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INTERACTIONS BETWEEN HAWAIIAN HONEYCREEPERS
AND METROSIDEROS COLLINA ON THE ISLAND OF HAWAII

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ABSTRACT

Studies are in progress on the island of Hawaii which we hope will determine 1) the strategy and energetic cost of the outcrossing system of Metrosideros collina polymorpha, 2) the strategy and energetic efficiency of the foraging system of the three most common species of honeycreepers in a M. collina forest, and 3) the efficiency of energy transfer from the producer M. collina to the honeycreeper nectivores. Preliminary results indicate that ohia produces larger amounts of nectar than would be necessary if its avian pollinators were more sedentary in their foraging habits, but sufficient nectar to support the more mobile foraging system as described herein.

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INTRODUCTION

One of the most fundamental problems of ecology is the study of appropriation and allocation of energy, be it at the level of the organism, the species' population, the community or the ecosystem. The flow of energy through specific ecosystems has been or is being modeled (Teal 1957, Odum 1957, current undertakings of the International Biological Program). One result has been the stimulation of several general hypotheses concerning the role of energy in evolution and community organization. One of these is that given enough time, the process of coevolution results in the maximization of energy utilization within the community, that is, energy is lost from the biotic realm of the ecosystem to the physical realm more slowly (Odum, 1971). Although general, such an hypothesis is testable by comparing the organization of an ecosystem in which little coevolution has taken place, to the organization of an ecosystem in a similar physical environment but which is older, species-rich, and biologically complex.

The studies proceeding on the island of Hawaii by the Island Ecosystems IRP/IBP afford an opportunity to provide information potentially usable in testing such general hypotheses. The Hawaiian islands are geologically newer than the continents; furthermore, as young islands, they are species-poor and many species associations are new. Both these factors mean that coevolution in competition, predation and pollination systems has probably not proceeded to the extent that it has on mainland areas with similar climates (see MacArthur & Wilson, 1967 for a discussion of evolution on islands). Thus, it would be fruitful to compare the

allocation of energy on these islands to that of comparable settings in the mainland tropics.

The present study is focusing on the energy flow between parts of two trophic levels composed of species native to the youngest island, Hawaii. These are the tree ohia (Metrosideros collina, Myrtaceae) and three species of Hawaiian honeycreepers (Drepanididae): the Amakihi (Loxops virens), the Apapane (Himatione sanguinea), and the Iiwi (Vestiaria coccinea). The study began with the work of R. E. MacMillen (1972) and the present work is being conducted by both authors in conjunction with the continuing laboratory work of R. E. MacMillen.

We have developed hypotheses concerning energetic efficiencies in two systems, the pollination strategy of the ohia and the foraging strategies of the birds.

MATERIALS AND METHODS

Pollination Ecology of *Metrosideros collina*

The study site was located at 1,366 m elevation near Puu Oo trail, Keauhou Ranch, Kau District, Hawaii. Work was conducted the last week of July and the second half of August, 1973. For the studies on the pollination ecology of ohia, we selected ten small trees (4.5 to 9 m tall) and an eleventh tree 17 m tall. In each of the ten small trees we selected three inflorescences in bud stage: one inflorescence we covered with a fine-mesh nylon tulle bag to exclude all nectivores over 1 mm in size; a second inflorescence was covered with a similar tulle bag that had many 3- to 5- cm diameter holes cut in it to exclude birds but allow in insects; we left a third inflorescence, marked with a small wire loop, uncovered as a control. Except for brief removal of bags to sample nectar, we left the inflorescences undisturbed for three weeks while the buds opened and the flowers developed. This bagging regime was intended to determine the degree of selfing in ohia (percent seed set inside fine-mesh bags), the percent pollination by insects (percent seed set inside bags with holes minus percent seed set inside fine-mesh bags), and the percent pollination by birds (percent seed set in uncovered inflorescences minus percent seed set inside bags with holes). We measured rates of nectar production in the inflorescences that were bagged against all nectivores (fine-mesh bags) in five of the ten trees by periodically taking nectar by capillary action into microcapillary tubes of known volume (10 μ l and 50 μ l).

In the 17 m tree, Paul Banko used climbing gear to reach three heights in the tree: 5.2 m, 10.1 m and 14.5 m. He selected four open inflorescences at each of these three levels and sucked the four inflor-

escences at each level dry with a Pasteur pipette. He then bagged two of the four inflorescences with fine-mesh bags. He also cut and gently lowered three or four similar inflorescences from each level to the ground for measurements of absolute amounts of nectar. Twice subsequently, he resampled the nectar from the bagged and the unbagged (control) inflorescences at each level. This yielded data on nectar production rate and on relative usage of nectar at different heights in the tree.

The concentrations (percent sucrose) of all nectar samples taken from the small trees and from the 17 m tree were measured with a Bausch & Lomb sugar refractometer registering to 60 percent. Sampling of nectar for nectar production rates was performed in morning, early afternoon, and late afternoon on the small trees and in the morning and late afternoon on the 17 m tree so as to reveal any nocturnal and diurnal patterns of nectar production. The total number of inflorescences was counted in the 17 m tree with binoculars; because the foliage and blossoms were sparsely distributed along the length of the tree rather than in a dense mushroom-shaped canopy, most inflorescences were visible and an accurate absolute count could be made.

Birds freshly captured in mist nets were immediately examined with a 10X hand lens for the presence or absence of the pale yellow ohia pollen on their heads or bills.

Foraging strategies of the honeycreepers

Four 2 x 9 m mist nets were set up in the dense ohia forest at the study site. Three nets were placed more or less linearly end to end separated by a few meters. The fourth net was placed in similar habitat about 100 meters from the others. The nets were raised 10 m above ground by means of telescoping poles. All three species of honeycreepers

were captured and each individual was given a distinct color-coded plastic leg band. Birds were released at the same locality where caught, either soon after capture following some manipulations (e.g., banding, checking for pollen) or one to two days after capture after laboratory measurements had been made by R. E. MacMillen.

The vertical pattern of bird foraging activity in the 17 m tree was determined by visually dividing the tree into four levels (0-5.2 m, 5.2 - 10.1 m, 10.1 - 14.5 m, 14.5 m - top) using the bags in the tree as boundary indicators. The number of birds at each level in the tree was then counted for 15 minutes each hour. Counts were made over three successive days until one 15-minute count had been made for every hour the birds were active.

RESULTS AND DISCUSSION

Ohia reproductive system

The inflorescence of Metrosideros has been described by J. R. Porter (1973). The average inflorescence on our 17 m tree contained 19.6 flowers (number of inflorescences sampled = 25, S.D.=6.45), and on four of the ten small trees 23.8 flowers (S.D.=7.12). The individual flowers in an inflorescence may be protogynous since the style and stigma are exerted from the opening buds before the many stamens are, and the stigma seems receptive (sticky) at that time. Contrary to Baldwin's report (1953), we found that nectar secretion occurred throughout most of the life of the flower, beginning copiously when only the style was exerted and continuing throughout the time that the stamens exerted, matured and dehisced pollen. Sometimes, however, nectar secretion stopped before the last few anthers had matured. The life of most inflorescences was two weeks to less than a month, an observation that supports observations by Porter (1973) and Baldwin (1953).

The results of the bagging program to determine the percentage of selfing, insect pollination and bird pollination are, as yet, inconclusive. At the end of the study period only three or four of the 20 bagged inflorescences seemed to be setting any seed regardless of the type of bag, whereas most of the ten unbagged inflorescences showed some signs of seed set. We will be able to judge success of seed set in these 30 inflorescences with much greater certainty when we return in December 1973.

Regardless of the results in those ten trees, however, we consider them inconclusive because we were not satisfied with the bags themselves. First, since the inflorescences are terminal (occur at the ends of twigs), the top of the bag usually touched part of the inflorescence and may have

interfered with normal floral development, e.g., inhibition of normal stamen exertion. Second, we felt that the bags designed to permit normal insect foraging but exclude birds may have tended to exclude insects as well simply because the tulle material was visually obvious and the entry holes probably would have to be sought by the insects once they landed on the bag. Therefore, we spent several days designing new kinds of bags that would solve these problems and also include more inflorescences within the bag. We built cylinders of 2.5 cm mesh chickenwire 1 m long and 0.5 to 0.75 m in diameter, and covered one end of the cylinder with more chickenwire. For the bag that was to exclude only birds but not insects we simply placed the naked chickenwire cylinder over the end of a lowered branch containing 21 marked inflorescences in bud stage and sealed the bottom of the cylinder with more chickenwire. The cage was secured to the branch so that when we raised the caged end of the branch back to its normal position in the canopy, the cage would not slide down onto the terminal inflorescences.

For the bag designed to exclude all nectivores, we covered the chickenwire cylinder with fine-mesh nylon tulle and sealed all seams by folding over the seam edges and sewing them carefully. The base of the cylinder was sealed with more fine-mesh tulle and taped to the bark of the branch with several layers of masking tape. This cage included 18 marked inflorescences in bud stage.

The two cages were on different trees. For each cage, we selected on the same tree as the cage a control branch of unbagged inflorescences and we marked the same number of inflorescences as was marked inside the cage (21 for the tree with the first cage, 18 for the second). In

addition we selected two control trees separate from the two trees with cages but in the same vicinity and habitat type. We marked 20 inflorescences in one tree and 24 in the other and left them unbagged. All four trees (the two controls and the two experimentals with both caged and control branches) were 4.5 to 7.7 m tall. When the branches that we had lowered in order to bag were raised back to normal position, the marked inflorescences were 3 to 6 m above ground.

Finally, all marked inflorescences were sprayed with a short-lived insecticide. This was done mainly to ensure that no live insects were included inside the bag that was supposed to exclude all nectivores, but it had to be done to all other study subjects so as to standardize the conditions. We hope that when we return in December to check on seed set, this procedure will have proven adequate for measuring selfing and determining the relative importance of the two groups of pollinators. If so, we plan to enlarge our sample size and bag many more branches during our next two study periods (December 1973-January 1974 and June-September 1974).

Pollinators

The general appearance of most of the varieties of ohia on the study site is that of a typical "bird flower": red or orange color, long-stamened and long-styled, copious nectar (Heinrich and Raven 1972; Grant 1966; Raven 1972, and others). Of nine Apapane examined for pollen, six had pollen on the forehead, chin and rictal bristles (short "whiskers" extending from the corners of the mouth). The pollen was loosely attached and seemed ideally situated for transfer to a flower during a foraging visit. Of six Iiwi examined for

pollen, none showed any pollen on bill or forehead. However, three individuals had pollen caked in the small hollow at the base of the mandible, a situation that did not seem well suited for pollen transfer. Of three Amakihi examined, none carried pollen. We intend to continue more of this work, including cleaning of each individual's bill and head feathers with water and microscopically examining the rinse.

We noticed several kinds of small black Hymenoptera which were attracted to the flowers and could possibly serve as pollinators. We intend to collect systematically insects foraging at blossoms and examine them microscopically for pollen. From cursory observations, however, it seemed that these insects restricted their activities to the nectar cup and did not crawl around on the anthers gathering pollen, a behavior that would be necessary for them to effect pollination, given the long-styled, long-stamened structure of the flower.

While climbing the 17 m tree, P. Banko noticed honeybees foraging at ohia blossoms. Since some of them were crawling on the anthers, they probably effect some pollination. Of course, honeybees are introduced and therefore have not yet played a role in the evolution of the pollination strategy of ohia on Hawaii. However, they could affect the efficiency of the strategy and the energetics of the bird pollinators.

Nectar production

Overall nectar production was determined by measuring the nocturnal and diurnal rates of production over periods from 24 to 168 hours in five small trees and one tall tree. Values for two of the small trees were discarded because they were obtained at the end of the life of the inflorescences. Values for each of the four remaining trees were averaged,

and the mean for all trees calculated. The mean overall rate of nectar production was 0.75 μ l nectar per flower per hour, or 15 μ l per inflorescence per hour assuming 20 flowers per inflorescence. This overall value is relatively meaningless, however, because there was a dramatic difference in rate of nectar secretion depending on the time of day. The mean production rate during the night was only 0.42 μ l/flower/hour (S.D. = 0.18) whereas during the day it was 2.5 times greater, 1.07 μ l/flower/hour (S.D. = 0.40). A two-tailed t-test shows the difference to be statistically significant ($p < 0.05$).

There also was a trend for the tall tree with many (600) inflorescences to produce less nectar per flower than the small trees, which had relatively few inflorescences. The overall rate of secretion in the three small trees was 0.90 μ l/flower/hour (S.D. = 0.57) and in the tall tree 0.46 μ l/flower/hour (average taken of the values for three inflorescences, one at each of three levels in the tree; S.D. = 0.38). A t-test corrected for unequal variances does not indicate that the difference was statistically significant, but the sample sizes were small. We plan to gather more data on large and small trees to test the hypothesis that small trees with relatively few inflorescences must compensate for lesser visual attractiveness to the birds by producing more nectar than does a large tree with many inflorescences.

The inflorescence at the highest measured level in the tall tree (14.5 m) produced about three times more nectar than did the inflorescences at the intermediate and lowest levels. This is another trend we hope to document further. If the trend is substantiated, then its significance is clear and will become apparent below in the discussion of honeycreeper foraging strategies.

Nectar concentrations were extremely variable, ranging from 9 to 59 percent (in sucrose equivalents). Very low concentrations were obtained when the flowers had been exposed to drizzling rain. The causes for high concentrations (>30%) are still unknown but several factors seem to enter in. First, if an inflorescence has not been sampled for several days, it may have a high concentration. This presumably is because the water in the nectar evaporates gradually and although volume may remain the same because of continual secretion, the concentration rises. Secondly, old inflorescences often seemed to produce very concentrated nectar; this occurred a day before nectar secretion ceased completely. Third and most interesting, the smaller trees may produce more concentrated nectar than do large trees. The average concentration of three small tree inflorescences was calculated, eliminating the values likely affected by rain, excessive evaporation, or old age. The average concentration of three inflorescences sampled in the tall tree also was calculated. A statistical comparison of these means is probably not biologically meaningful because of the way the few data were collected. However, a trend is apparent: the small trees averaged 22.5% (S.D. = 4.92) and the tall tree averaged 18.4% (S.D. = 2.81). This is another trend we wish to follow up, as it is another test of the hypothesis that small trees must have more attractive blossoms than large, heavily blooming trees.

Using our measurements of nectar production rate and number of inflorescences in the tall tree, we were able to estimate total nectar production over 24 hours in that tree:

$$\begin{aligned} &0.46 \mu\text{l/flower/hour} \times 19.6 \text{ flowers/inflorescence} \times 600 \text{ inflorescences} \\ &\quad \times 24 \text{ hours} = 130 \text{ ml/tree / day.} \end{aligned}$$

From this value we have calculated the number of honeycreepers that this tree theoretically could support. We assumed that the mean ambient temperature over 24 hours in August was 19° C (Bridges and Carey 1973). We used the metabolic rates and honeycreeper weights measured by R. E. MacMillen in his concurrent work. Thus, we assumed an average metabolic rate of 4.5 cc O₂/g/hr at 19° C, an average body weight of 15.09 g, and a caloric equivalent of 5 cal per cc O₂. From this, the caloric requirements of one honeycreeper over a 24-hour period are:

$$4.5 \text{ cc O}_2/\text{g/hr} \times 5 \text{ cal/cc O}_2 \times 15.09 \text{ g} \times 24 \text{ hours} = 8.338 \text{ Kcal/24 hrs.}$$

Since one gram of sucrose provides 3.87 Kcal (Diem 1962), then 130 ml of 18% sucrose or sucrose equivalents (1 fructose + 1 glucose) provides 90.56 Kcal and the tall tree could support 90.56/8.34 or 10.86 birds. The rationale for the pollination strategy of the ohia depends on the foraging strategy of its main pollinators, which for the time being we will assume are the honeycreepers (the preliminary work on bagged inflorescences supports this assumption). Foraging strategies therefore will be discussed next, followed by a discussion of the ohia pollination strategy.

Foraging strategies of the honeycreepers

Since nectar is a resource that is constantly renewed, a bird whose major source of energy is nectar would forage most efficiently if it visited flowers in a systematic way so that after each visit it allowed the flower enough time to recuperate. This requires some kind of "knowledge" of the location of its nectar sources and of any other individuals competing for those sources. There are two ways to satisfy these requirements. First, the bird might establish a territory which it defends against other nectivores and within which it follows a systematic

pattern of flower visitation. This is the strategy that hummingbirds are believed to employ (Ortiz-Crespo, MS).

This strategy could potentially cause serious problems for a given plant if it is an obligate outcrosser and if territoriality is employed by its chief pollinators. If the plant comprises the entire territory of one or more of the pollinators so that the pollinators do not need to forage at any other plant, then no outcrossing will occur if territorial defense is effective in excluding other individuals. The best way for the plant to deal with this problem is to produce enough energetic reward (nectar) to be attractive to pollinators but not enough reward to fill their total energetic needs (Heinrich and Raven, 1972). This will force the pollinators to include more than one plant in their territories and outcrossing will then occur.

We can predict that if ohia is in fact an obligate outcrosser chiefly pollinated by birds and if the honeycreepers are territorial, then a single tree should produce less than 8.34 Kcal (12 ml of 18% nectar) in 24 hours (see page 12). The fact that the tall tree produced almost 11 times that amount suggests that the honeycreepers must not be territorial. In fact, although all three species defend small nesting territories (Berger 1972a), none is known to defend feeding territories. Our own observations reveal no hint of territoriality, although we have seen Iiwis occasionally chase individuals of other species from their immediate vicinity. We have never seen aggression in Apapanes, the most abundant of the three species. Furthermore, over a period of 35 days we obtained no recaptures of the 31 honeycreepers (3 Amakihi, 11 Iiwi, 17 Apapane) netted, banded and released in the area, and the rate of capture did not decline with time. This suggests that the birds were

very mobile and that new individuals were continually passing through the area. We plan to do more netting and banding in the future and hope to release the birds as soon after capture as possible to minimize trauma during capture and thereby enhance potential recapture,

The second way for a bird to visit flowers systematically and keep track of its competitors is to forage in a flock. Flock-foraging presumably would benefit the individual by aiding the discovery of untapped nectar sources. Also, a flock might retain a "memory" of areas recently foraged in and would not retrace its tracks too soon for the nectar to recuperate. This would reduce the likelihood of an individual wasting time and energy on an area whose nectar sources, unbeknownst to him, had recently been tapped. Such a strategy is reminiscent of the one suggested for some seedeaters (Cody 1971), whose foods are inconspicuous and difficult to locate. However, it is unknown in nectivores.

Do the honeycreepers forage in flocks? Flocking behavior such as that shown by seedeaters should be as easily observable as is territoriality in hummingbirds, yet we saw no evidence of such flocking behavior. The confusing fact was that individual honeycreepers seemed to be foraging randomly with respect to every other individual. The chief consistent aspect of their foraging was that an individual never stayed very long in one tree. However, two observations suggested that foraging might not be random but in fact systematic. First, bird counts at different levels in the tall tree throughout the day showed a distinct vertical pattern to foraging activity (Fig. 1). Foraging begins high in the morning, gradually gets lower during the day, reaches its lowest in mid-afternoon, and then gets higher once again just before dark.

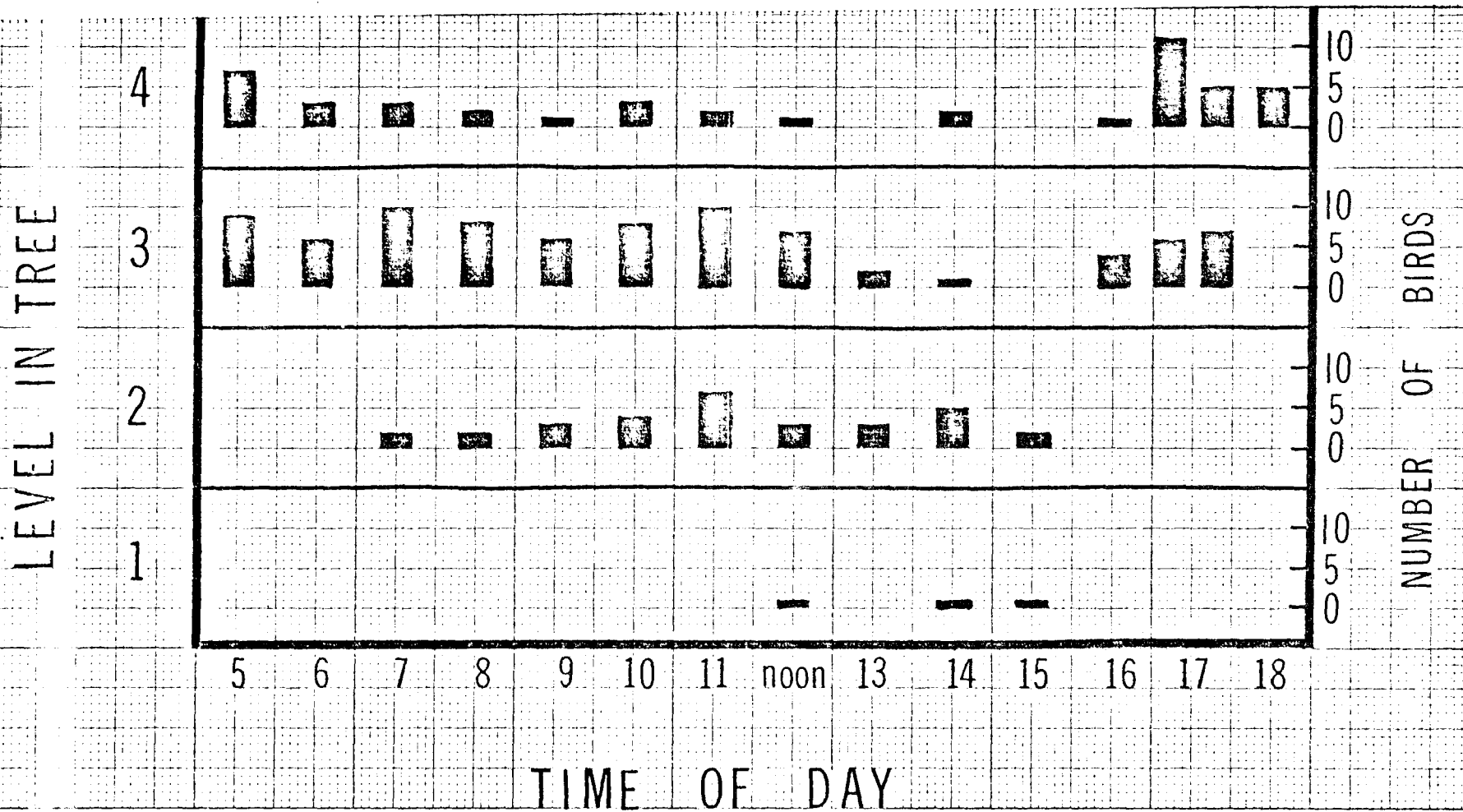


FIG. 1. VERTICAL DISTRIBUTION OF HOURLY ACTIVITY IN A TREE. The number of birds was counted from dawn to dusk at each of four levels in a 17 m ohia tree, and showed that activity began high and ended high but that most mid-day activity was low in the tree.

The second observation that suggests a possible pattern to foraging is the sighting by ourselves, P. Banko and others (Berger 1972b) of loose "flocks" of hundreds of Apapanes and Iiwis flying up the slopes of Mauna Loa in the evening. This may mean that a large proportion of the honeycreeper population roosts high on the mountain, perhaps to avoid roosting in the energetically-demanding nocturnal fog and rain that form a belt at lower elevations in the summer (see Fig. 4 in Berger 1972a).

These two observations taken together suggest the following strategy: the birds roost high up the mountain; in the morning they begin foraging and systematically descend the mountain, thereby encountering untapped nectar sources. Perhaps because of some predilection for foraging high in the trees, the birds in the front of this gigantic descending wave of birds forage high. But the birds in the rear will encounter already-tapped flowers if they also commence foraging high in the trees, so they are forced to forage lower, thereby also encountering untapped flowers as they descend the mountain. This would account for the kind of observation shown in Fig. 1, made at a single location at a middle elevation: first the high-foraging birds reach the location, followed progressively by lower foraging birds. In the late afternoon foraging is high again as the high-foraging birds return up the mountain. This strategy is not true flocking but is more closely related to the hypothesized flocking strategy than to the hypothesized territorial strategy.

This hypothesis is easily testable by gathering three kinds of data:

1. Bird counts at dawn high and low on the mountain.
2. Quantification of the mean direction of flight between foraging bouts: it should be downhill all morning and then reverse itself in late afternoon.

3. Counts like those in Fig. 1: the low foragers should reach trees at higher elevations earlier in the day.

Furthermore, the effectiveness of the strategy in preventing over-exploitation of some inflorescences and lack of exploitation of others can be quantified by determining the periodicity of visitation of marked inflorescences. If the strategy is efficient then a recently-visited inflorescence should be less likely to be visited than one that has had time to recuperate. We already know that during the day 21 μ l of nectar is produced by the average inflorescence in an hour. Time energy budgets of the birds will indicate the amount of nectar reward required for a bird to visit an inflorescence efficiently (Wolf et al. 1972; Hainsworth et al. 1972), and from this the minimum time for adequate recuperation of a visited inflorescence can be calculated and compared to the observed mean time between bird visits.

Ohia pollination strategy

If the above-hypothesized foraging strategy is forced upon the birds by the climate and topography of the area, then the ohia must adapt its pollination strategy to that fact of life. It must produce copious nectar all day long to provide every newcomer with some reward so that it will stay long enough to effect pollination. We have already calculated that our tall tree produced enough to support an average of 10.86 birds. This means that at any point in time during the day, an average of 11 birds should be seen in the tree. The data in Fig. 1 can be reworked to show the observed numbers of birds in the tall tree at 15 points in time during the day (Fig. 2). The average for those 15 points in time is 10.93 birds (S.D. = 4.93), a value that agrees

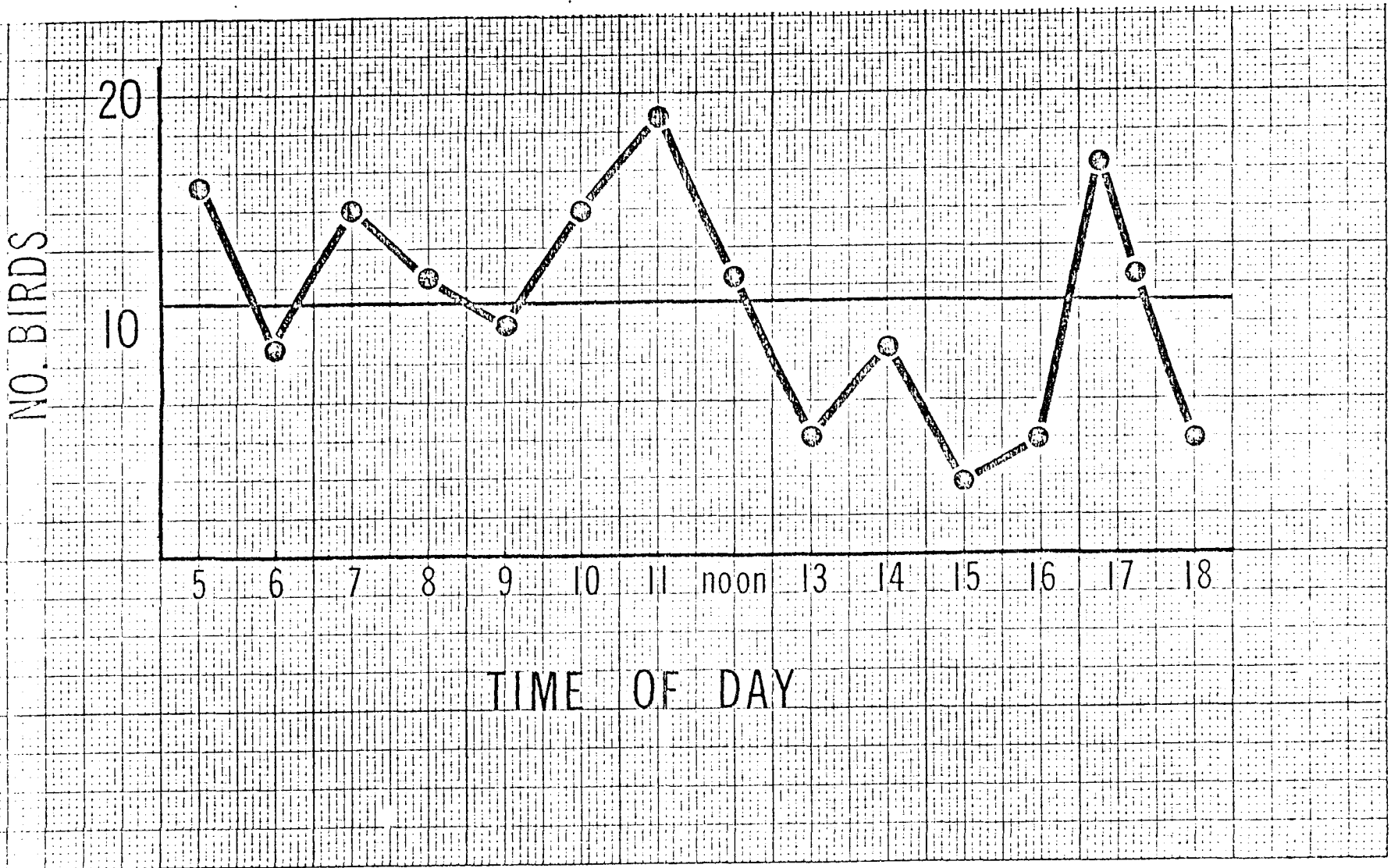


FIG. 2. HOURLY NUMBER OF BIRDS IN AN OHIA TREE. The number of birds in a 17 m ohia tree was counted during one 15 minute interval for each hour of the day in August 1973.

almost exactly with the predicted value. The closeness of this agreement must be largely fortuitous and we plan to gather more data of this kind. For example, we might expect the observed number of birds in a small tree to be considerably less than the number predicted on the basis of the amount of energy produced by the small tree. This would reveal the selection pressure operating to force small trees to produce larger volumes and higher concentrations of nectar, trends that we have already discussed.

The implications of the bird foraging strategy for the ohia are apparent, not only from the point of view of pollination energetics, but also from the point of view of gene flow. As long as a tree produces enough reward to attract the birds and cause them to linger long enough to effect pollination, the result will be tremendous pollen dispersal because of the great mobility of the pollinators.

CONCLUSIONS AND SUMMARY

Our preliminary work on the honeycreeper-ohia interaction indicates that ohia may be an obligate outcrosser that is primarily bird-pollinated. The Apapane seems especially important as an agent of pollen transfer. The pollinators are not territorial and seem to be highly mobile; as a result, each ohia must produce large amounts of nectar in order to be attractive and hold the pollinators for any time at all.

Small trees may be at a disadvantage because of the apparent tendency of the honeycreepers to forage high in the forest canopy. Small trees show a tendency to compensate for this by producing slightly larger inflorescences and larger volumes and higher concentrations of nectar.

From the ohia's point of view, given that a tree is sufficiently attractive, it probably gets its genes transferred efficiently and over long distances, a benefit which undoubtedly compensates for the high cost of attracting its highly mobile pollinators.

The fact that one tree studied supported on the average the same number of birds as predicted on the basis of nectar production and number of blossoms suggests that the honeycreepers may possess an efficient foraging strategy in spite of their great mobility. An hypothesis has been proposed regarding the nature of their strategy.

We hope in future work to obtain a measure of the efficiency of energy transfer from ohia to the honeycreeper population. This could be compared to efficiencies in mainland ecosystems to test the hypothesis that island ecosystems show less specialization than do mainland ecosystems.

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