high levels in the canopy most of the day (Baldwin 1953, Carpenter and MacMillen 1973; MacMillen and Carpenter, in prep.).

Heinrich and Raven's (1972) hypothesis suggests that above an optimal nectar availability, seed set should decline. I tested this two ways, first with a between-season comparison, and second with a within-season comparison of trees with different nectar flows. C treatment seed set values were corrected to a standard height in tree (3.7 m) according to the equation in Figure 10. B treatment seed set values were corrected to 1500 m elevation according to the equation in Figure 9.

I predicted that seed set should be lower, because of geitonogamy, at the peak of blooming when large numbers of blossoms occur per tree, than in the decline of blooming. C treatment seed set was significantly lower resulting from pollination in April, the peak of the bloom, than that resulting from pollination in summer toward the end of the bloom (one-sided t-test, $p < .05$). However, B treatment seed set was not significantly lower at the peak than in the decline (one-sided t-test, $p > .15$). Thus, birds may have been more sedentary at the peak of the bloom than later, and the resultant geitonogamy lowered seed set. Insects, however, seemed to not be affected by the change in the blooming regime.

Seed set declined in trees with nectar flow rates greater than 0.4 cal per floret per hr (Fig. 11), both in C treatments ($F=11.32$, $.005 < p < .01$) and in B treatments ($F=8.00$, $.01 < p < .025$). The standard errors of the regression coefficients were 15.75 and 17.07 for C and B treatments, respectively.

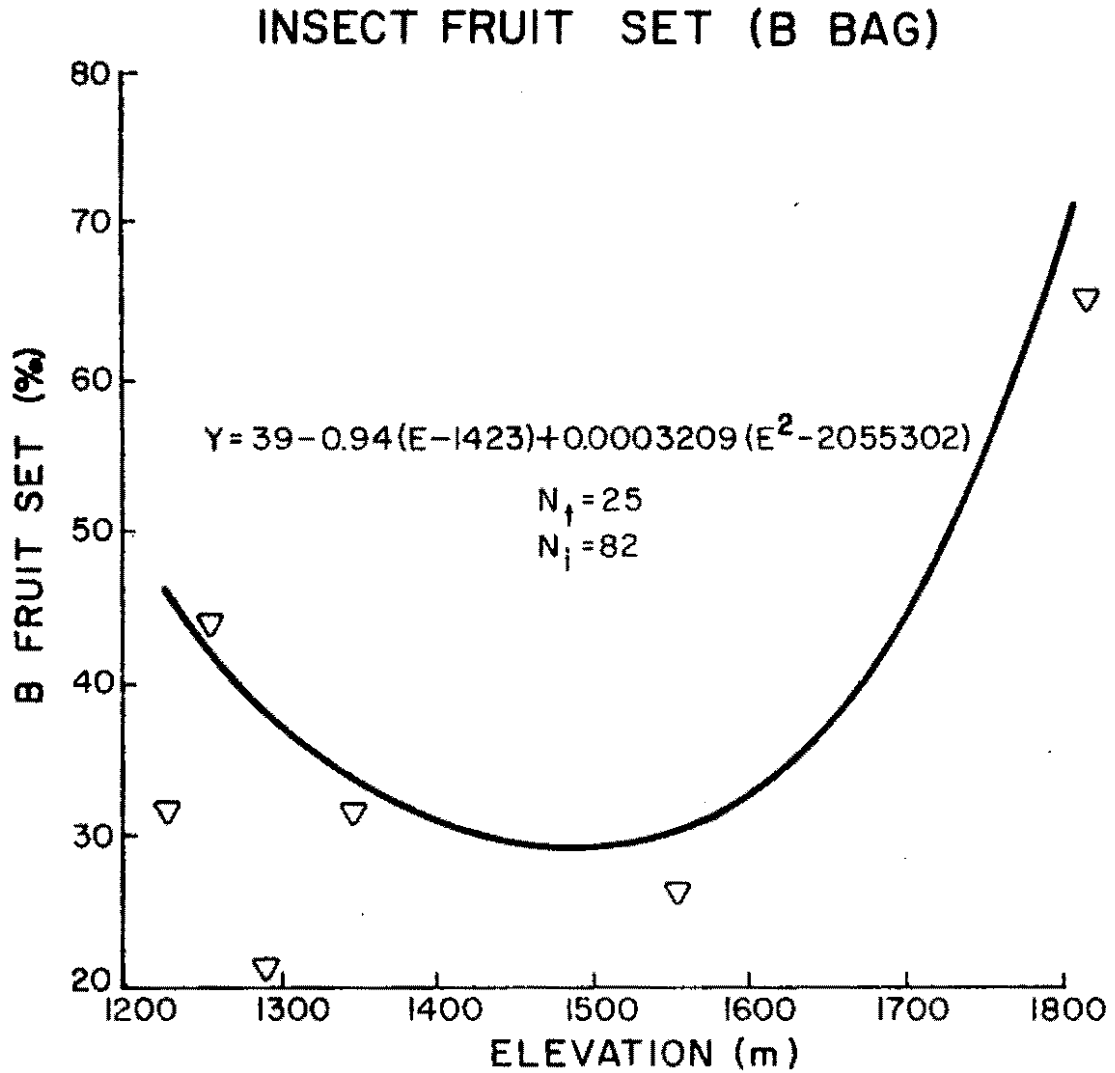


FIG. 9. Insect seed set (B treatment) against an elevational gradient. Weighted means for each elevation are indicated by open triangles, and the line is the best-fit equation shown on the graph.

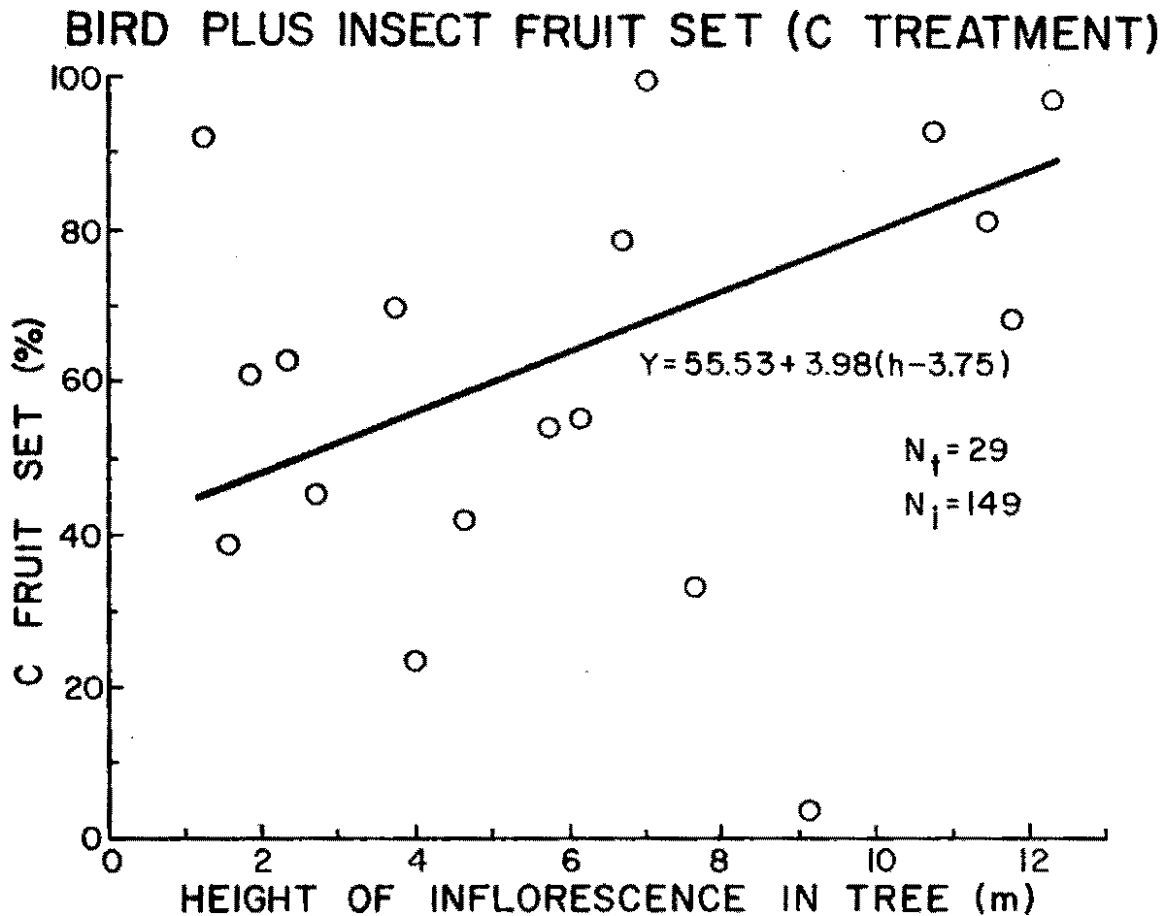


FIG. 10. Bird plus insect seed set (C treatment) as affected by height of inflorescence in tree. The open symbols are weighted means for each height in tree. The sample sizes (N_i) for each height in tree vary from one at $x=9$ m to 46 at $x=3.7$ m. The line is the best-fit equation shown on the graph.

Maximal seed set occurred in trees that had a nectar flow of about 0.4 cal per floret per hr, apparently falling off rapidly in trees with lower nectar flow rates, as was also predicted. Polynomial regressions were not fit to the data in Figure 11 because of too few data points from low nectar producers. Trees were selected randomly with respect to their rates of nectar secretion (unknown at the time of selection), and the small sample of low producers may mean that few of these individuals occur in the population as a whole. The rapid decline in seed set below the rate of about 0.4 cal may act as strong selection pressure against these individuals.

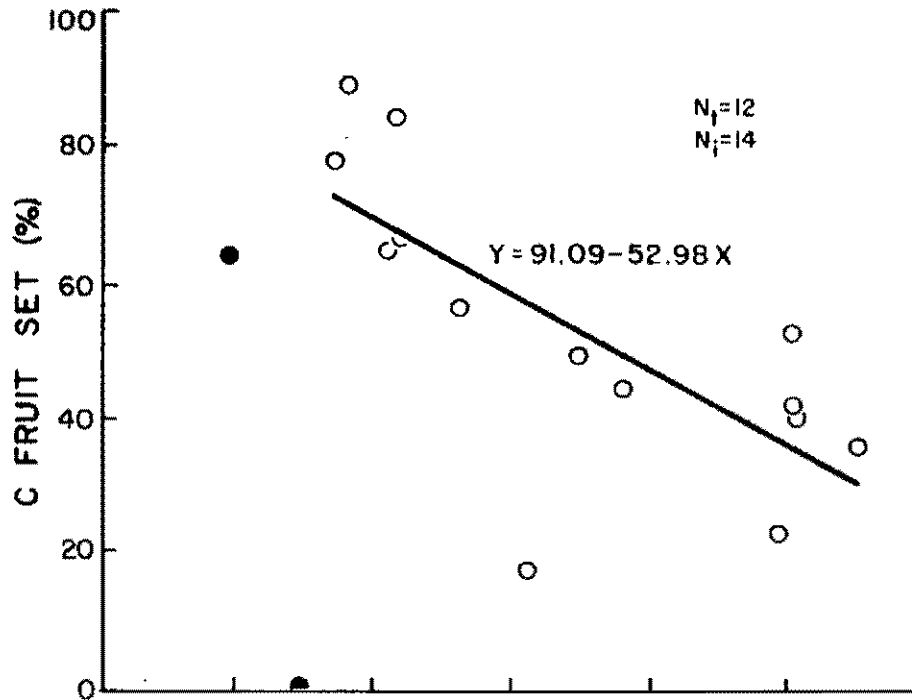
That highest seed set at intermediate nectar flows was caused in fact by satiation of pollinators was supported by higher levels of nectar left unused at all times of the day in fast nectar producers than in slow (one-sided t-test, for B treatment $p < .025$; for C treatment, trend only with $.10 < p < .15$). Thus, satiation of pollinators seemed to occur at high flows, with concomitant decline in outbreeding, causing lower seed set because of partial self-incompatibility.

If this be the case, we should be able to predict that outbreeding would be a mirror image of the nectar secretion curve against elevation (Fig. 3). To get an approximate measure of outbreeding, I subtracted the insect component (B seed set) from the total insect plus bird seed set (C) to get a bird-only component. When plotted against elevation, a curve resulted that was a mirror image of Figure 3, with maximum contribution of bird pollination occurring at the elevation of slowest flow, 1560 m (Fig. 12). Thus outbreeding via bird activity compensated for the low insect activity at intermediate elevations.

All of these results taken together suggest that, given constant pollinator activity, seed set depends on nectar flow; however, seed set declines regardless of nectar flow when pollinator activity falls too low.

Iiwis (*Vestiaria coccinea*) were capable of pollination (Table 5), but often established territories in single trees (Carpenter and MacMillen 1975a). Given that seed set declines directly with the decline in degree of outbreeding in ohia, I was able to test whether the geitonogamy effected by Iiwis on single-tree territories resulted in lower than average seed set. Seed set in the C treatment of the one Iiwi tree for which I had data fell below the lower limit of the 98% confidence interval of nonterritorial trees whose blossoms secreted at about the same rate, whereas, insect pollination (B treatment) in the territorial tree was normal ($p > .30$, one-sided t-test). Data from another tree in the general Iiwi

EFFECT OF NECTAR PRODUCTIVITY ON FRUIT SET EFFECTED BY BIRDS AND INSECTS



EFFECT OF NECTAR PRODUCTIVITY ON FRUIT SET EFFECTED BY INSECTS

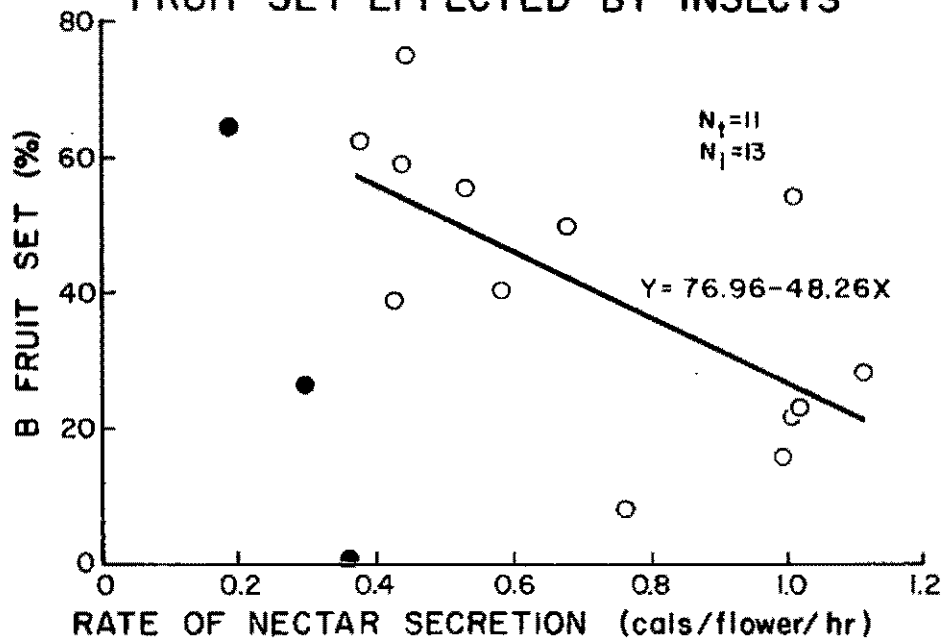


FIG. 11. Effect of nectar productivity on seed set effected:
top: by birds and insects (C treatment)
bottom: by insects alone (B treatment)
Only data represented by open symbols were included in the regression analyses. Total sample sizes including data represented by closed symbols were $N_c=14$, $N_i=16$ for both B and C treatments.

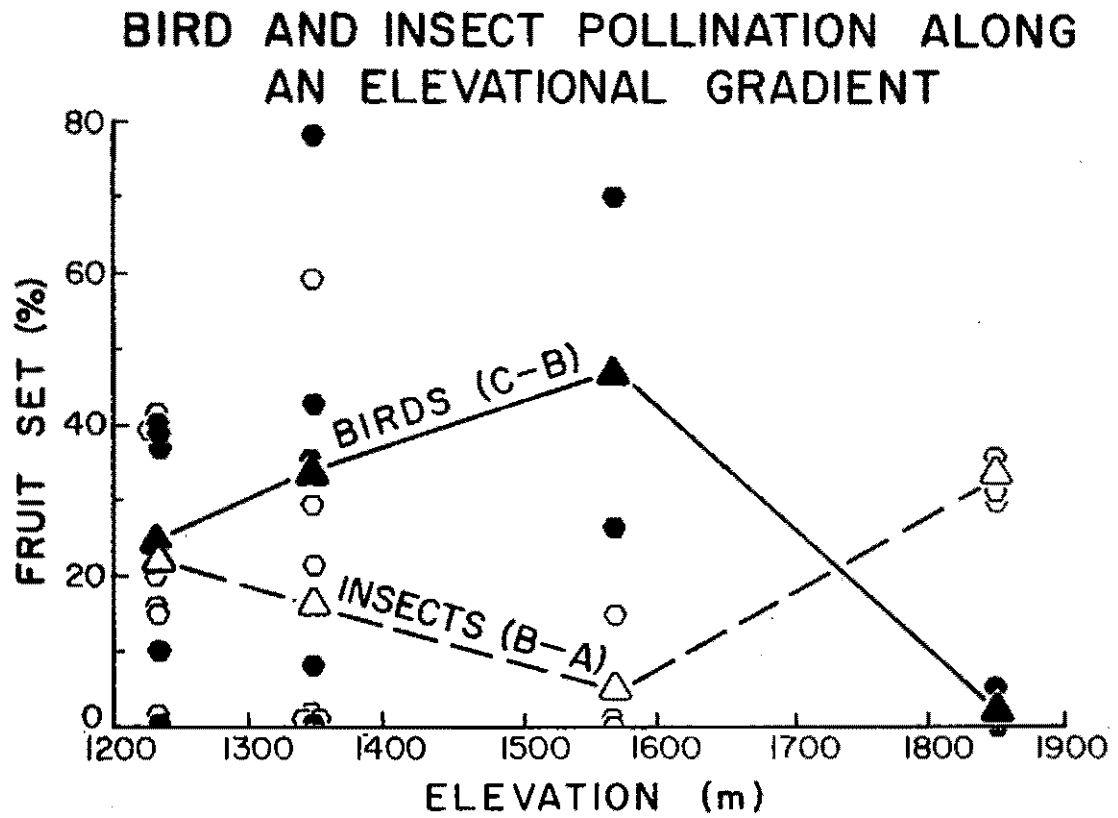


FIG. 12. Bird and insect pollination along an elevational gradient. Closed symbols represent birds, open symbols represent insects. Data points are mean values per tree, triangles are means for each elevation.

area were available; when combined with the known single-tree territory and compared against similar non-Iiwi trees by a one-sided t-test, a trend toward reduction in C seed set was found ($.05 < p < .10$), while, again, B seed set was normal.

DISCUSSION

Factors affecting nectar flow

The rate of nectar flow in red-flowered ohia depended primarily on stage of flower, elevation, and time of day. The apparent tendency of peak nectar flow to coincide with maximal stigmatal receptivity should be corroborated with more observations since my sample size was small. However, such a phenomenon would be adaptive in ohia because even selfing probably requires a pollinator, and pollinator visits should be a function of nectar availability, all other factors being equal.

The non-linear effect of elevation on nectar flow suggests a complex of interacting factors. Rate of nectar production is directly related in some plants to both insolation (Shuel 1955, Beutler et al. 1957) and ambient temperature (see Percival 1965). On Mauna Loa, temperature declines inversely with elevation ("lapse rate" = 1.7°C per 308 m rise, Stearns and Macdonald 1946), so one would expect a decline in nectar production with increasing elevation. This did occur between 1290 and 1560 m. But what accounts for the rise in productivity at still higher elevations? We casually but commonly observed that the study sites at lower and intermediate elevations were likely to be foggy from the cloud layer that often forms on the slopes of Mauna Loa, but that the highest sites, especially that at 1850 m, were usually clear even when fog occurred below. That a break in the cloud layer may occur commonly between the 1500 and 1850 m sites was suggested by the data of Juvik and Perreira (1973): the absolute amount of precipitation contributed by fog increased between 1000 and 1500 m elevations but declined above 1500 m. Furthermore, Jones (1941) states that rainfall is maximal at elevations below 1850 m. It is possible then that the lapse rate in ambient temperature affects nectar production from the lower to the middle elevations, which are frequently cloud-covered, but that still lower temperatures at the highest elevations are counteracted by increased surface insolation, due to decreased water vapor

and/or droplets, which stimulates nectar productivity. It is notable that the activity of poikilothermic insects seemed to vary with elevation in the same way as nectar production. Their activity should be directly related to total heat load in the environment which will decline with decreasing ambient temperature, but increase with increasing surface insolation. It was probably fortuitous that the blooming curve in summer 1974 also showed the same parabolic relation to elevation, since the bloom varies seasonally at each elevation (Baldwin 1953, Porter 1973), yet my study showed that nectar flow rate does not. Thus, I simply happened to measure blooming percentages at a time (summer) when the middle elevations had finished flowering, the peak having occurred in April.

If nectar production is temperature- and insolation-dependent, this would also explain the external cause of the diurnal rhythm of secretion, with its midday peak. Different plant species have different diurnal rhythms, including those with nocturnal peaks, and secretion rhythms are thought (Baker 1961) to be adapted to the activity patterns of the appropriate pollinators. Ohia's peak coincides with the peak of activity of insects during the day, but also with an afternoon peak of activity of Apapane (MacMillen and Carpenter, in prep.). Other nectar-feeding birds seem to increase activity in late afternoon (Pearson 1954, Stiles and Wolf 1970, Carpenter and MacMillen 1973, 1975a), and this is suggested by Figure 6 for the birds using ohia in our study area. Thus, the high afternoon secretion rates benefit both insects and birds. However, the fact that considerable secretion continues during at least part of the night suggests adaptation for birds rather than insects. Nocturnal secretion, even though lower than diurnal, results in large amounts of accumulated nectar at dawn, when feeding is intensive by the fast-breaking birds (MacMillen and Carpenter, in prep.; see also Stiles and Wolf 1970). Because they are still lethargic in the cool mornings, insects cannot fully exploit the accumulated nectar when birds are excluded, and thus it is difficult to imagine that the overall copious nectar flow and the nocturnal secretion of ohia could be adapted primarily for diurnal insects. The situation in New Zealand Metrosideros umbellata may shed light on this matter. This species is associated with the native meliphagids, the Tui, Prothemadera novaeseelandia, and the Bellbird, Anthornis melanura (Falla et al. 1966). These birds are larger than the Apapane and Iiwi (Peterson 1961, and Falla et al. 1966) and, therefore, have higher total energy requirements. They are also distributed at higher latitudes

(> 40°S), which should result in cooler nocturnal temperatures and thus more energy spent by the birds while roosting. I measured nectar flow in one tree in December 1974: diurnal secretion was 0.58 cal per floret per hr, nocturnal secretion was 0.47 cal per floret per hr, and the resultant 24 hr rate was 0.50, similar to the ohia mean. The higher nocturnal flow resulted in even larger amounts of accumulated nectar by the critical early morning period for the New Zealand birds. The colder early morning temperatures at that latitude should inhibit early morning nectar exploitation by insects even more than in Hawaii.

In addition to floral stage, elevation, and time of day, soil type may have affected nectar flow in ohia. The low flow rates in the scrub forest could not be accounted for by difference in climate. The trees were smaller, but data from the higher-elevation forest showed no effect of tree size on secretion rate. The most conspicuous difference between the scrub and forest was difference in soil depth and base rock type (Mueller-Dombois and Fosberg 1974). The scrub was growing on shallow ash and soil over smooth, ropey pahoehoe lava that does not decompose quickly. The forest was growing on maturer soils built from the jagged chunks of aa lava, which breaks down quickly. It seems reasonable that trees growing on pahoehoe might be limited severely by water or nutrients or both, and that this would limit nectar production. Both water and nutrients are known to affect nectar secretion in other plants (see Percival 1965).

Nectar availability and utilization

In spite of low flow rates in the scrub, large amounts of nectar accumulated in scrub ohia blossoms because of low insect and bird usage. One of the assistants observed unusually low numbers of honeycreepers in the scrub during the summer of 1974; this observation was confirmed by the censuses of Conant (1975). According to my nectar usage measurements (Fig. 7) insects also seemed to be unusually scarce in the scrub. The reason for such apparent avoidance of the scrub by pollinators is not clear. Large numbers of honeycreepers were censused in the scrub in winter and spring 1974 (Conant, pers. comm.) so it would seem that the scrub is suitable habitat. However, the census may have picked up masses of birds passing through on their way to higher elevations beginning in the winter, as Baldwin (1953) showed such movements must take place.

So perhaps the scrub is not suitable for extended visitations of honeycreepers. Insects might avoid the scrub because of less shelter from wind and rain.

As a result of these several patterns, the amount of nectar available to insects and birds varied with elevation and time. Within the forest, middle elevations had less nectar available in the summer of 1974 than did higher or lower elevations because 1) fewer trees were blooming, 2) the number of blossoms per tree was lower, and 3) the nectar flow rate was lower. Nectar availability for the pollinators is patchy temporally also. Baldwin (1953) showed that the birds respond to the temporal patchiness by vast seasonal movements across the mountain slopes, following the bloom. Other nectar feeding birds seem to perform similar movements (see review in Stiles 1973). One would expect then that the birds should respond to spatial variations in bloom by adjustments of their own densities. This may have occurred during my study, as Figure 7 indicates that the total usage of nectar by birds and insects together remained relatively constant along the forest transect in spite of varying blooming intensities, a situation not held for insects alone. This means that the ratio of birds to nectar availability (determined partly by insect usage) may have been relatively constant throughout the patchy environment. To test this, I extracted both bloom abundance and bird abundance data from Baldwin (1953: Fig's. 4, 10, 11, 12) to see if they were positively correlated. Values for blossom and Apapane abundances were available for 12 months in three study sites for Iiwi and 10 study sites for Apapane. When correlation analysis was performed on all values from all sites for each of the bird species, the correlation was significant for Iiwi ($p < .05$) but was not significant ($p > .10$) for Apapane in spite of obvious coincidence of Apapane peaks and blooming peaks (see Baldwin 1953). The lack of correlation probably was caused by two factors: 1) Apapane may be less nectar dependent than Iiwi and turn to insects as the bloom declines in an area, and 2) blooming can begin and peak so rapidly in any given area that Apapane lag in detecting and invading such areas. Factor 1 (above) would contribute to this lag. That lags occur is obvious in Baldwin's (1953) data (compare Fig's. 10 and 11 with Fig. 4 in his paper). However, in spite of lack of precise correlation, Apapane do follow the blooming with a two to four week lag, and they tend to distribute themselves more evenly with respect to blossom abundance than would occur by random sorting. This is shown by the fact that Apapane numbers were correlated significantly with blossom

abundance in 4 of the 10 study sites of Baldwin (1953) when each site is analyzed independently of the others.

Pollination

1. Selfing in ohia

The pollination ecology of ohia suggests a relatively generalized pollination strategy, encompassing selfing and outbreeding effected by two major groups of pollinators, insects and birds. Ohia seems to have a moderate degree of self-incompatibility that may be partly genetic and partly structural. Darwin (1876) found a gradation of (genetically determined) self-incompatibility, from total to none at all (see also Faegri and van der Pijl 1971). Ohia apparently falls midway along that gradient being partially self-compatible but setting highest seed when outbreeding is greatest. Percival (1965, p. 118) refers to similar system in Eucalyptus calophylla. Some plants attain self-incompatibility by means of chemicals in the stigma and style that inhibit growth of pollen tubes of the same genotype (Pandey 1960). Inhibition can be total, or it merely can slow the growth of pollen tubes such that tubes from different genotypes grow faster and are therefore favored in the race to pollinate ovules. Furthermore, sometimes such chemicals dissipate during the life of the flower, so that by the end of nectar production, the flower is completely self-compatible and selfing can occur as an emergency measure in the event that little or no outbreeding has taken place by then (Lamprecht 1929, Ascher and Peloquin 1966, Pandey 1960). More work needs to be done on the ohia pollination system to confirm partial self-incompatibility and determine its basis.

Although the sample size of non-red forms was small, the results suggest that the rate of nectar flow depends partly on flower color, different colors seeming to represent different pollination syndromes. The yellow, and perhaps also the orange, forms seem to have lost any genetic self-incompatibility and to be evolving a floral structure which encourages selfing. Concomitant with this is an increase in nectar productivity, which should enhance selfing by geitonogamy. It is possible that the yellow tones increase the attractiveness of these flowers to insects relative to birds (see Faegri and van der Pijl 1971, Grant and Grant 1968). Insects would be more likely to be satiated by large quantities of nectar than would be birds, because of their relatively lower

energy requirements. Insects, therefore, would be good agents of geitonogamy in ohia, especially in the presence of high nectar flows as in the yellowish forms. Furthermore, in my study area honeybees seemed to be the most active of the ohia flower insects, and they possess strong site constancy behavior (Grant 1950, Butler 1945, Free 1962). Outward pollen flow effected by honeybees on crops has been found to decline precipitously 10 m beyond the source (see review, Heinrich 1975). Both site constancy and low energy requirements enhance the likelihood that these insects would effect primarily geitonogamy in the yellowish ohia forms. I interpret the yellow and orange forms as derivatives of the red because red is the predominant color in the genus (Dawson 1968, 1970, 1972, 1975). If the yellowish forms are evolving autogamy, the situation is ripe for genetic isolation from the red form, and thus, speciation. The possible selection pressures for this are discussed in the section "Pollinators as limiting factors".

2. The significance of birds in ohia's pollination strategy

For red-flowered trees to attain the levels of seed set found in the yellow trees, both birds and insects are required, apparently because outbreeding is necessary. The fact that seed set was so much higher when birds used the flowers suggests that birds--in particular, Apapane--rather than the comparatively sedentary insects, effect most of the outbreeding. Reasons for considering insects to be primarily agents of geitonogamy were explained for the yellow flowers, but the same applies to red flowers. Figure 6 showed that insects rarely completely exhaust the nectar supply even of the lower-producing red flowers. In fact, the reason B seed set was the same in summer as in the April blooming peak may have been because insects were effecting principally geitonogamy in both seasons, the availability of nectar in summer still being high enough to satiate them. This was not true for the birds, as C seed set increased with the decline of blooming in the summer and the chronically empty C blossoms showed that nectar was being exhausted, except in the fastest nectar producers, presumably forcing more movement between trees by both birds and pollen.

However, although seed set in the C treatment was on the average almost three times higher than in the B treatment on the same tree, this does not mean necessarily that birds are three times more important as pollinators than are

insects, because my bagging techniques could not isolate their role from that of the insects. The birds could be either more or less than three times as important as insects. Because of their higher energy requirements and rapid foraging, birds undoubtedly take much more nectar from ohia than would be indicated by subtracting nectar taken by insects (B treatment) from nectar taken by birds plus insects (i.e. total produced). B bags allowed insects free access to nectar without competition or interference from birds; thus, B bag seed set may exaggerate the role insects actually play when in the presence of birds. On the other hand, because nectar essentially was unlimited in B treatments to the insects, it is probable that the insects effected relatively more geitonogamy than they would have if birds had lowered the nectar levels first each morning. However, it is obvious that birds are crucial for high seed set and may effect a majority of the outbreeding in ohia. In particular, outbreeding probably occurs primarily during the beginning and decline of the bloom in an individual tree, and also in years when that individual does not bloom heavily at all. Baldwin (1953) showed that mass movements of Apapane and Iiwi follow the blooming peaks in different areas throughout the year. There is some evidence (Carpenter and MacMillen 1973) that mass movements of Apapane may occur on a daily basis at times. Long distance flights by pollen-bearing birds should increase gene flow throughout the ohia population in my entire study area. Gene flow is also increased by the dispersal by wind of the tiny, light-weight seeds.

On the other hand, the tree must achieve most of its total yearly seed set by geitonogamy effected by both birds and insects at the peak of a heavy bloom, because at these times, huge numbers of blossoms are produced. Although seed set per inflorescence (measured in this study) is relatively low at these times, never-the-less seed set per tree must be high, and probably greater than at the beginning and decline of bloom. In fact, both Baldwin (1953) and Porter (1973) stated that the intensity of bloom in any given tree is variable from year to year and unpredictable by climatic conditions. This may ensure both outbreeding--in light bloom years--and good total seed set--in heavy bloom years. (Whether birds help set more or less total seed than insects on an annual basis cannot be determined from my data.) The anomaly of profuse flowering in tropical mainland trees is still an unexplained phenomenon--profuse flowering in the partially self-compatible ohia serves to produce large numbers

of seed, but many of the tropical species are known to be self-incompatible (see Heinrich 1975, for a review).

From 1290 m up to 1560 m the role of birds in pollination seems to increase in importance relative to that of insects. Perhaps related to this was the observation that yellow-flowered ohias occurred most frequently at lower elevations: I found none above 1350 m, two at 1350 m, three at 1200 to 1230 m, and noticed that yellow and orange were common if not predominant at two sites below 900 m. In Mexico hummingbirds become more important than insects in floral ecology as elevation increased, and the reason suggested was that homeotherms should be more dependably active under the stressful climatic conditions associated with high elevations than are poikilothermic insects (Cruden 1972; see also Vogel 1958 and Hedberg 1964). Similarly, the diversity of bird-flowers increases disproportionately at higher elevations in other tropical areas (Faegri and van der Pijl 1971, van der Pijl and Dodson 1967) and in California (Grant and Grant 1968). According to this argument, the results at my highest (1850 m) site are anomalous, as not only does the importance of insects increase but that of birds relative to insects decreases. Again, the peculiarities of Hawaiian cloud formation on the slopes could explain the increase in insect activity at elevations above 1500 to 1600 m. The decline in importance of birds relative to insects may be an artifact of the concentration of Iiwis at this site during summer 1974 (MacMillen and Carpenter, in prep.). One of the two trees upon which the mean for the 1850 m site was based in Figure 12 was known to be an Iiwi's single-tree territory; observations were not made on avian foraging on the other tree but it occurred in an area known to be inhabited by several territorial Iiwis. Thus, both of these trees were likely to have experienced primarily Iiwi-effected geitonogamy, and therefore, should not have set any more seed than did flowers in the same trees visited only by insects (B treatment). I would expect that when and where Iiwis are not present or at least not territorial at these high elevations, bird-effected seed set would increase once again, relative to insect-effected seed set. That the trees at these high elevations may be adapted primarily for bird rather than insect pollination is suggested by the increasingly large floral dimensions (Fig. 4) and by the absence of non-red individuals from the population.

If Iiwis were the most abundant nectar eating bird species in the forest, selection should have acted to reduce nectar flow in ohia. But Iiwis are the

rarest of the three honeycreeper species that we studied (Baldwin 1953, Conant pers. comm.). They always may have been rare relative to Apapane, as they are the most specialized of the three species (Baldwin 1953, MacMillen and Carpenter in prep.), and specialized species of birds tend to have less dense populations than do generalized species in the same areas (MacArthur 1972). Three other species are now extinct that previously used ohia as a nectar source on Hawaii (see review in Berger 1972 a): the Akialoa (Hemignathus obscurus) and the Mamo (Drepanis pacifica), both drepanidids that seemed to be associated more with lobeliads than with ohia, and the Oo (Moho nobilis-Meliphagidae). All three of these species were larger and apparently even more nectar-specialized than is the Iiwi. Their long bills (Table 6) would probably not have resulted in effective pollination of ohia, whose stamens and style rarely exceed 2.5 cm in length (Fig. 4). It seems likely then that the Apapane is the species that has played the most important pollinating role during the history of ohia on Hawaii.

3. Balanced adaptations in ohia's pollination strategy

Ohia has opted for a generalized pollination strategy that attains a balance between selfing as a safety measure in the absence of birds, and outbreeding for maximum genetic variability (Faegri and van der Pijl 1971). To do this it has adapted to the community of birds and insects. Ohia possesses many characteristics that seem specifically adapted for bird pollination: copious nectar production (Heinrich and Raven 1972), low concentration of newly secreted nectar (Baker 1975), predominantly red flower color (Grant 1966). Furthermore, the average nectar flow rate of the overall population (0.57 cal per floret per hr) was slightly higher than the optimum for pollination by insects or by insects plus birds (0.4 cal per floret per hr) and this may be an adaptation to the birds alone. But by maintaining an open flower ohia does not exclude insects as do many hummingbird-pollinated flowers (Grant and Grant 1968) and, therefore, insects can effect pollination during years when or at locations where the bird population might be low. The high sugar concentration of nectar at the end of the life of the floret may be an adaptation that attracts insects in the event that bird pollination has failed, since most nectar-feeding insects prefer more concentrated nectars (von Frisch 1960, Percival 1965). Bee flowers are on the average 1.5 to 2.0 times more

TABLE 6. Bill lengths of extant and extinct nectar-feeding birds on Hawaii.

Species ¹	(N)	Bill length ²
<u>Loxops</u> <u>coccinea</u>	(14)	0.99 - 1.05
<u>Zosterops</u> <u>japonica</u>	(14)	1.11 - 1.19
<u>Loxops</u> <u>virens</u> ♀	(7)	1.24 - 1.30
<u>L. virens</u> ♂	(7)	1.40 - 1.46
<u>Himatione</u> <u>sanguinea</u>	(14)	1.63 - 1.69
<u>Moho</u> <u>nobilis</u> ♀	(4)	2.34 - 2.60
<u>Vestiaria</u> <u>coccinea</u> ♀	(7)	2.48 - 2.64
<u>V. coccinea</u> ♂	(7)	2.79 - 2.85
<u>M. nobilis</u> ♂	(7)	2.86 - 2.98
<u>Drepanis</u> <u>pacifica</u> , sex?	(2)	3.87 - 4.77

¹ Data are presented separately for the sexes only in those species for which a significant ($p < .05$) difference in bill length exists between the sexes.

² 95% confidence intervals in cm.

concentrated in nectar than are hummingbird flowers (Baker 1975). Percival (1965) points out that Acanthis mollis flowers secrete less, but more concentrated, nectar with age and that their attractiveness to insects therefore does not decline. Furthermore, ohia's open flower allows nectar to concentrate by evaporation if not soon removed by birds, thus exchanging attractiveness to birds for attractiveness to insects when birds are not present. A similar situation has been observed in Orange blossoms (Vansel et al. 1942): in the morning nectar is secreted at 16% and bees ignore it preferring nearby flowering crucifers; by afternoon the sun concentrates the nectar to 25 to 50% and the bees switch preferences to the Orange.

The orange- and yellow-flowered ohia individuals seem to be primarily adapted to insect pollination by their color and smaller florets, which are more likely to be susceptible to pollination by the small insects than are the wider-cupped red florets. Thus, the open flower and changing nectar concentrations seem to be adaptations at the individual level for insects, and the flower color variations are likewise, but at the population level.

The M. collina group is characteristically a good colonizer, both of islands (Dawson 1970) and of new lava flows on those islands (Eggler 1971). Ability to set large quantities of seed in variable environments is crucial for success at colonizing (Baker 1965). Although ohia does not possess autogamy, nor complete self-compatibility as do the plants that have colonized the Galapagos (Rick 1966), nevertheless, it comes close in its pollination strategy to the "general purpose genotype" suggested by Baker (1965) for herbs in disturbed environments. The cost of this strategy has been production of enough nectar for both birds and insects.

Pollinators as a limiting factor to plants

This study suggests that selection pressures on ohia fluctuate throughout the year. When blooming is light both within trees and overall, pollinators are not limiting and the number of pollinators available per flower is large. Populations of both bees and Apapane can be maintained by two different devices: bees can live off stored reserves during hard times, and Apapanes can turn to insectivory. However, when the bloom gets heavier in an area, pollinators may become limiting to ohia because their numbers are likely to lag behind the increase in flower numbers. At these times there is likely to be competition

for pollinators.

We can hypothesize three regimes of limiting factors on outbreeding plants and what the evolutionary effects of each regime should be. First, pollinators may be severely and constantly limiting to plants. Under this regime, one would expect the plants to evolve self-compatibility and eventually, automatic selfing mechanisms such as cleistogamy (Uphof 1938), with little or no production of pollinator attractants. This has occurred in Arctic and alpine regions where conditions are not favorable for pollinator activity (Iversen 1940, Hocking 1965, and Docters van Leeuwen 1933, Clausen and Hiesey 1960) and in extreme deserts (Hagerup 1932). Second, pollinators may alternate between being limiting and being unlimited, as seems to be the situation in ohia. Depending on the importance of maintaining genetic variability in the population, this regime should result in the maintenance of outbreeding systems because pollination can occur, and in the evolution of efficient systems with energy attractants finely tuned to the energetics of the pollinators, as Heinrich and Raven (1972) propose. Lastly, pollinators theoretically could be constantly superabundant--never limiting. By definition, these pollinators could not be highly nectar-dependent, as such populations would likely be limited by plant nectar production and would decline until their numbers were no longer superabundant relative to their food supply. However, if the pollinators were generalized enough to be able to maintain large populations in spite of low nectar availability, but still preferred nectar and used all available, the plants could afford to reduce nectar flow if selection pressure existed on them for energetic conservation. A limit would exist to this reduction, however, as it would benefit the pollinators to lose their nectar preference once foraging costs exceeded energy intake (Wolf and Hainsworth 1971, 1975). Thus, under this third limitation regime, a stable system should result when the pollinators involved are generalized. See Figure 13 for summary. The path of evolution may follow the abscissa either to the left or to the right. So, for example, if the yellow-flowered ohias are evolving a selfing from an outbreeding strategy, we can see more clearly why they must first increase nectar productivity. This gives the population time to evolve true autogamy, after which nectar production may be lost. There are examples of strictly autogamous species that still produce considerable nectar--Taraxacum and Oxalis pes-caprae (Baker, pers. comm.), Myrmecodia tuberosa (Burck 1890)--and these are most easily

SELECTION EFFECT OF POLLINATOR AVAILABILITY ON NECTAR PRODUCTIVITY AND PLANT REPRODUCTIVE SYSTEMS

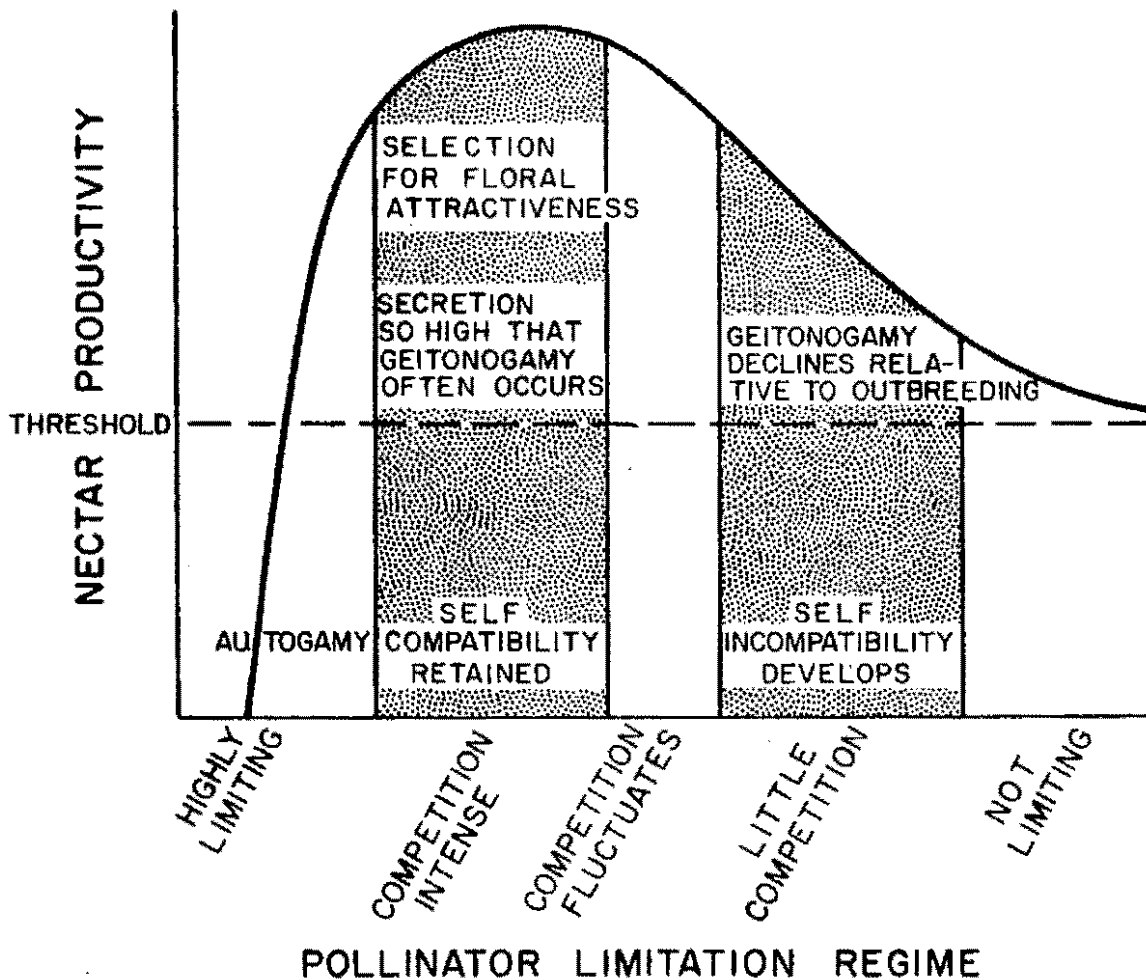


FIG. 13. Model of the selection effect of pollinator availability on nectar productivity and plant reproductive systems. The threshold indicated is the nectar productivity which just balances the foraging costs of the pollinators.

interpreted in terms of a scheme like that above. If the limitation regime for ohia sometimes shifts toward the intensive competition end of the abscissa, this would encourage evolution of selfing morphs within the generally outbreeding population and the strategy of ohia as a whole could be classified as a polymorphic generalism to deal with fluctuating environments (Levins 1968).

The neatness of ecological segregation among the major component species of Hawaiian forests suggests that pollinators are frequently limiting and that resultant competition has acted as an important selection pressure. Some ways in which plants may avoid interspecific competition for potentially shared pollinators, yet still outbreed and avoid the risks of overspecialization on single pollinator species are: 1) occur in a geographical area or habitat different from that of the most intense competitors, 2) evolve a different life form (e.g. shrubs and trees may not compete intensely because of some pollinators' preferences for specific foraging heights, see Gravatt 1969, MacMillen and Carpenter, in prep., and Levin and Kerster 1973), or 3) bloom at a different time of year. These are some of the differences to look for, then, in the study of differentiation of the pollinator niches within plant communities.

In the present study individuals of Metrosideros collina were shown to compete for pollinators. If nectar secretion was too low in an individual, seed set also was low, presumably because of lower attractiveness of those individual trees. Furthermore, pollinators often seemed to be scarce relative to the flowers available: large amounts of nectar were left unexploited in the trees in the scrub forest at 1200 m elevation. Nectar was also not fully exploited in those individual trees that produced nectar at the highest rates. In one season of heavy bloom (summer 1973) large amounts of nectar were left unexploited. All this information shows that pollinators can be in short supply in some habitats, in some seasons, in some years, and in some individual trees.

Since intraspecific competition is intense, it is reasonable to suppose that interspecific competition potentially occurs between tree species using these same pollinators. The three commonest tree species in our Mauna Loa study sites besides M. collina were Myoporum sandwicense (Myoporaceae), Acacia koa and Sophora chrysophylla (both Leguminosae). These four trees exhibit strong pollination segregation. A. koa has pale yellow wattle flowers with little nectar apparent and are probably only insect pollinated; it blooms in the winter overlapping temporally with S. chrysophylla. M. sandwicense has white, shallow

bowl flowers that are probably also insect-pollinated, but it blooms in the summer, overlapping temporally with M. collina. S. chrysophylla and M. collina likely could compete for bird pollinators, as the honeycreeper species associated with M. collina are also associated with S. chrysophylla. S. chrysophylla has bright yellow flag-type blossoms, a color and shape often associated with bird pollination (Faegri and van der Pijl 1971). The curved corolla fits the bill morphology of Vestiaria coccinea well, and this honeycreeper is strongly associated with this legume (Baldwin 1953). Like ohia, Sophora is a profuse bloomer but measurements showed that nectar production by a Sophora flower is only 20% that of an ohia floret (Carpenter and MacMillen 1975b), which could prevent Iiwis from setting up single-tree territories. However, S. chrysophylla and M. collina have staggered their blooming periods so that almost no temporal overlap occurs in areas where they overlap geographically (Fig. 14, top). That these mechanisms are effective in preventing pollen loss and wastage in M. collina was shown by the fact that pollen smears of the birds contained almost no other types of pollen. In areas where these two species do not overlap, their blooming seasons are shifted (Fig. 14, bottom), suggesting character displacement in the overlap areas. Thus, among the principle tree species in the Mauna Loa forests, pollinator segregation occurs either by morphological specialization for different groups of major pollinators or by staggering of blooming seasons.

Several species of both Metrosideros and Sophora occur in New Zealand, and three species of honeyeaters (Aves: Meliphagidae) apparently play important roles as pollinators (Thompson 1926; McCann 1952, 1975). The New Zealand forests, especially those of the North Island, are more diverse than are the Mauna Loa forests, and several tree species are thought to be bird-pollinated (McCann 1952, 1975; Cockayne 1958): three species of Metrosideros, two of Sophora, Vitex lucens (Verbenaceae), and Knightia excelsa (Proteaceae). Strong ecological segregation occurs between almost all of these forms (Table 7). The Metrosideros species are the most abundant element in the forests, and the three species that assume the arboreal life form (several others are small shrubs or lianes) are largely isolated from each other geographically and by habitat. The Sophora species are habitat isolated from each other, and are isolated either by habitat or by blooming season from Metrosideros. In the diverse forests of the North Island, staggering of bloom is the major isolating factor, with different

STAGGERING OF FLOWERING SEASONS

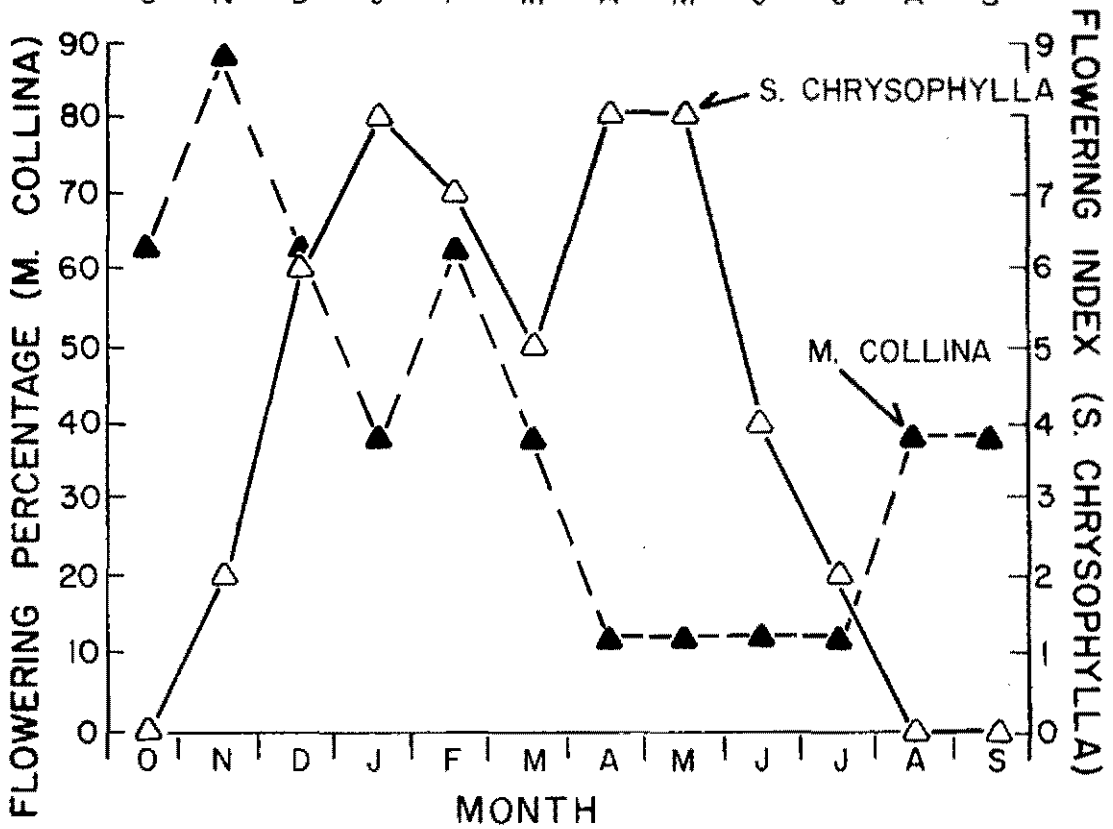
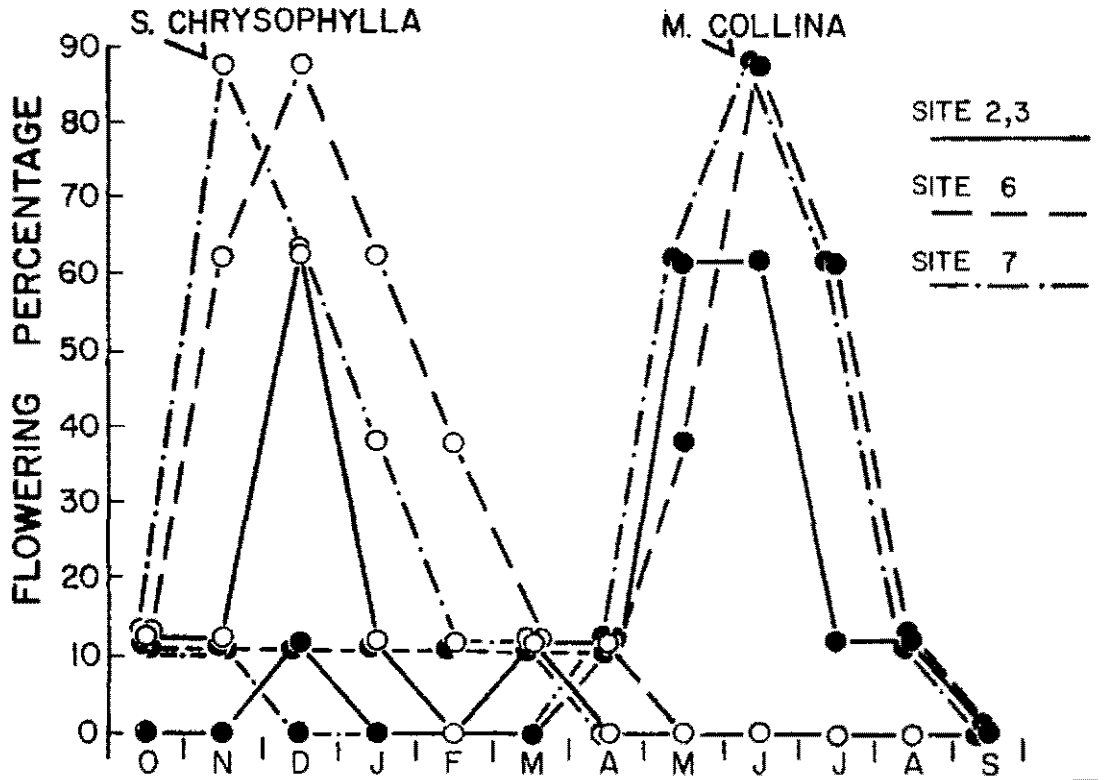


TABLE 7. Pollinator segregation in New Zealand trees.¹

Species	Primary geographic range	Primary habitat	Blooming season
<u>Metrosideros excelsa</u>	Auckland Provinces, North Island	seaside	December-January
<u>M. robusta</u>	North Island ²	forest	November-January
<u>M. umbellata</u>	South Island ³	forest	November-January
<u>Vitex lucens</u>	North Island ⁴	forest	all year with peak June-October
<u>Knightia excelsa</u>	North Island	forest	October-November
<u>Sophora microphylla</u> ⁵	North and South Islands	forest	July-October
<u>S. prostrata</u>	South Island	open, rocky places	November-December

¹ Data extracted from Salmon (1963), Wardle (1971), Moore and Adams (1963).

² Occurs in extreme northern South Island also.

³ Also occurs sporadically in three small areas on North Island and on two islands off the coast of North Island (Wardle 1971).

⁴ Northern half of the North Island only.

⁵ S. microphylla includes the localized form tetraptera, with which S. microphylla hybridizes (see Johnson 1968).

species blooming from June or July to October, from October to November, and from November to January. One case of overlap occurs with Vitex and Sophora microphylla, but there is some suggestion that the latter may occur in more open forest than Vitex (Salmon 1963, Johnson 1968). Gravatt (1969) mentions that honeyeaters visit Vitex more frequently during the times other bird-trees are not blooming. Thus, Vitex may follow an opportunistic pollinator strategy, having some flowers available whenever blooming of another species fails. Of the five forest bird-trees in Table 7, it has the most limited geographical distribution.

It appears that evolution has acted in a parallel manner on New Zealand and Hawaii, and by staggering blooming periods has reduced interspecific competition between sympatric species using the same pollinators. The main difference in the two communities lies in the greater plant species diversity of the North Island forests. This has resulted in shorter blooming periods for each species--two to three months usually, compared to four to six months (Fig. 14) for Sophora and Metrosideros on Hawaii. Staggering of bloom occurs in the highly diverse mainland tropical forests and abbreviation of blooming periods is also seen. In Costa Rica, the average duration of bloom in almost 200 seasonally flowering species was about six weeks (Frankie et al. 1974). The members of some species synchronously bloom on a single day (Richards 1952). The forest communities of tropical mainland areas, of the tropical North Island of New Zealand, of the tropical island of Hawaii, and of the temperate South Island of New Zealand form a graded series from high species diversity to low. This series fits the predictions from biogeographic theory (e.g. MacArthur and Wilson 1967) that island size, age, and latitude are among the factors that determine the number of species on an island or in a community. As with other systems studied to date (e.g. Colwell 1969) this system also shows that species diversity and niche breadth are inversely related.

The neat ecological segregation seen among species of Hawaiian forest trees is not seen so clearly in the nectar-feeding birds (Baldwin 1953, MacMillen and Carpenter in prep.); in particular, the Apapane and Iiwi overlap greatly in their nectar foraging ecologies. This is independent evidence that in the Hawaiian forests, nectar supplies are generally abundant relative to bird populations, and that the plants experience a limitation regime to the left of the midpoint of the abscissa in Figure 13.

Plant-pollinator interdependency

There are many known examples of highly specialized relationships between plants and their pollinators, some of which are so obligate that extinction of one member species would probably cause extinction or rapid evolutionary change in the other. Most of these obligate relationships occur with insects as the pollinators, and sometimes the insects require the fruit of the plant as a brood-site: Trollius europaeus has such a relationship with a fly, Yucca spp. with a moth, and Ficus spp. with gall-forming Agaonids (examples from Faegri and van der Pijl 1971). Tightly-bonded relationships are often characterized by strict coincidence of geographic distributions (Aconitum and Bombus, see Baker and Hurd 1968) and of phenological timing. Examples of the latter are the hibiscus bee Emphor bombiformis, and Hibiscus lasiocarpus (Robertson 1925); Halictoides novae-angliae, a solitary bee, and the Pickerel-weed, Pontederia cordata (cited in Percival 1965); and Eucerine solitary bees Melandrena spp. and Oenothera spp. (Linsley and MacSwain 1955, Linsley et al. 1955)--in these examples the emergence of insects and blooming of flowers or presentation of nectar or of pollen are timed exactly to coincide within a few days or even hours of each other.

Such refined interdependency seems to occur rarely in bird-plant associations. Birds are relatively long-lived organisms and cannot afford to depend on a single species of plant. Furthermore, bird-plant relationships are probably more recently evolved (Baker and Hurd 1968) and therefore may have lacked the time to develop complex interdependencies. However, several plant species are thought to be pollinated primarily or strictly by specific birds: Protea spp. by Promerops cafer (Porsch 1926, Broekhuysen 1959), Eucalyptus calophylla by meliphagids (cited in Percival 1965), New Zealand flax Phormium tenax by the Tui Prosthemadera novae-seelandiae (McCann 1952), Anigozanthos spp. by honeyeaters (Wakefield 1960). Porsch (1926) thought that the interdependency between Protea and Promerops was as complete as that between Aconitum and Bombus. However, because most nectar-feeding birds do not seem to be as bonded to single flower species as insects sometimes are and will feed on whatever nectar-producing blossoms are available, this has led some to refute the idea that birds and plants have coevolved (Melin 1935), a rather extreme position. Sometimes the timing of breeding is strongly correlated with the blooming of one or two species, as Stiles (1973) has shown convincingly for the hummingbird

Calypte anna and Ribes spp. and as has been suggested for Promerops spp. with Protea spp. (Broekhuysen 1959, 1963; Skead 1963), Panterpe insignis with Macleania gabra (Wolf and Stiles 1970), Colibri thalassinus and Salvia spp. (Wagner 1945), and Phaethornis spp. with Heliconia spp. (Stiles 1973). The ability to remain resident over winter at high elevations in the Peruvian Andes is determined for the hummingbird Oreotrochilus estella by the winter flowering of Chuquiraga spinosa, which it pollinates (Carpenter 1972, 1976); if Chuquiraga were eliminated, this bird would have to migrate to lower elevations because in some areas, at least, no other native plant suitable for birds blooms in the winter.

The relationships between Apapane and ohia and between Iiwi and Sophora plus ohia are not as obligate as in these examples. Both honeycreepers breed from about January or February through June (Baldwin 1953, Berger 1972a), while blooming of Sophora declines in January and ohia does not attain good bloom in most areas before May (Fig. 14). The densities of Apapane do not correlate well with blooming intensities of ohia; this honeycreeper can occur in numbers where there is no bloom and therefore seems to be able to exist at least temporarily on insects alone. However, their population movements do follow the ohia bloom with a lag (Baldwin 1953). If the ohia should cease to produce blooms, the Apapane would be forced during the breeding season into competition with the insectivorous members of the family, particularly with the Loxops group. It is impossible to guess the outcome of such a radical change in its life history. If, on the other hand, the Apapane disappeared from the forests, what would be the effect on ohia? Because of its general strategy, it would probably continue setting moderate amounts of seed. However, gene flow would be drastically reduced. Selection for reduced nectar flow consistent with the energetics of its insect pollinators could result, with increased gene flow once again, or else the population could break into genetically isolated units, encouraging speciation. In contrast, even though the Iiwi's breeding is not precisely timed to coincide with the blooming of either Sophora or ohia, both its population movements and densities throughout the forest are correlated with the blooming of both tree species; it therefore seems to be nectar dependent. Its bill morphology also suggests specialization, and therefore, presumably, dependency on nectar. The pollination ecology of Sophora needs to be studied to determine its dependency on Iiwi pollination. However, even here, as tight

a bond as exists between hummingbirds and sunbirds and their flowers seems not to occur.

The situation with Hawaiian lobelias (Campanulaceae) is not resolved. Perkins (1913) believed that these flowers had an obligatory pollination relationship with certain honeycreepers, including the Iiwi, but Rock (1919) disagreed. Baldwin (1953) observed preference in Iiwi for ohia over the nearby blooming lobelias, but Spieth (1966) described Iiwis feeding at the flowers and emphasized the "nicety of fit" between bill and corolla, propounding a reciprocally evolved relationship between curve-billed honeycreepers and the lobelias. Faegri and van der Pijl (1971) cite Porsch (1930--not referenced) and Amadon (1947) as believing that the autogamy now present in these plants was a necessary escape from lack of pollinators when the several species of long-billed honeycreepers went extinct. However, Percival (1965) points out that most of the lobelia species violate the typical bird pollination syndrome by having inconspicuous flower colors, especially pale pinks, dark purples, and whites. It is unlikely that the reproductive seasons of the lobelias and of the honeycreepers coincided: the extant species of nectar-eating honeycreepers breed in winter and spring (Berger 1972a) so presumably this was the breeding season also of the long-billed extinct species; most lobeliads for which there is information appear to bloom in the summer (Rock 1974). Thus, the degree of interdependency between these plants and the honeycreepers is at this point impossible to state.

Qualitatively, at least, one can say that the Hawaiian flora seems to lack the preponderance of bird-pollinated species at high elevations that characterize mainland floras, and also lacks tightly bonded interrelationships between flowers and birds. I do not know if this is true also for insects and their flowers in Hawaii. I also cannot say whether or in what way the lack of specialization is a result of low species diversity on the island. One possible consequence of low species diversity is strictly probabilistic: e.g. mainland communities may possess only one specialized pollination interrelationship for every 100 generalized ones: the Hawaiian situation therefore could be simply a probabilistic effect of low species diversity. On the other hand, the generalized strategies so prevalent in island communities are often interpreted as ecological release caused directly by low numbers of competitors. Ohia may follow this pattern. This study suggests a polymorphic generalist pollination

strategy, which could be stable. In New Zealand--a possible source area for Polynesian invasions by Metrosideros (Dawson, pers. comm.)--the three Metrosideros species that assume arboreal growth forms are ecologically segregated by habitat or geography and seem to show less variation in floral color and structure (Cockayne 1958, Johnson 1968, Moore and Adams 1963, Salmon 1970) than ohia does. It is possible that the variability of Hawaiian Metrosideros is a kind of ecological release in the presence of an environment with no closely related species and few other abundant tree species.

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