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SYSTEMATIC PATTERNS OF FORAGING FOR NECTAR BY AMAKIHI (*LOXOPS VIRENS*)

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ABSTRACT

The visits of color-banded, territorial Amakihi to marked clusters of mamane bloom were recorded. The results indicated the existence of three systematic patterns in foraging behavior: (1) Amakihi avoid revisiting flower clusters they have recently visited; (2) when revisits do occur, they tend to be temporally spaced so as to allow time for nectar replenishment; (3) at least in some cases, the male and female Amakihi do not feed randomly with respect to each other, but rather a portion of the territory is utilized only by the female. Each of these characteristics of Amakihi foraging for nectar probably increases the foraging efficiency of the birds.

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INTRODUCTION

When a nectar feeding bird takes nectar from a flower, that flower will remain empty for a period of time that depends on the rate at which the flower produces new nectar. Therefore, it is theoretically possible for the nectar feeding bird to increase its foraging efficiency by adopting a systematic pattern of flower visitation which minimizes repeat visits to recently fed upon flowers. The purpose of the present study was to determine if members of one species of Hawaiian Honeycreeper (Drepanididae), the Amakihi (*Loxops virens*), in fact show such a pattern in the field.

The potential utility of such systematic foraging by nectar feeders has been commented upon by a number of authors (e.g., Carpenter & MacMillen 1973, 1975; Gill & Wolf 1975; Gill, Wolf, & Peters, in prep.; Ortiz-Crespo). Carpenter & MacMillen have been directly concerned with drepanids. In their 1973 paper they commented that a nectar feeder could "forage most efficiently if it visited flowers in a systematic way so that after each visit it allowed the flower enough time to recuperate." However, perhaps because of their primary interest in the pollination strategies of nectar-bearing trees, Carpenter and MacMillen have not reported any data which rigorously test the hypothesis of systematic foraging in drepanids. As Gill et al. (in prep.) have shown, testing this hypothesis requires the recording of visits by identifiable individual birds to marked flowers. With this information, the actual distribution and timing of the visits of individual birds to specific flowers can be obtained and compared to the results that would be produced by random visitation.

In the present study, such data were obtained by recording the visits of territorial, color-banded Amakihi to specific clusters of the flowers of the mamane (*Sophora chrysophylla*). Since mamane flowers are curved and relatively closed, they must be probed to determine their nectar content. Thus the birds could not see whether the flower contained nectar by visual inspection from a distance; the insertion of the bill into the flower, however, provided an easily observed criterion of flower visitation. At the same time, because mamane flowers are quite small, it was necessary to score visits to clusters of flowers rather than individual flowers.

METHODS

Site

The study site was located in the Kaohe Game Management Area at approximately 2140 m elevation, on the western slope of Mauna Kea near the road to Puu Laau (Fig. 1). This area is a relatively dry, open parkland type forest, dominated by mamane and naio (*Myoporum sandwicense*) trees (Fig. 2; see van Riper 1975, for a detailed description of this area). Data were collected during the Amakihi breeding season on several field trips from February to May, 1975.

Procedures

Because the typical Amakihi territory included thousands of mamane flower clusters distributed among two or more trees, it was necessary to select a sample of these clusters for observation. The first step in this process was to choose trees in which visits to flower clusters would be recorded. Five trees in five different territories were chosen. All five of these met three criteria: (1) each was located in the territory of a pair of Amakihi and was defended against intruding Amakihi by the pair; (2) both resident Amakihi were color-banded; and (3) at least one side of the tree could be clearly seen from a distance of 10-15 m. Three of the trees selected (sites 1-3) appeared to be primary feeding trees, in heavy bloom compared to other trees in the territory. The other two trees (sites 4 and 5) contained the nest and only light bloom.

The second step was to select the specific flower clusters which would be observed in these trees. In trees 1-3, with many clusters, colored markers were hung in the tree and flower clusters located near these markers were each given a unique designation (e.g., Black 1-9, Red 1-7, etc.). In trees 4 and 5, where far fewer clusters were present, virtually every visible flower cluster was assigned a number. These clusters, all visits to which were recorded, will be referred to as the "designated clusters." The number of designated clusters watched during observational periods varied from 56 to 116. When markers were used, they were left in place for one to two days before data collection began to allow the birds to habituate to the presence of the markers. Furthermore, the first observation session conducted at each site was treated as a "practice session" with the data collected excluded from data analyses. This gave the observer an opportunity to become familiar with the spatial distribution of the designated clusters and gave the birds an opportunity to habituate to the presence

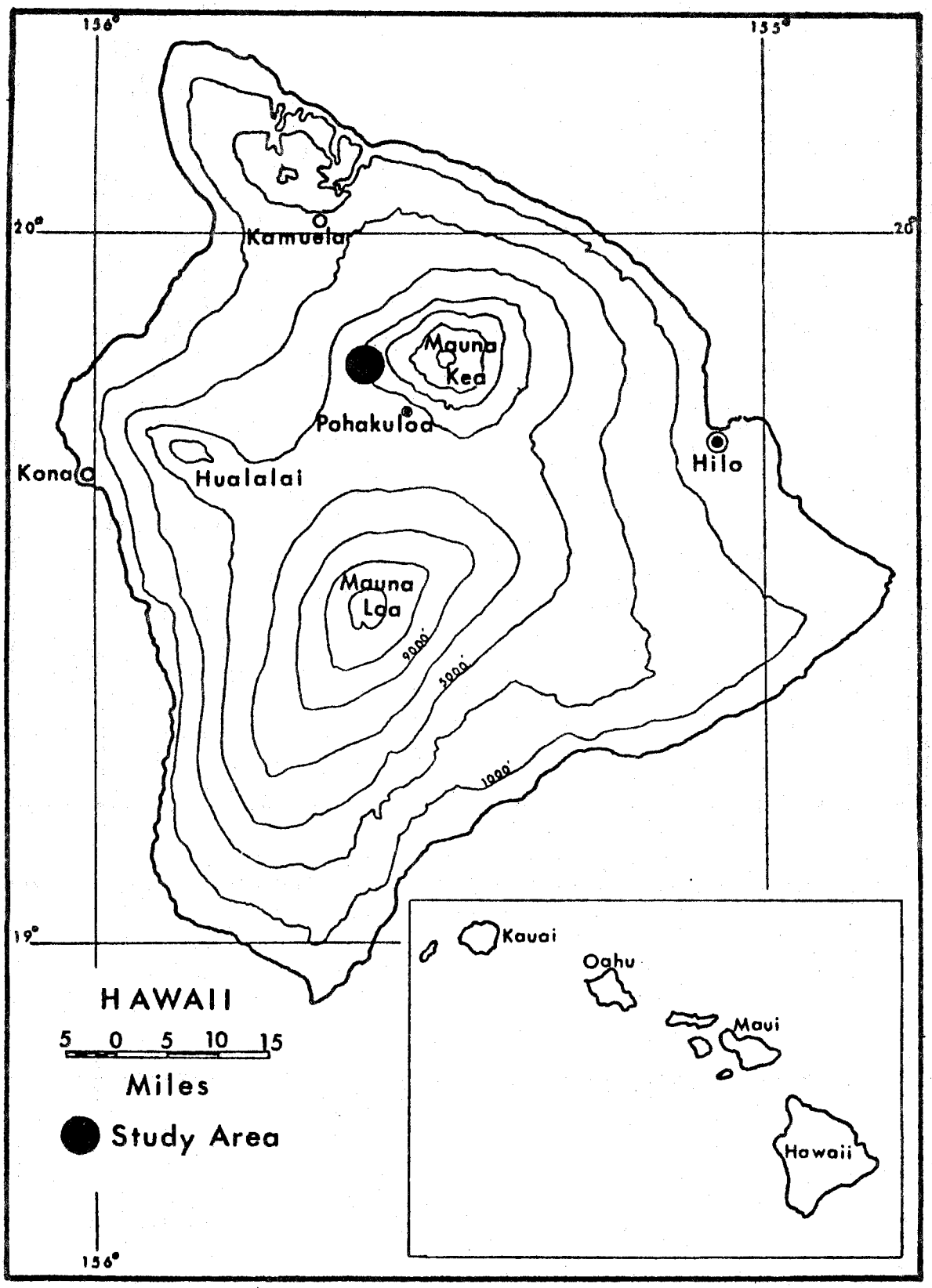

FIG. 1. Orientation map of the Hawaiian Islands, with the island of Hawaii showing study area location.

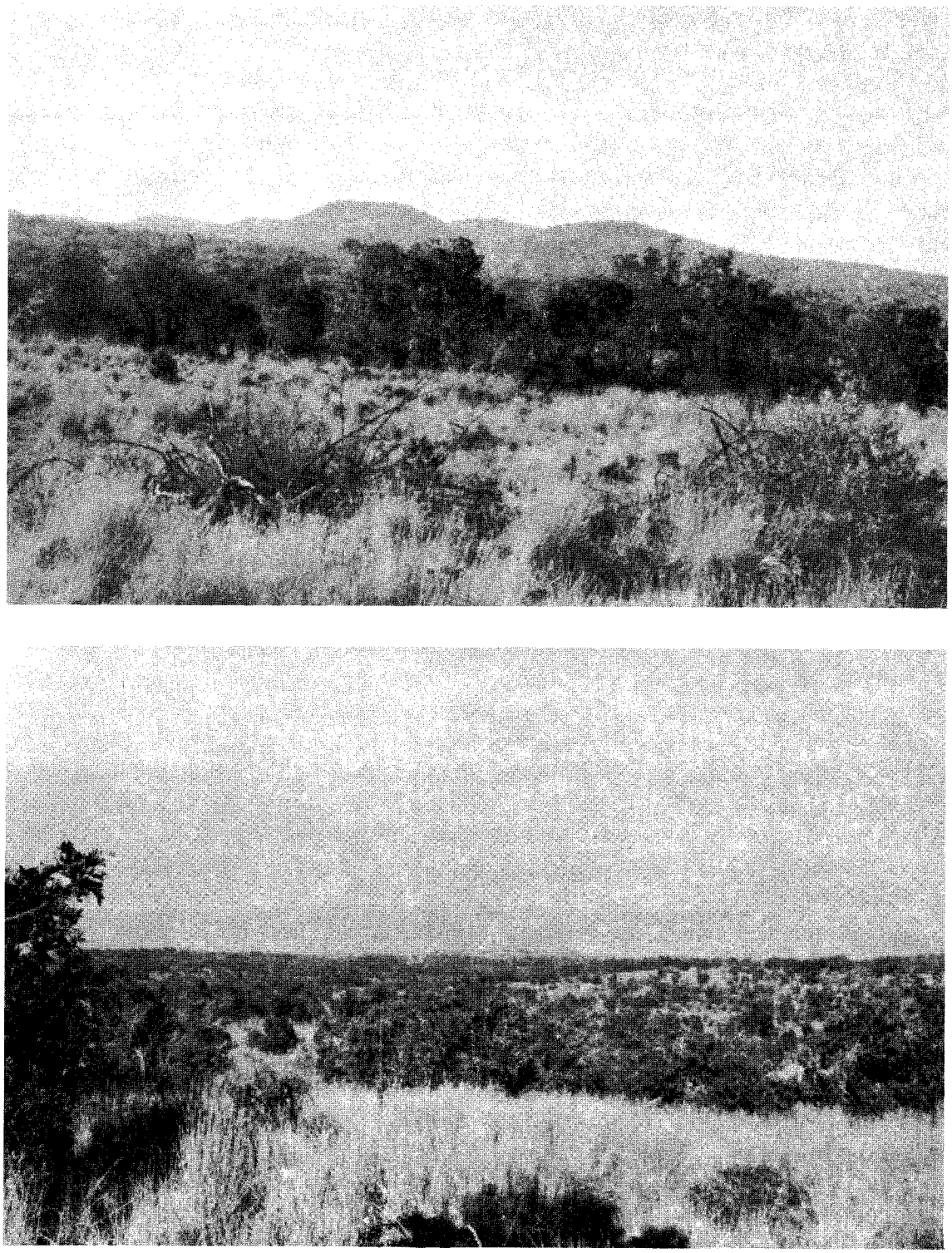

FIG. 2. Puu Laau on the slopes of Mauna Kea at an elevation of 7,300 ± feet.

of the observer.

Data were collected during observational sessions of 4-6 hours duration, usually beginning between 0730 and 0800 hours. The observer would position himself 10-15 m from the tree, equipped with 8 x 40 field glasses and a portable tape recorder. Each time an Amakihi or White-eye (Zosterops japonica), the only nectar feeding birds seen during the study, was observed feeding on nectar in the tree, three things were recorded on tape: (1) the identity of the bird (band colors or the absence of any bands in the case of some of the intruders); (2) the time the feeding bout began; and (3) the identity of designated flower clusters visited, if any. Thus, the number of visits to each designated cluster, the identity of the bird making each visit, and the approximate time of each visit were available for later analysis.

In order to measure the accuracy of this method, an estimate of its interobserver reliability was obtained. Two observers simultaneously recorded visits to the same designated clusters for two observational sessions. During these two sessions, 173 clusters were observed and the observers agreed on the number of visits of 159 (91.9%) of these. In each of the 14 disagreements, the degree of discrepancy was one visit. In addition to this high level of agreement, it was apparent that some of the disagreements were caused by factors that would not affect normal data collection: the fact that the two observers, of necessity, observed from slightly different vantage points and therefore had slightly different views of the designated clusters, and because of the relative inexperience of one of the observers.

RESULTS

Flower visitation

In 74 hours and 20 minutes of observation a total of 1171 visits to designated clusters were observed, of which 1093 (93.3%) were made by resident Amakihi. Of the 78 (6.7%) visits to designated clusters made by intruders, three were made by White-eyes and 75 by intruding Amakihi. These figures indicate that the resident Amakihi were very efficient at excluding nectar feeding intruders, most of whom were chased soon after entering the territory. While intruding Amakihi were almost invariably chased, White-eyes were chased only occasionally. If the hypothesis of systematic foraging is correct, then the resident birds, who consistently feed within the same restricted area, should show fewer visits

to already visited flowers than the intruders. Of the 1093 visits by residents, 369 (34.0%) were visits to previously visited clusters; of the 78 visits by intruders, 52 (67.8%) were repeat visits. These proportions differ significantly (χ^2 test, $p < .005$).

For each observational session, separate frequency distributions were compiled for each resident, indicating the number of times that a resident had visited each designated cluster. If visits to the designated clusters were distributed randomly, these obtained distributions should approximate the Poisson distribution. Table 1 shows the distributions obtained for all cases in which the ratio of the number of visits to the number of designated clusters exceeded 0.20, along with the Poisson distribution for each case. Of the 19 obtained distributions, 12 (63.2%) deviated significantly from the Poisson distribution in the direction which indicates that the resident Amakihi were tending to avoid clusters which they had already visited. Less clusters were visited zero times, less clusters visited more than once, and more clusters visited exactly once than would be expected by chance. One (5.2%) of the distributions deviated significantly in the opposite direction, with more repeat visits than expected. Finally, of the six (31.6%) distributions which did not deviate significantly from the Poisson, five showed fewer repeat visits than expected by chance.

Intervisit times

The temporal patterning of those repeat visits to designated clusters was also examined. Each time a designated cluster was visited more than once, the duration of the interval between successive visits was calculated. These intervisit times were tabulated separately for several categories of repeat visits (summarized in Table 2). The intervisit times for two successive visits by the same resident on days for which the frequency distribution of visits deviated significantly from the Poisson distribution with less repeat visits than by chance (SAME-NP) was compared with that for the remaining days (SAME-P, those not deviating significantly from the Poisson plus the one day deviating in the direction of more repeat visits than by chance). The difference in intervisit times for these two classes was not statistically reliable, whether tested in terms of the means (t-test, $p > 0.3$) or the temporal distribution (χ^2 test, $p > .25$; see Fig. 3). Therefore, these two classes were combined into one category (SAME) for all revisits where both visits were made by the same resident

TABLE 1. The distribution of visits to designated clusters.

Date, Sex	# visits/# clusters	Distribution	# visits 0	1	2	≥3	p
Feeding Site 1							
2-22, ♀	52/70	obs:	27	36	8	--	<.01
		Poisson:	33	25	12	--	
2-26, ♀	32/82	obs:	51	30	1	--	<.025
		Poisson:	56	22	4	--	
3-1, ♀	61/88	obs:	36	45	7	--	<.01
		Poisson:	44	30	13	--	
4-3, ♀	56/72	obs:	23	42	7	--	<.01
		Poisson:	33	26	13	--	
4-6, ♀	40/80	obs:	41	38	1	--	<.01
		Poisson:	49	24	7	--	
Feeding Site #2							
2-25, ♀	93/86	obs:	32	29	16	9	ns
		Poisson:	29	32	17	8	
2-25, ♂	25/86	obs:	62	23	1	--	ns
		Poisson:	64	19	3	--	
2-28, ♀	99/90	obs:	21	46	18	5	<.01
		Poisson:	30	33	18	9	
Feeding Site #3							
4-9, ♀	36/72	obs:	41	27	4	--	ns
		Poisson:	44	22	6	--	
4-10, ♀	33/101	obs:	71	27	3	--	ns
		Poisson:	73	24	4	--	
4-10, ♂	22/101	obs:	79	22	0	--	<.10
		Poisson:	81	18	2	--	
4-14, ♀	51/116	obs:	70	42	4	--	<.05
		Poisson:	75	33	8	--	
4-14, ♂	49/116	obs:	72	40	4	--	<.05
		Poisson:	76	32	8	--	
Feeding Site #4							
4-15, ♀	58/66	obs:	23	31	12	--	<.10
		Poisson:	27	24	15	--	
4-16, ♀	95/74	obs:	7	44	19	5	<.005
		Poisson:	20	26	17	11	

TABLE 1 (Continued).

Date, Sex	# visits/# clusters	Distribution	# visits 0	1	2	≥3	p
Feeding Site #5							
4-24, ♀	28/55	obs:	29	24	2	--	<.025
		Poisson:	33	17	5	--	
4-26, ♀	82/55	obs:	18	9	18	10	<.025
		Poisson:	12	18	14	11	
4-28, ♀	93/56	obs:	4	21	21	10	<.025
		Poisson:	11	18	15	13	
4-28, ♂	35/56	obs:	25	29	2	--	<.01
		Poisson:	30	19	7	--	

TABLE 2. Summary of intervisit times for different categories of repeat visits to the same designated cluster.

Category	Mean	S.D.*
SAME-POISSON	110.4	7.31
SAME-NON-POISSON	102.3	4.84
SAME	105.7	4.19
DIFF	80.4	4.13

* The S.D. figures given throughout this paper are standard error for the mean reported.

SAME-POISSON = revisits by the same resident Amakihi on days which did not have significantly fewer revisits than by chance.

SAME-NON-POISSON = revisits by the same resident Amakihi on days with significantly fewer revisits than by chance.

SAME = intervisit times when the revisit was made by the same resident Amakihi (includes both SAME-POISSON and SAME-NON-POISSON)

DIFF = intervisit times when the revisit was made by a different individual

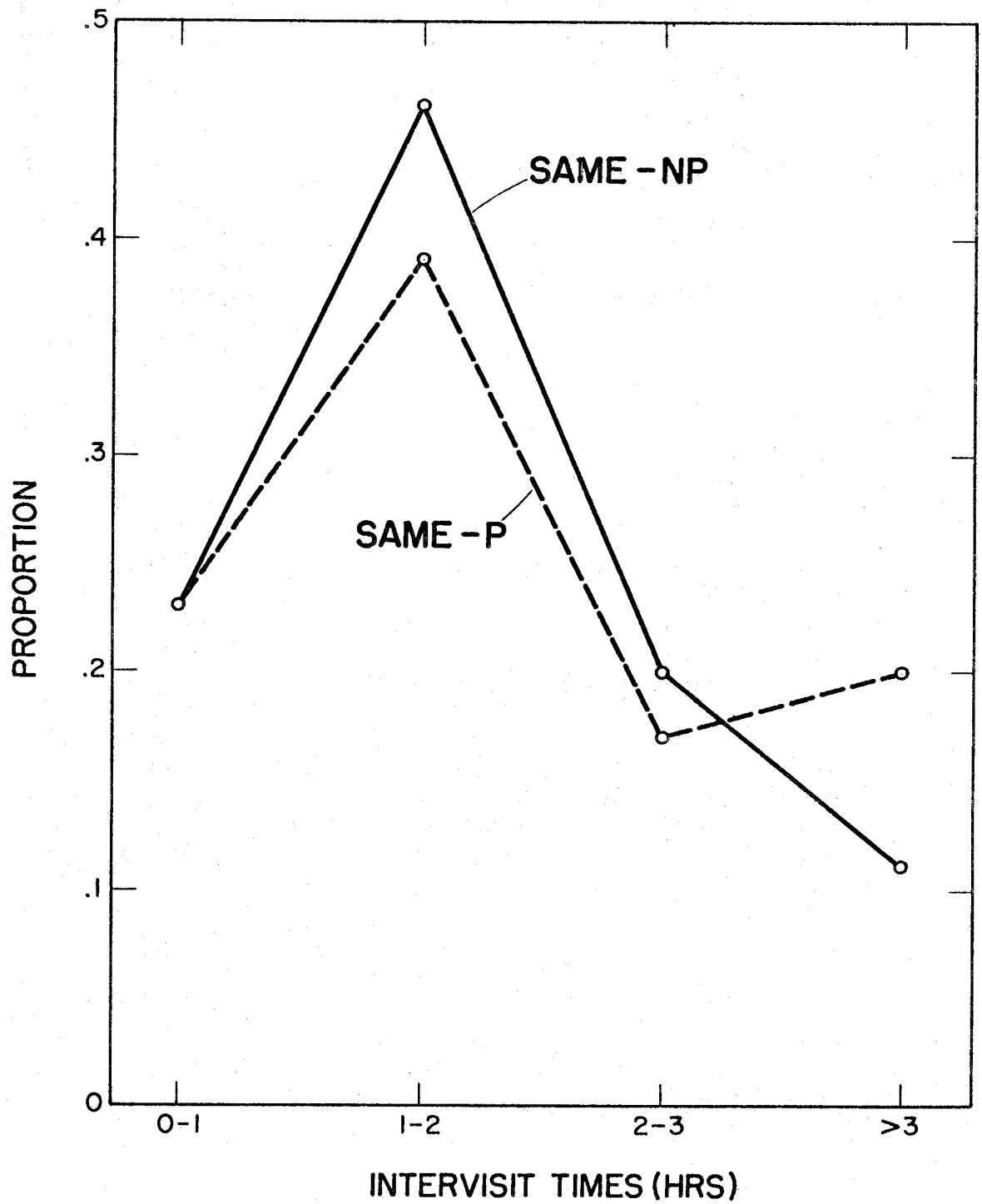

FIG. 3. Temporal distributions of intervisit times. SAME-NP indicates repeat visits by the same Amakihi on days with significantly fewer revisits than by chance. SAME-P refers to days which did not have significantly fewer revisits than by chance.

Amakihi. This was then compared to intervisit times for those cases where the revisit had been made by a different individual (DIFF; Fig. 4). Repeat visits to the same cluster by different individuals occurred significantly closer together in time than repeat visits by a single individual, in terms of the means (t-test, $p < .001$) or temporal distributions (χ^2 test, $p < .005$). It should be noted that although the difference in mean intervisit times for the SAME and DIFF cases was small (25.3 min), the DIFF mean was increased by the results of one session in which an intruder appeared and fed upon designated clusters 124 minutes after the last visit to designated clusters by a resident. When these visits are eliminated, the difference in means rises to 34.8 minutes.

Division of the territory

During the course of this study, it became evident that, is some cases, the resident male and female Amakihi did not simply feed randomly with respect to each other's feeding activities. It appeared that the female had exclusive use of a portion of the feeding territory, which the male did not feed in. This pattern was clearest in the case of the pair at Site 1. This feeding tree was a large one, with most designated clusters lying on three main limbs facing the observer's vantage point. However, other parts of the tree and a very small tree in heavy bloom to the north of the primary tree were also in view. The feeding area which was utilized exclusively by the female was located in the central part of the tree and included all designated clusters. The male almost never fed in this area although he was observed chasing intruders from this part of the tree several times. This pattern is indicated by the following data: in 25 hours and 55 minutes of observation time, the female was observed initiating feeding bouts 86 times, and the male 83 times, in the total area which could be seen from the vantage point. Yet, while the female frequently fed in the area of the designated clusters, making 241 visits to them, the male entered this area to feed only 4 times, visiting a total of 6 designated clusters. In fact, the male made less visits to designated clusters than did intruders, who visited 43 in the same period of time. Clearly, if the residents of this territory fed randomly with respect to the locations at which the other fed, the two residents should have made an approximately equal number of visits to designated clusters. Similar patterns were observed at Site 4 and 5 trees (which contained nests), where the males were rarely observed feeding on bloom near the nest. However, it must be

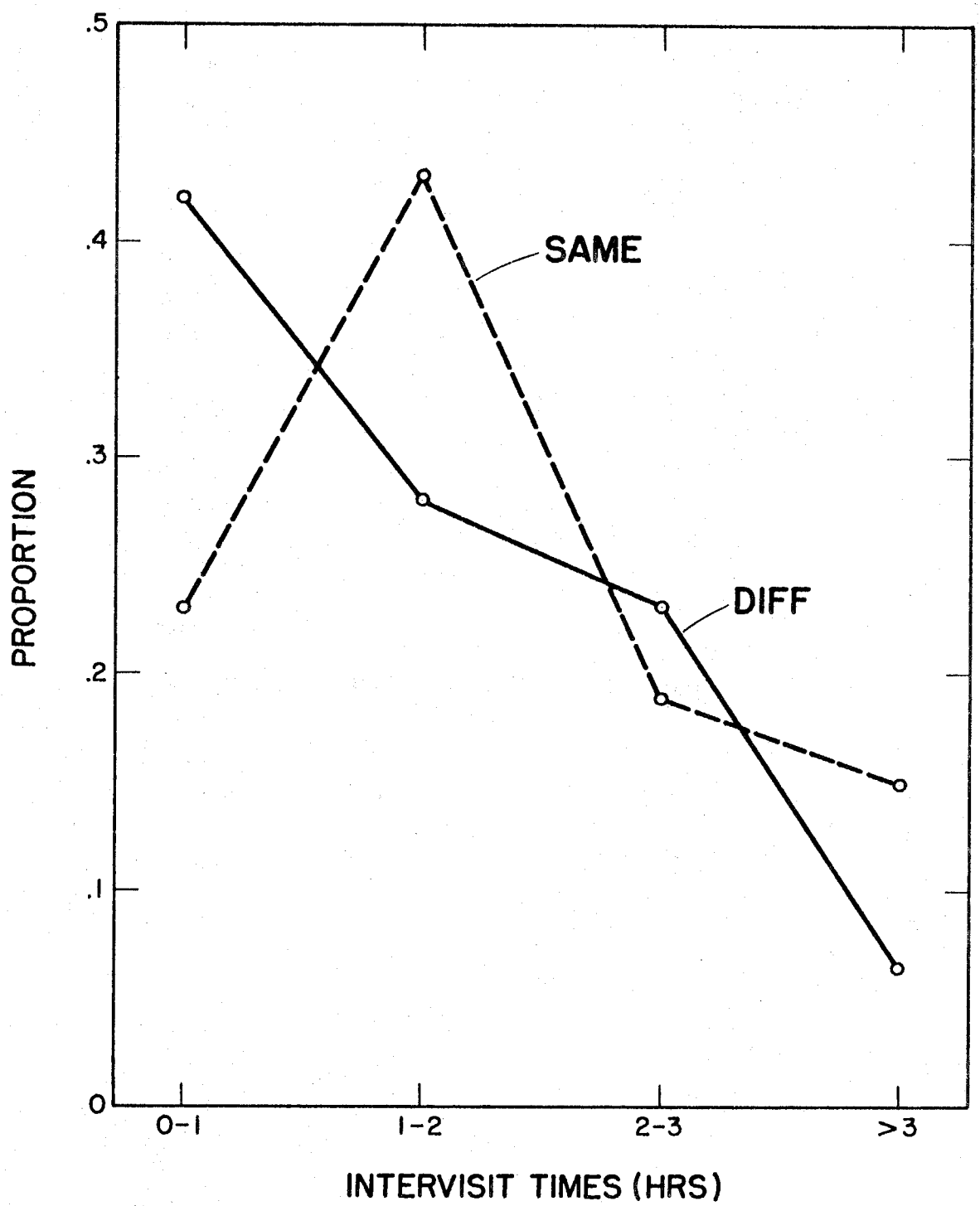

FIG. 4. Temporal distributions of intervisit times for repeat visits made by the same birds (SAME) and those made by different birds (DIFF).

emphasized that no indication of this type of division of the territory was seen at Sites 2 or 3.

DISCUSSION

These data demonstrate that territorial Amakihi systematically pattern their visits to flower clusters in three ways, each of which probably functions to increase nectar foraging efficiency.*

(1) Amakihi make relatively few visits to flower clusters which they have already visited. Thus a disproportionately large proportion of the clusters which are visited are being visited for the first time, and such unvisited flowers undoubtedly contain more nectar than clusters which have been visited previously during the observational session.

(2) When an individual Amakihi does make repeat visits to the same cluster, these visits are spaced temporally further apart than would be expected by chance (if we regard the DIFF intervisit times as an estimate of the temporal spacing of random revisits). This allows more time for nectar replenishment than would be obtained with random foraging.

(3) At least in some cases, the resident pair of Amakihi appear to divide their territory for feeding purposes so that only the female utilizes a portion of it. Division of a territory has been observed in other feeding species (e.g., Wolf and Stiles 1970), and probably functions to reduce the extent to which each animal visits clusters recently depleted by the other (Ortiz-Crespo).

One problem with the analysis of the distribution of visits to the designated clusters is the observation that some distributions did not differ significantly

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* Data were also gathered on the rate of nectar production by mamane clusters in order to estimate the amount of nectar obtained by Amakihi on each visit to designated clusters. Analysis of these data is not yet complete, but some preliminary results can be reported here. Nineteen clusters in six different trees were covered so as to exclude both buds and insects. These clusters were then periodically emptied of nectar for 3-10 days (114 measures of the amount of nectar production per day were obtained). Virtually all nectar production took place during the day, with no marked difference between morning and afternoon. The average rate of nectar production during the day was 1.63 μL/hr per cluster (S.D. = 0.17). The mean sugar content of the nectar was 25.5% (S.D. = 1.93; based on 27 measurements). Preliminary estimates of nectar availability based on these figures indicate that systematically foraging resident Amakihi enjoyed a 15-25% advantage over intruders, in terms of μL of nectar available per visit to designated clusters.

from the Poisson distribution (also a feature of the data of Gill et al. in prep.), and one even showed more repeat visits than by chance. While the number of such distributions is low, and does not call into question the basic conclusion above, this variation is of interest. There seem to be two possible explanations. Either the birds do, in fact, vary in their tendency to avoid flower clusters they have already visited, or this tendency is consistent but the technique used to detect the pattern was fallible. Fallibility of the technique seems more likely for a number of reasons. Methodologically, the frequency distributions obtained could be seriously affected by the outcome of the process of selecting designated clusters for observation. If a substantial number of designated clusters were in a part of the tree which the birds avoided entering (for example, areas low in the tree, which may have been avoided on occasion because of the presence of the observer), this would artificially increase the number of designated clusters receiving no visits. This, in turn, would decrease the probability of detecting any systematic avoidance of already visited clusters in the part of the tree which was fed in by the birds.

In terms of the data, there are two reasons to conclude that lack of sensitivity in the statistical procedures caused the variation in the statistical analyses. First, most of the obtained distributions which did not differ from the Poisson distribution tended to show less repeat visits than expected. In one case (Site 3, 4-10, male) no repeat visits were observed, but the power of the test was very low because there were few visits to designated clusters. Second, intervisit times for non-Poisson days did not differ significantly from those of Poisson days. This shows that even though the birds made more revisits to designated clusters on Poisson days, these revisits themselves were distributed systematically. Even in the case in which significantly more repeat visits were made than expected by chance (Site 5, 4-26), the mean intervisit time by this individual was greater than that for the overall SAME distribution (117.7 min, S.D. = 14.99).

It is interesting to compare these data with those obtained by Gill et al. (in prep.). They recorded the visits of color-banded Golden-winged Sunbirds (*Nectarinia reichenowi*) to marked *Leonotis* inflorescences. These birds were not breeding, but maintaining individual territories, and because there were only 200-300 inflorescences per territory, it was possible to record visits to a much higher proportion of the flowers on the territory than was possible in the

present study. Gill et al. also detected two systematic tendencies--reducing the number of revisits to individual inflorescences and temporally distributing revisits so as to allow time for nectar replenishment. The presence of these two behavioral patterns in both drepanids and nectarinids suggests that they may be widely found in nectar feeding species.

It is also interesting to compare the present data with the data Carpenter and MacMillen (1975) used to conclude that territorial Iiwi (Vestiaria coccinea) visit flowers in a systematic way allowing for nectar replenishment. Actually, this conclusion was apparently based on a single observation: "We watched a single branch of flowers on a territory and timed the owner's visits to that branch. The visits were spaced 31 minutes apart (S.D. = ± 5 min) for seven consecutive visits." Actually, this observation is of no use in evaluating the question of systematic flower visitation. Although the verbal statement implies a fairly fixed intervisit interval, the standard deviation indicates variation. Any set of numbers will have a mean and standard deviation, and we have no way of deciding whether or not a mean intervisit time of 31 minutes is significantly different from a random pattern of flower visitation.

Carpenter and MacMillen (1975) also reported that the Amakihi they observed showed no specialized nectar feeding strategy, specifically not defending feeding territories. This clearly conflicts with the observations reported here. However, the difference is probably due to the different areas in which the studies were carried out and perhaps due to their being conducted at different times. Carpenter and MacMillen collected their data in the relatively wet, ohia dominated areas on Mauna Loa where three nectar feeding drepanid species are fairly common: Iiwi, Apapane (Himatione sanguinea), and Amakihi. Because both Apapane and Iiwi easily displace Amakihi in interspecific encounters (Carpenter and MacMillen 1975, pers. obs.), it may be difficult or impossible for Amakihi to maintain a territory which includes a substantial amount of bloom where these other species are present. Furthermore, it is not clear whether or not Carpenter and MacMillen collected data during the Amakihi breeding season. It is possible that Amakihi maintain territories which include feeding areas only during the breeding season and in areas where Apapane and Iiwi are uncommon. This would be consistent with Eddinger's failure to observe Amakihi feeding territories (Berger, pers. comm.) in Kokee State Park on Kauai, where both Apapane and Iiwi are present.

The patterns of foraging behavior observed in this study raise the question of what behavioral mechanisms make them possible. One possibility is that in feeding on a flower a bird somehow changes the appearance of the flower. Then the bird need only avoid flowers which show signs of having been fed on recently. But this possibility can be eliminated because of the finding that intervisit times were consistently longer for revisits made by the same bird than for those made by different birds. If physical changes in the flower were used to mediate systematic foraging, these changes should be apparent to any Amakihi, not just to the particular bird who made the initial visit to the flower.

It seems most likely that some type of memory is involved and that Amakihi remember where they have fed (perhaps in terms of general area and not specific clusters) and avoid feeding there again. This is supported by the results of a laboratory experiment I have just completed. During this experiment, Amakihi could maximize their intake of sugar solution and minimize their contact with a mild quinine solution by learning to avoid visiting a feeding site at which they had recently fed (10-15 sec earlier). All three Amakihi tested learned this task readily. These results do not prove that Amakihi learn systematic foraging in the field, nor can they be regarded as a rigorous test of the ability of the Amakihi to remember information over longer time periods. But they do show that Amakihi are capable of learning to use cues based on the site of previous feeding to systematically pattern their feeding behavior. Since the field situation is structured in such a way that repeat visits to the same cluster in a short period of time will go relatively unrewarded, such learning must be regarded as a definite possible mechanism underlying the systematic foraging of Amakihi.

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