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Foraging Interactions of Small Hawaiian Forest Birds

C. John Ralph and Barry R. Noon
USDA Forest Service, Redwood Sciences Laboratory, Arcata, Calif., U.S.A. 95521

Abstract
In a search for competition, limiting factors, and other patterns in a community of small passerine birds in Hawaii, we recorded the foraging behaviors, resource abundances, and climatic variables believed to influence resource levels. Some definite patterns were found, showing that the rare, endangered birds were specialists; however, some specialists were quite abundant. We also identified some potential competitive interactions by an introduced species; however, no overriding theme of organization was apparent. Rather, each species appeared to have its own suite of adaptations, largely independent of others in the bird community.

Introduction

In this study, we were attempting to determine the potential suites of competing species and factors potentially limiting a species' abundance, especially those of the endangered species in these communities. In general, we were trying to determine if there were any overall patterns of adaptation related to the foraging niche used by the birds.

As foraging activities were a principal focus of the study, it is important to outline factors influencing foraging behavior, and what we considered a foraging act. The foraging niche of a species is more complex than an amalgamation of several foraging acts. These influences can be divided into those aspects that are in the past or external to the bird, and those in the present or internal to the bird. The past or external influences are the factors that determine the abundance of fruit, flowers, or insects upon which the birds in the community feed. These factors involve abiotic, primarily climatic, and biotic influences. Biotic influences are largely a function of the population densities of birds and other consumers of these same resources. These densities of animals, coupled with their food use, all interact on this resource production to result in the

resource availability for a particular species. We were able to estimate this resource availability through quantification of the abundance of the fruit and flowers throughout the entire study, and of insects in one of the areas for 3 yr.

At this point, the present or internal factors come into play to determine the foraging act of an individual species, i.e., the behavior resulting in food acquisition. The innate factors, such as morphological and behavioral constraints, and the behavioral and physiological needs, such as breeding or molting, interact with the past or external factors to determine the food choice of the species. These constraints and influences on resource acquisition are finally manifested as a foraging act, which we could observe in the field. The combination of all foraging acts results in what we term the foraging niche of the species.

Methods

This project was carried out through an intensive study spanning more than 5 yr on Hawaii Island in a mid-altitude, temperate, wet native forest, as outlined in detail by Ralph (in press). This study was on a 16-ha site in a modified ohia (*Metrosideros collina*) and koa (*Acacia koa*) forest about 10 km north of the headquarters of Hawaii Volcanoes National Park at 1800 m elevation.

We observed birds in timed activity observations of varying lengths, averaging about 30 s, and recorded various details of the methods and sites of the birds' activities. Each activity observation contributed a single datum to the analysis. All the observations of foraging of a species in a single month were compiled and classified into 30 categories—the foraging acts. These categories were combinations of the plant species used, the resource taken, the substrate chosen, and the foraging method used.

We gathered usually 25 to 35 activity observations of each species in each month throughout the study period. At the study site discussed in this paper, this resulted in 55 months of continuous quantification of foraging.

We estimated bird densities by the Reynolds *et al.* (1980) census technique, using the variable-distance circle count. The data were analyzed by the method suggested by Ramsey and Scott (1979).

On a monthly basis, we counted the number of flowers and fruits on usually more than 100 individuals of the plant species that we observed birds feeding upon regularly. In addition to the two dominant trees, these included the naio (*Myoporum sandwicense*), akala (*Rubus hawaiiensis*), olapa (*Cheirodendron trigynum*), pilo (*Coprosma* spp.), and kawau (*Ilex anomala*).

We used the monthly mean of the natural logarithm of each plant species count. We calculated the mean monthly rainfall (referred to in Table 1 as RAIN) and temperature (TEMP) from readings taken at 0800 hours at Park headquarters. The month was entered into data sets by making variables of the sine (DATE1) and cosine (DATE2) of each month, thus providing a continuous variable with 1 January of each year as the starting point.

The bird community contained four introduced and eight native passerine species, three of which have such low populations that they are considered by the U.S. Fish and Wildlife Service to be endangered. The total density of all species combined was among the highest of any community studied in the world,

averaging about 35 birds per hectare. The densities for a given month often exceeded 100 birds per hectare (Ralph, in press).

Results

We attempted to determine patterns in (a) the timing and abundance of resources; (b) changes in densities of co-occurring species; (c) foraging differences between species; (d) the degree to which species specialized on specific resources or behaviors; and (e) the correlation of foraging diversity with density of the birds.

Changes in the Timing and Abundance of Resources

The climatic events that at least partially determined the abundance of resources available to a given species have been investigated with a stepwise multiple regression model (Ralph, in press). Seasonal climatic changes, primarily date and rainfall, explained much of the variation in the production of fruit and flowers. However, relatively little seasonality in insect production was found. In general, the abundance of insects had only about a 50% coefficient of variation annually. Further, the peak of abundance was not seasonal, i.e., not regularly spaced. Essentially, one could regard insects as being fairly constant throughout the year.

Changes in Densities of Birds

There were quite marked seasonal changes in the abundances of various bird species in the community. We used stepwise multiple regression analysis to investigate the amount of variation of the densities of birds related to variation in the number of fruits and flowers, climate, or date (Table 1). There were 17 different models of population density with significant contribution by one or more of the variables.

Density of the Northern Cardinal (scientific names are given in Table 1), the Apapane, and the Iiwi could be fairly well explained by the independent variables. Only the density variation of the introduced Japanese White-eye could not be explained. For most species, the regression models explained only 25–50% of the variation in their densities. Included in this group are species that are primarily insectivorous and that we believed to be relatively independent of the timing of fruiting and flowering. Some of these species, such as the Hawaiian Creeper, Elepaio, Akepa, and the Common Amakihi, all had less than 30% of their density variation explained by the independent variables. It should be noted that population densities explained by climatic and resource variables are probably not being determined by any competitive interactions.

In an additional analysis, we investigated the possibility of competitive interactions by estimating the correlation of each species' density with those of the other species. We assumed competition was implied if the density of one species increases while that of another declines. First, we computed simple correlations of each species' density with those of all the others (Table 2). Then we computed partial correlations among the species' density estimates, after removing the effects of variation in plant phenology. Partial correlations were

Table 1. Stepwise multiple regression analysis: estimated monthly species densities (dependent variable) regressed on the abundance of various species of fruits (FR) and flowers (FL), weather, and date (independent variables). A second analysis omits the weather and date variables.

	With weather, date		Without weather, date	
Bird species	R^2	Model variables (and significance)[a]	R^2	Model variables (and significance)
Elepaio (*Chasiempis sandwichensis*)	0.28	-DATE1***	0.33	NAIO FL.***, -OHIA FL.*
Hawaiian Thrush (*Phaeornis obscurus*)	0.31	NAIO FR.***, NAIO FL.***	Same	
Melodious Laughing-thrush (*Garrulax canorus*)	0.25	NAIO FL.**, OLAPA FR.*	Same	
Red-billed Leiothrix (*Leiothrix lutea*)	0.35	NAIO FL.***, AKALA FR.**	Same	
Japanese White-eye (*Zosterops japonicus*)	None		None	
Northern Cardinal (*Cardinalis cardinalis*)	0.57	DATE1***, -OHIA FL.***, DATE2**, NAIO FL.*	0.33	OLAPA FR.***, -OHIA FL.**, NAIO FR.**
House Finch (*Carpodacus mexicanus*)	0.26	AKALA FR.**, NAIO FL.**, -TEMP.*	0.20	AKALA FR.**, NAIO FL.*
Common Amakihi (*Hemignathus virens*)	0.18	-AKALA FR.**	Same	
Akiapolaau (*H. munroi*)	0.38	-DATE1**, -TEMP.**, OLAPA FR.**	0.22	NAIO FL.**
Hawaiian Creeper (*Oreomystis mana*)	0.11	-AKALA FR.*	Same	
Akepa (*Loxops coccineus*)	0.11	-NAIO FR.*	Same	
Iiwi (*Vestiaria coccinea*)	0.48	OHIA FL.***	Same	
Apapane (*Himatione sanguinea*)	0.51	-TEMP.***, AKALA FL.***, -RAIN*	0.37	AKALA FL.**, -NAIO FL.**

[a]Only significant variables are shown. Significance of difference: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Table 2. Simple correlation coefficients (above) of bird densities on each other and partial correlations (below), with the effect of phenology of fruit and flowers removed.

	Apapane	Iiwi	Elepaio	Hawaiian Thrush	Japanese White-eye	Amakihi	Hawaiian Creeper	House Finch	Red-billed Leiothrix	Akepa	Akiapolaau	Northern Cardinal	Melodious Laughing-thrush	Skylark
Apapane	×													
Iiwi	0.444	×												
	0.350													
Elepaio	−0.280	-	×											
	(−0.001)													
Hawaiian Thrush	0.266	-	0.331	×										
	0.375		0.294											
Japanese White-eye	-	(−0.220)	-	-	×									
		−0.264												
Amakihi	-	-	0.456	-	0.273	×								
			0.448		0.292									
Hawaiian Creeper	-	-	0.289	-	-	0.369	×							
			0.309			0.286								
House Finch	(0.150)	0.433	-	0.304	−0.272	-	-	×						
	0.345	0.441		(0.170)	−0.265									
Red-billed Leiothrix	−0.281	(0.195)	0.512	0.379	-	-	-	0.610	×					
	(−0.076)	0.421	0.422	(0.186)				0.534						
Akepa	-	-	0.338	-	-	0.275	0.549	-	-	×				
			0.266			(0.192)	0.553							
Akiapolaau	-	(−0.016)	0.308	-	(−0.222)	-	0.288	0.396	0.487	0.556	×			
		0.331	(0.056)		−0.262		0.309	0.468	0.429	0.547				
Northern Cardinal	-	(0.261)	-	0.358	−0.311	-	-	0.438	0.396	-	-	×		
		0.424		(0.112)	−0.306			(0.252)	(0.199)					
Melodious Laughing-thrush	-	(0.233)	0.432	-	-	-	-	0.427	0.400		0.347	0.512	×	
		0.320	0.365					0.282	(0.203)		(0.234)	0.439		
Skylark	-	-	-	-	0.380	0.315	(0.239)	-	-	(0.160)	-	-	-	×
					0.393	0.353	0.267			0.272				

Summary of Correlations

Simple

	+	−	0	Total
+	21	0	7	28
Partial −	0	2	2	4
0	9	2	-	11
Total	30	4	9	43

Note: The 5% level of significance of correlation was $P > 0.262$. Nonsignificant correlations are not shown (-) unless the other correlation was significant in the pair, in which case it is shown in parentheses.

computed because the species may have tracked the same resource, resulting in a positive, simple correlation; however, when the effects of variation in that resource were removed, the species may covary negatively. Also, species may have a negative simple correlation because they track distinct resources that covary negatively.

The clearest evidence of competitive interactions would be both a negative simple and a negative partial correlation: i.e., both species use the same resource and interfere with each other in its use. The next clearest line of evidence would be a simple correlation being not significantly different from zero, but partial correlations significantly negative. This outcome could be caused by two species tracking the same resource, or two or more distinct resources that covary positively.

These two patterns of a negative simple and negative partial and the neutral/negative were uncommon, with only two (5%) relationships showing each of them. However, all four involved the introduced Japanese White-eye (Table 2). The white-eye is a prime candidate for competitive interactions, being both abundant and a generalist.

Foraging Differences between Species

We found six major groups, as defined by foraging acts (Table 3): the bark foragers included two endangered species, the Akiapolaau and Hawaiian Creeper; a flycatcher, the Elepaio; a terminal bud feeder, the endangered Akepa; two nectar feeders, the Apapane and Iiwi; two fruit eaters, the Hawaiian Thrush and the introduced Red-billed Leiothrix; and two foliage gleaners, the Common Amakihi and introduced Japanese White-eye.

The foraging pattern of the community as a whole was deduced by first computing the proportion of the total monthly foraging observations of each species in each of the 30 foraging acts and arranging these data into row vectors that summed to one. Accumulating these vectors across months for each species and across species generated a large 30-column matrix. From this matrix, we computed the 30×30 correlation matrix for the foraging act variables. With this as a basis, we extracted the major axes of variation from this metric by principal components analysis and retained for interpretation those axes with eigenvalues greater than 1.0. From this analysis, it was apparent that several aspects of the species' foraging behaviors were important in determining the foraging pattern of the community.

The first factor derived from the community foraging matrix was aligned with variation ranging from bark pecking by the Hawaiian Creeper and Akiapolaau to feeding on ohia flowers and foliage by the rest of the community (Fig. 1). The second axis was aligned with frugivory of the thrush and leiothrix at one extreme and feeding on foliage and flowers by the rest of the community at the other. Each of the subsequent components tended to separate out no more than a single species, so that when the eigenvalue was less than 1.0 (at nine factors), only 53% of the variation had been explained. This failure to greatly reduce the dimensionality of the foraging space suggests that the species in the community had quite distinct foraging patterns, with some foraging acts being

Table 3. Mean percentage of time spent on various combinations of substrates, foraging motions, and plant species used by ten of the forest birds on Hawaii Island.

Variable	Bird species									
	Red-billed Leiothrix	Hawaiian Thrush	Elepaio	Iiwi	Apapane	Japanese White-eye	Common Amakihi	Akepa	Hawaiian Creeper	Akiapolaau
Fruit										
Naio	0.11	0.44	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.00
Olapa	0.10	0.21	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00
Akala	0.13	0.03	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00
Other	0.04	0.09	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00
Flower										
Ohia	0.01	0.00	0.00	0.35	0.36	0.20	0.17	0.06	0.01	0.00
Naio	0.00	0.00	0.00	0.06	0.13	0.04	0.10	0.00	0.00	0.00
Akala	0.00	0.00	0.00	0.03	0.00	0.01	0.04	0.00	0.00	0.00
Flycatch	0.02	0.05	0.38	0.01	0.01	0.01	0.00	0.00	0.00	0.00
Glean foliage										
Naio	0.10	0.03	0.11	0.12	0.07	0.10	0.18	0.00	0.02	0.02
Ohia	0.13	0.02	0.26	0.17	0.15	0.24	0.11	0.35	0.07	0.00
Koa	0.01	0.00	0.02	0.01	0.03	0.04	0.04	0.03	0.02	0.04
Probe foliage										
Naio	0.07	0.02	0.03	0.05	0.03	0.05	0.06	0.01	0.04	0.05
Ohia	0.10	0.02	0.07	0.09	0.13	0.10	0.08	0.48	0.11	0.02
Koa	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.02	0.03	0.12

Glean bark										
Naio	0.01	0.01	0.03	0.00	0.00	0.01	0.04	0.00	0.04	0.04
Ohia	0.04	0.01	0.03	0.01	0.01	0.02	0.02	0.01	0.12	0.01
Koa	0.01	0.01	0.01	0.00	0.00	0.01	0.00	0.00	0.05	0.11
Peck bark										
Naio	0.00	0.01	0.01	0.00	0.01	0.02	0.03	0.00	0.09	0.13
Ohia	0.03	0.02	0.02	0.01	0.01	0.01	0.02	0.01	0.19	0.04
Koa	0.01	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.19	0.38

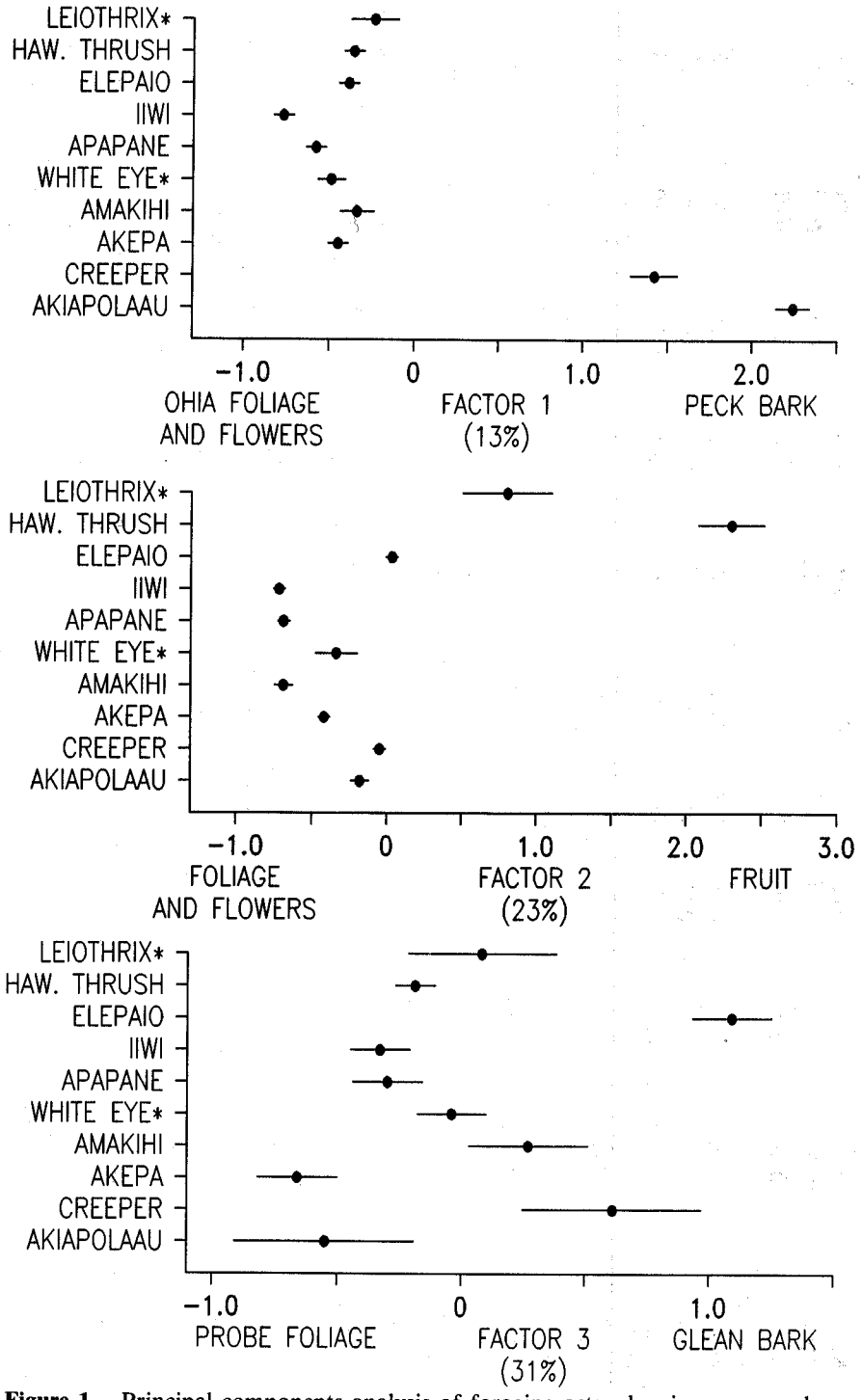
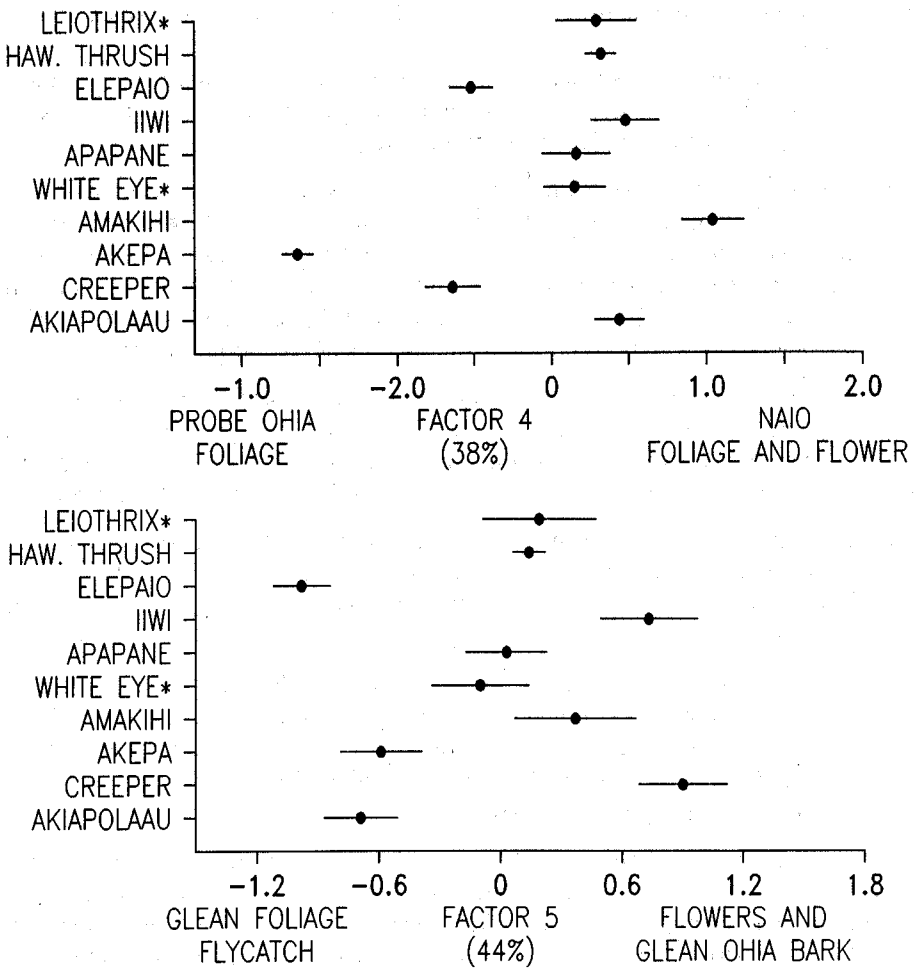


Figure 1. Principal components analysis of foraging acts, showing mean and standard error. The percentage of the variation explained by each factor is indicated below, and the principal variables important in each factor are indicated under the positive or negative loadings of the factors.



used extensively by only one or a few species. Further, the failure to clearly distinguish the species by their foraging behaviors indicates that the major axes of variation in foraging behavior were not aligned with differences among the species. The analysis suggests that most species foraged extensively in the foliage and flowers, particularly of the ohia tree (Fig. 1).

Determination of Specialists vs. Generalists

The question concerning a species' functioning either as a specialist or generalist in its food habits has many implications. These involve the implied flexibility of a generalist to take advantage of differing abundances of food resources and the relative inability of a specialist to respond favorably to changing resource levels. Given the variability in the resource levels we measured, we would have expected the specialists to be less abundant and the generalists more abundant. We measured the degree of foraging specialization with the Shannon diversity index (H′). Each datum in the analysis was the proportion that each of the

30 foraging acts made up of each month's total for each species in the community.

We did not find a strong specialist-generalist dichotomy, rather a range in values of H′. This spectrum of foraging diversity could be conveniently and somewhat arbitrarily divided into four groups:

(a) true specialists—This group was characterized by a low average foraging diversity, about 2.0, with a stable, consistent H′ value, shown by a narrow range of values. This pattern indicated that the species used a low diversity of food resources consistently throughout the year. Three species showed this pattern (Fig. 2)—the Apapane, Iiwi, and Elepaio. The first two species are nectar/flower foragers, and the latter a flycatching specialist.

(b) opportunistic specialists—These species also had a low diversity of foraging acts seen as the median H′ value, but the species were more variable than the preceding group, having a greater range of H′ values. This group was made up of two endangered species—the Akepa and the Akiapolaau.

(c) true generalists—This group was characterized by a higher average diversity of foraging acts (median = 2.5) and relatively stable H′ values. This group consisted of the endangered Hawaiian Creeper, but also the abundant Amakihi.

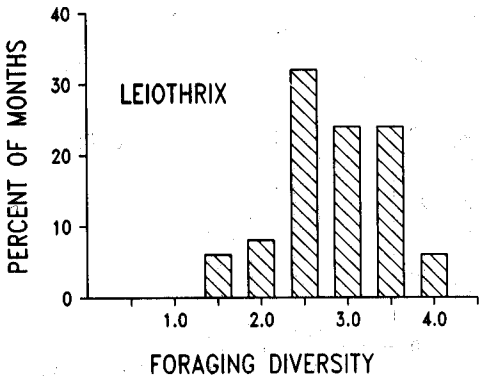
(d) opportunistic generalists—A high diversity of foraging acts, as in the previous group, was coupled in this group with a wide range of H′ values. Birds with this pattern were the three species most commonly eating fruit (Table 1)—the Hawaiian Thrush, Red-billed Leiothrix, and the more omnivorous Japanese White-eye.

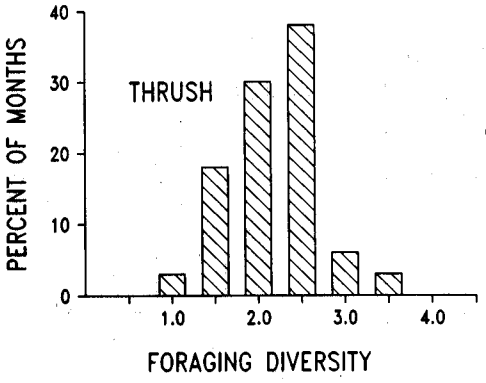
Although two of the endangered species appeared to be specialists, they differed extensively from each other. Further, the commonest species in the community, the Apapane, was a marked specialist. Thus, at this level of analysis, there was no strong association between a species' abundance and its degree of foraging diversity.

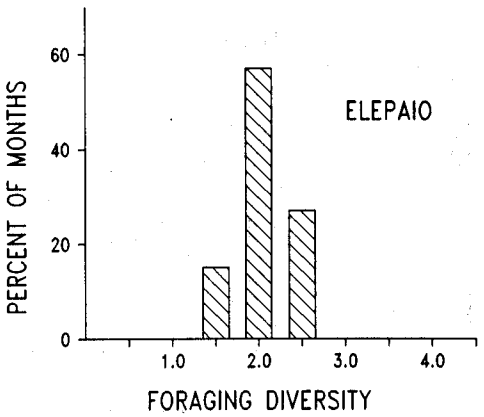
Correlations of Foraging Diversity with Density

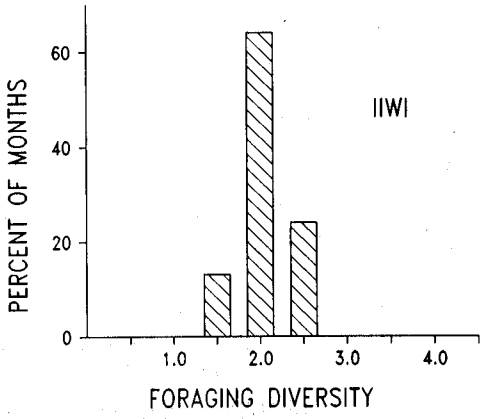
To look in a different way at the relationships between abundance and foraging diversity, we compared the monthly diversity, as measured above, with the monthly density estimate of each species by a correlation analysis (Table 4). Overall, we found two patterns—one involving the more specialized species, and the other the more generalized foraging species. This classification is defined by this analysis alone.

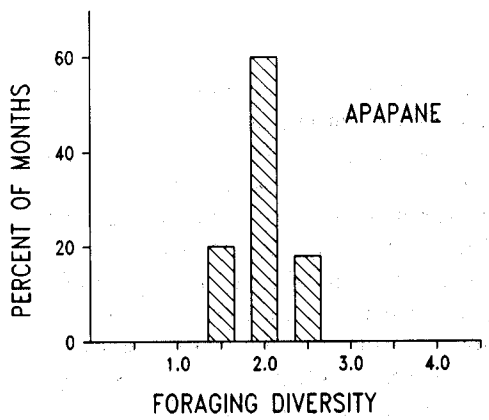
Species with negative correlations of their foraging diversity with their own density, as well as with the density of other species in the community (Table 4), can be considered specialists, as illustrated by the Akepa. One possible explanation for this pattern is that as there was an increase in the specialists' densities, as well as in the densities of other species in the community, the specialists were forced to concentrate their attention on specific resources by competitive pressures. Thus, the variability in foraging diversity may be in part related to densities of other species.

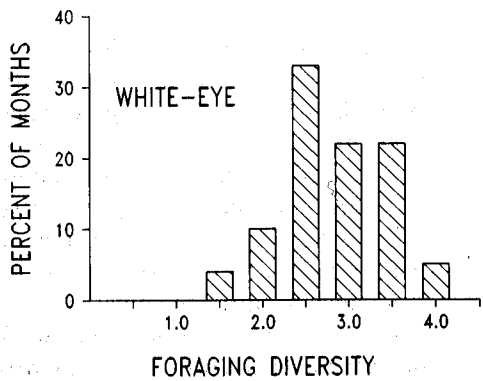












(Figure 2 continued over leaf)

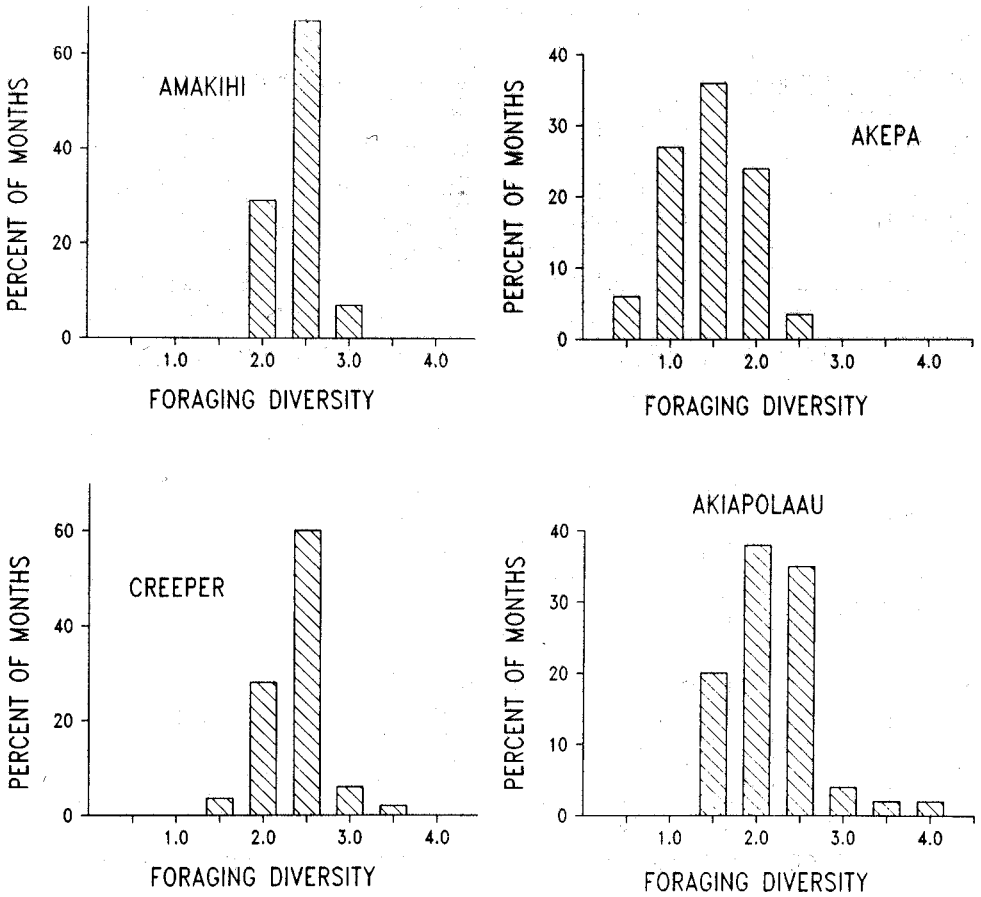


Figure 2. The percentage of months having different levels of diversity of foraging acts.

For the generalists, there were many positive correlations of foraging diversity with their population densities, as well as with the abundance of other species in the community. An example is the white-eye (Table 4), whose foraging behavior became more diverse as its densities and those of other species increased. Thus, these species responded to an increase in bird abundance, both intra- and interspecifically, by diversifying their foraging patterns.

As was the case in the previous analysis, we observed a variety of responses to a similar source of variation—in this case, variation in the community-wide abundance of birds. Such variety of responses, and the relative uniqueness of the foraging pattern of most species, appear to preclude generalizations about the foraging patterns of Hawaiian forest birds. Here again, each species is pursuing a basic strategy, but there is no common thread connecting the various ways in which a bird responds to changes in its environment.

Table 4. Significant ($P < 0.05$*) correlations of the diversity of foraging tactics with the monthly population density.

Population density	Foraging diversity (H′)									
	Apapane	Elepaio	Hawaiian Thrush	Iiwi	Japanese White-eye	Common Amakihi	Hawaiian Creeper	Red-billed Leiothrix	Akepa	Akiapolaau
Apapane	−0.27	–	–	–	–	0.29	–	–	–	–
Elepaio	–	–	–	–	–	–	–	–	–	–
Hawaiian Thrush	–	0.30	–	–	–	–	–	–	–	–
Iiwi	–	–	−0.29	−0.41	–	–	–	–	–	–
Japanese White-eye	–	–	–	–	–	–	–	–	–	–
Common Amakihi	–	–	–	–	–	–	–	–	–	–
Hawaiian Creeper	–	–	–	–	–	–	–	–	−0.28	–
House Finch	–	–	–	–	0.42	–	–	–	−0.28	−0.40
Red-billed Leiothrix	–	–	–	–	0.43	–	–	–	−0.34	–
Akepa	–	–	–	0.27	–	–	−0.44	−0.28	−0.36	–
Akiapolaau	0.28	–	–	–	0.40	–	−0.43	–	−0.62	−0.33
Northern Cardinal	–	–	–	−0.42	–	–	–	–	–	–
Melodious Laughing-thrush	–	–	–	−0.33	0.29	−0.29	–	–	–	–

*Significance of correlations is as follows: $P < 0.05 = 0.28$–0.33; $P < 0.01 = 0.34$–0.42; $P < 0.001 = 0.43$–0.60; $P < 0.0001 = > 0.61$.

Discussion

In this study, the species showed complex interactions with varying resource levels; they partitioned resources in a variety of ways; and they were exposed to varying levels of intra- and interspecific competition. There was some evidence that the introduced Japanese White-eye was interacting with the other species. Mountainspring and Scott (1985) suggested that their data showed similar potential for competition by this species.

The categories of specialist and generalist, at least as applied to this community, did not show consistent relationships and were dependent upon the metric used to define the degree of specialization. Although specialists could be rare, they could also be abundant. Although specialists could concentrate on a certain resource, there were alternative ways of exploiting this resource. Further examples from other communities would help a great deal in understanding the apparent subtleties of foraging niches.

All of the species' foraging behaviors are constrained to some unknown degree by their body size and physiological requirements. At least in this Hawaiian forest bird community, we were unable to detect any common theme connecting the various species and their adaptations to their environment.

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