

SCALES OF HABITAT SELECTION BY FORAGING 'ELEPAIO IN UNDISTURBED AND HUMAN-ALTERED FORESTS IN HAWAII¹

ERIC A. VANDERWERF²

Department of Zoology, University of Florida, Gainesville, FL 32611

Abstract. I examined habitat selection by foraging 'Elepaio (*Chasiempis sandwichensis*) in relatively undisturbed and human-altered forests in Hawaii at three hierarchically-nested scales by comparing birds with random sites. The fine scale was based on a sphere with a radius of 0.75 m, the intermediate scale used a cylinder from ground to canopy with a radius of 1.5 m, and the broad scale was based on the point-quarter method. At a fine scale, 'Elepaio in both forests selected foraging sites with high foliage density, large bark surface area, and many twigs and branches. 'Elepaio in disturbed areas compensated for lower available foliage density by being "hyperselective" toward high density sites. At an intermediate scale, 'Elepaio in both forests favored sites with above average foliage density at all heights. Birds in undisturbed habitat preferred sites with native ground cover and used sites with feral pig damage or exotic grasses less than expected, while birds in disturbed forest did not favor any ground cover type. At a broad scale, tree and shrub densities were much lower in disturbed areas, but 'Elepaio did not select sites with high tree or shrub density in either forest. 'Elepaio in both forests preferred 'Ohia, and used Koa less than expected. Disturbed areas may be lower quality foraging habitat because less space consists of sites with preferred high fine-scale foliage density. The broad scale is commonly used to measure habitat around nest sites and song perches, but it did not detect patterns of foraging site selection and may be too coarse for measuring foraging habitat of forest birds.

Key words: *Chasiempis sandwichensis*; 'Elepaio; habitat selection; habitat disturbance; Hawaii; scale.

INTRODUCTION

Habitat structure affects foraging opportunities for birds by determining abundance and distribution of prey and which search and attack methods birds can employ to capture prey (Robinson and Holmes 1982, 1984; Holmes and Schultz 1988). For insectivorous forest birds, foraging opportunities may be the primary determinant of habitat selection (Holmes 1981, Sherry and Holmes 1985). It is not surprising, therefore, that human alteration of habitat structure has an impact on foraging behavior and habitat selection (e.g., Szaro and Balda 1979, Franzreb 1983).

In studies of avian habitat selection, correlations often are found between distributions of bird species and habitat characteristics, particularly vegetation structure (Hildén 1965, reviews in Cody 1985). Habitat selection presumably has adaptive significance (Rotenberry 1981), but to understand why these relationships exist and if they are biologically meaningful, we must determine how birds choose habitat (Holmes 1981,

Sherry and Holmes 1985, Sedgwick and Knopf 1992). In the majority of cases, the mechanisms and criteria for habitat selection in birds are poorly known (Cody 1985, Orians and Wittenberger 1991). Insight into these processes can be gained by comparing patterns of habitat selection by a single species in two habitats that differ in structure (Holmes 1981, Robinson and Holmes 1982).

Habitat alteration in Hawaii has been extensive both historically (Stone and Scott 1985) and prehistorically (Kirch 1982, 1983), and native Hawaiian birds may be especially sensitive to disturbance (Olson and James 1984, Sakai 1988). Abundance of native Hawaiian birds is often negatively correlated with habitat disturbance (Scott et al. 1986). However, to determine if and how habitat alteration affects these species, one must understand what aspects of habitat structure are important to them and the mechanisms by which they select habitat.

Patterns of habitat use at the population and geographic levels are ultimately the result of how individuals respond to variation in habitat structure (Martin 1986). Individual variation in behavioral responses to habitat differences is therefore essential to discovering processes by which

¹ Received 1 March 1993. Accepted 26 May 1993.

² Present address: University of Hawaii, Department of Zoology, Edmondson Hall, 2538 The Mall, Honolulu, HI 96822.

birds select habitat because patterns of individual selection should most clearly reflect responses to habitat characteristics (Wiens et al. 1987b).

Variations in habitat structure to which individual birds may respond exist in a hierarchy of spatial scales (Maurer 1985, Kolasa and Pickett 1991), and this hierarchical heterogeneity should be considered when attempting to determine patterns of habitat selection (Kotliar and Wiens 1990, Orians and Wittenberger 1991). The scale at which habitat is measured influences what patterns are detected and what underlying processes can be inferred from them (Sherry and Holmes 1985, Wiens and Rotenberry 1986, Wiens et al. 1987a). Thus, the appropriate scale depends on the goals of the study. To determine how individual birds select foraging sites and to what aspects of habitat structure they respond, a local scale is required (Brown 1984, Wiens et al. 1987a, Sedgwick and Knopf 1992). A useful approach is a design that includes a nested hierarchy of scales that encompass the range of habitat parameters to which birds may respond (Maurer 1985, Kolasa and Pickett 1991, Bergin 1992).

I devised a method of measuring habitat parameters that individual birds might use to select foraging sites at three hierarchically-nested scales. Although I termed them broad, intermediate, and fine scales, most authors would consider all three to be microhabitat or local scales (e.g., Morris 1987, Wiens et al. 1987a). The fine scale encompassed an area a foraging bird might search from a single perch and measured foliage density, bark surface area, and numbers of branches and twigs. The intermediate scale covered an area a bird might search from two consecutive perches and measured groundcover type and foliage density in several height categories. The broad scale was similar to that often used to describe avian habitats and measured tree and shrub densities (James and Shugart 1970). To determine patterns of selection, I compared measurements from points where I saw a bird forage to those from random points (Moser et al. 1990).

I used this method to examine patterns of foraging site selection by an endemic, insectivorous Hawaiian bird, the 'Elepaio (*Chasiempis sandwichensis*), in two forest types that differed in degree of human disturbance. By comparing selection of habitat parameters at several scales in relatively undisturbed and disturbed areas, I hoped to learn what aspects of habitat structure

are important to 'Elepaio, and whether 'Elepaio might be restricted somehow in their use of disturbed habitat.

METHODS

STUDY SITE AND SPECIES

This study was conducted from April through July, 1991 at Hakalau Forest National Wildlife Refuge, Hawaii. The site lies on the windward slope of Mauna Kea at 1,900 m elevation and experiences heavy rainfall (3 m/yr), frequent clouds and mist, and daytime temperatures rarely above 20°C. Scott et al. (1986) provide a detailed description of the topography and climate of the region.

The area was originally covered by montane rainforest, but in the last 100 years human activities such as cattle ranching and timber harvesting have transformed it into a mosaic of relatively undisturbed forest and highly modified open woodland. The "undisturbed" forest has been altered by the same activities, but to a lesser degree, and still retains a closed canopy, relatively dense understory, and ground cover mostly of native forbs and ferns. The disturbed forest has a shorter, more open canopy, almost no understory, and ground cover of exotic grasses, particularly Kikuyu Grass (*Pennisetum clandestinum*), Velvet Grass (*Holcus lanatus*), Sweet Vernalgrass (*Anthoxanthum odoratum*), and Meadow Ricegrass (*Microlaena stipoides*).

These two habitats did not have distinct boundaries, and areas intermediate in structure often intervened. I chose study plots that did not include areas of intermediate structure and that represented extremes of the continuum from undisturbed to disturbed. I established three study plots totalling 11.4 ha in undisturbed habitat and three plots totalling 10.6 ha in disturbed habitat that were as close as possible to each other (within 330 m) and were similar in size, shape, and elevation.

'Elepaio are common residents in both habitats at the study site, although population density may be slightly higher in undisturbed habitat (VanderWerf, unpubl. data). They are monogamous, nonmigratory, and remain paired and probably territorial throughout the year (MacCaughy 1919, Conant 1977, Berger 1981). 'Elepaio are insectivorous (Munro 1960, Conant 1977), and are extremely versatile foragers. They use a variety of foraging techniques that include

gleaning, hanging, and aerial hawking, and substrates ranging from leaves and twigs to trunks and even the ground (VanderWerf, unpubl. manuscript).

I used four methods to identify 45 individual 'Elepaio in the study plots: a unique combination of colored leg bands ($n = 16$), distinctive plumage caused by intergradation of two subspecies ($n = 5$, see Pratt 1980), being paired with a color-banded or distinctively-plumaged bird ($n = 10$), and known territory boundaries ($n = 14$). I compiled data separately for each individual.

DATA COLLECTION

I observed each foraging 'Elepaio until it attempted to capture prey or until I lost sight of it. If it attempted to capture prey, I recorded the plant species, height, and substrate where the attack occurred, and used the perch where the attack was initiated as the center from which to measure additional habitat use parameters at three scales.

For fine scale habitat use measurements, I imagined a 0.75 m radius sphere around the point of attack. I chose 0.75 m because this was the average length of 427 flights between perches in preliminary observations. The fine scale thus represented an area a bird might search from a given perch, on average. I estimated this distance using the length of an 'Elepaio, 15 cm, as a "ruler." Within this sphere I counted the maximum numbers of trunks (> 20 cm diameter), large branches (5–20 cm), small branches (1–5 cm), and twigs (< 1 cm) that passed through any one plane of the sphere. I estimated foliage density and bark surface area as the maximum in any one plane through the sphere in one of six categories (see Remsen 1985): 0 (0%), 1 (1–10%), 2 (11–30%), 3 (31–70%), 4 (71–90%), or 5 ($> 90\%$).

To measure intermediate scale habitat use, I imagined a 1.5 m radius cylinder centered on the point of attack and extending from the ground to the top of the canopy. Within this cylinder I recorded the dominant ground cover category (native forbs and ferns, exotic grasses, feral pig damage, or bare rock and soil). Damage by feral pigs was recognized by the churned, muddy soil, uprooted plants, and sometimes by their hoofprints and droppings. I estimated foliage density using the same categories as fine scale in four height strata: understory (< 3 m), lower canopy (3–6 m), mid-canopy (6–9 m in disturbed habi-

tat, 6–12 m in undisturbed), and upper canopy (> 9 m in disturbed habitat, > 12 m in undisturbed).

For broad scale habitat use, I measured tree and shrub densities using the point-centered quarter method, with the center on the ground directly below the point of attack (Cottam and Curtis 1956). Distances to nearest trees and shrubs were variable, but typically were 5–10 m for trees and 5–15 m for shrubs in disturbed habitat, and 2–5 meters for trees and 1–3 m for shrubs in undisturbed habitat.

I measured availability of the same habitat variables at the same three scales at random points. I found a random point by starting from the use point, selecting a compass bearing from a random numbers table, measuring the maximum distance a bird could travel in that direction from that point without leaving its territory or the foraging patch, and then randomly selecting a distance out of the maximum possible. Maximum distances ranged from a few meters to over 50 m and were generally longer in undisturbed habitat. I chose a height by measuring maximum canopy height at the random point and choosing a height out of the maximum possible with a random numbers table.

In an attempt to improve the precision of this method and remove subjectivity, I practiced by taking repeated measurements during preliminary observations until I felt proficient. To increase accuracy of bark surface area estimation, I converted diameters of trunks and branches into areas, assuming they were cylindrical. I made all observations myself, so there was no inter-observer variation.

ANALYSES

I averaged values for each variable over an individual and I used each individual as an independent observation. I required a minimum of ten observations per bird for inclusion in analyses and I obtained sufficient data on 22 individuals in undisturbed habitat and 23 in disturbed habitat. To determine which parameters 'Elepaio might use as selection criteria, I compared use and random points in each habitat with a paired *t*-test or, if several of the variables were related, with multiple analyses of variance (MANOVA). To determine whether 'Elepaio altered their selection criteria in disturbed areas and if they might be limited by disturbed habitat,

I compared both use and random points between habitats, again with either a paired *t*-test or a MANOVA.

For some variables I was interested in knowing patterns of selection for specific categories, such as tree species, height strata, and groundcover types. Habitat selection of this type is often analyzed using goodness of fit tests, with frequency of use of each category treated as observed values and availability as expected values. Such an analysis pools observations from all individuals, and thus assumes that all birds have equal access to the same resources. This assumption is not valid for territorial species in heterogeneous habitat because each bird has access only to the resources on its territory (Martin 1986). Furthermore, this type of analysis does not allow examination of individual variation in selection patterns. Dodge et al. (1990) suggest that regression is a superior method of comparing habitat use and availability. In this approach, each bird is used as a data point in a regression where use is the dependent variable and availability is the independent variable. Use and availability of each category are converted to proportions of the total number of observations. For example, proportional use of a tree species is found by dividing the number of foraging observations in that species by the total number of observations. Proportional availability is found by dividing the number of trees of that species by the total number of trees in the sampling points, weighted by basal area in this case. Because the dependent and independent variables are both proportions and have the same scale, they can be compared directly. If use is proportional to availability, each should increase at the same rate and the slope of the regression line will be one. The null hypothesis that use equals availability is tested by using a *t*-test to determine if the slope of the regression line is different from one. Use is greater than expected based on availability if the slope is greater than one, and less than expected if the slope is less than one. Regression without the constant is used to ensure that the line passes through the origin. Since values among categories for use and availability were relative proportions and were thus collinear, multivariate regression was not appropriate and I performed a series of simple regressions with each pair of use and availability values (Dodge et al. 1990).

RESULTS

COMPARISON OF USE AND RANDOM POINTS

Broad scale tree and shrub densities did not differ between use and random points in either habitat (Table 1). Densities at use points translate into average nearest neighbor distances of 3.4 m for trees and 2.8 m for shrubs in undisturbed habitat and 6.9 m for trees and 9.9 m for shrubs in disturbed habitat. Patterns of tree species selection were similar in undisturbed and disturbed habitats (Table 2). Use of *Metrosideros polymorpha* ('Ohia) and *Ilex anomala* was higher than expected from availability, use of *Acacia koa* (Koa) was lower than expected, and standing dead trees were not used at all. Other tree species, including *Myrsine lessertiana*, *Cheirodendron trigynum*, and *Coprosma* sp., were used in proportion to their availability in undisturbed habitat; some species were not used in disturbed habitat, such as *Cheirodendron* and *Coprosma*. Results for these species should be interpreted with caution because they were very sparsely and unevenly distributed. Patterns of their use are based on relatively few observations, and some territories in disturbed habitat did not contain all species of trees.

At an intermediate scale, 'Elepaio foraged in areas where foliage density was above average. Foliage density indexes at all heights in both habitats were higher at use points than at random points (MANOVA, overall $F_{4,39} = 16.82$, $P < 0.0001$ in undisturbed, $F_{4,41} = 11.33$, $P < 0.0001$ in disturbed). See Table 1 for partitioning of *F*-values). 'Elepaio did not seem to have a foraging height preference based on availability. The only height category used more than expected was mid-canopy in undisturbed habitat (Table 3). All other heights in both habitats were used in proportion to their availability.

Patterns of groundcover selection differed between habitats (Table 4). In undisturbed habitat, areas with native ground cover were used more than expected, and pig-damaged areas, exotic grass, and bare rock and soil were used less than expected. In disturbed habitat, all categories of ground cover were used in proportion to their availability, except bare rock and soil, which was used less than expected.

Fine scale foliage density indexes in both habitats were higher at use points than at random

TABLE 1. Tests of differences in habitat variables at use versus random points and between undisturbed and disturbed habitats. Use and random values are averages \pm standard errors from all individuals. t = Student's t from paired tests, F = MANOVA with other variables at the same scale within a habitat. Statistics in the right-most column represent tests between use and random points in either habitat, and statistics in rows show results of tests between habitats at either use or random points. n = 22 birds in undisturbed habitat and 23 in disturbed habitat. * = significance at α = 0.01, ** = significance at α = 0.001.

Variable	Habitat	Use	Random	Statistic
Broad scale				
Tree density (no./ha)	Undisturbed	864 \pm 58	868 \pm 68	t = 0.046
	Disturbed	208 \pm 16	198 \pm 41	t = 0.23
		t = 10.93**	t = 8.49**	
Shrub density (no./ha)	Undisturbed	1,246 \pm 106	1,633 \pm 261	t = 1.37
	Disturbed	102 \pm 13	150 \pm 59	t = 0.80
		t = 10.06**	t = 14.04**	
Intermediate scale				
Understory fol. den. index	Undisturbed	1.34 \pm 0.091	0.76 \pm 0.074	$F_{1,42}$ = 24.44**
	Disturbed	0.50 \pm 0.065	0.21 \pm 0.032	$F_{1,44}$ = 15.77**
		$F_{1,43}$ = 57.18**	$F_{1,43}$ = 47.52**	
Low canopy fol. den. index	Undisturbed	1.08 \pm 0.13	0.62 \pm 0.097	$F_{1,42}$ = 7.97*
	Disturbed	1.42 \pm 0.094	0.92 \pm 0.085	$F_{1,44}$ = 15.67**
		$F_{1,43}$ = 4.48	$F_{1,43}$ = 5.26	
Mid-canopy fol. den. index	Undisturbed	2.72 \pm 0.091	2.10 \pm 0.091	$F_{1,42}$ = 23.15**
	Disturbed	2.71 \pm 0.090	2.15 \pm 0.090	$F_{1,44}$ = 18.97**
		$F_{1,43}$ = 0.005	$F_{1,43}$ = 0.18	
Upper canopy fol. den. index	Undisturbed	3.44 \pm 0.065	3.04 \pm 0.081	$F_{1,42}$ = 15.14**
	Disturbed	2.73 \pm 0.091	2.22 \pm 0.084	$F_{1,44}$ = 17.21**
		$F_{1,43}$ = 39.35**	$F_{1,43}$ = 48.79**	
Fine scale				
Trunks	Undisturbed	0.18 \pm 0.047	0.054 \pm 0.013	$F_{1,42}$ = 7.16*
	Disturbed	0.088 \pm 0.018	0.042 \pm 0.017	$F_{1,44}$ = 3.57
		$F_{1,43}$ = 3.78	$F_{1,43}$ = 0.34	
Large branches	Undisturbed	0.92 \pm 0.056	0.55 \pm 0.054	$F_{1,42}$ = 21.77**
	Disturbed	0.96 \pm 0.071	0.47 \pm 0.041	$F_{1,44}$ = 36.71**
		$F_{1,43}$ = 0.25	$F_{1,43}$ = 1.77	
Small branches	Undisturbed	8.79 \pm 0.34	6.24 \pm 0.17	$F_{1,42}$ = 46.13**
	Disturbed	9.16 \pm 0.26	5.89 \pm 0.19	$F_{1,44}$ = 107.2**
		$F_{1,43}$ = 0.77	$F_{1,43}$ = 1.85	
Twigs	Undisturbed	15.28 \pm 0.50	11.91 \pm 0.27	$F_{1,42}$ = 35.12**
	Disturbed	15.69 \pm 0.38	11.28 \pm 0.20	$F_{1,44}$ = 106.2**
		$F_{1,43}$ = 0.43	$F_{1,43}$ = 3.59	
Foliage density index	Undisturbed	3.26 \pm 0.072	2.58 \pm 0.054	t = 7.89**
	Disturbed	3.15 \pm 0.053	2.32 \pm 0.052	t = 14.01**
		t = 1.25	t = 3.43**	
Bark surface index	Undisturbed	1.56 \pm 0.076	1.18 \pm 0.023	t = 4.93**
	Disturbed	1.37 \pm 0.058	1.14 \pm 0.027	t = 3.84**
		t = 1.96	t = 1.26	

points (Table 1). In addition, bark surface area was higher at use points than random points in both habitats. Numbers of large branches, small branches, and twigs were higher at use points than random points in both habitats, but number of trunks was higher at use points only in undisturbed habitat (MANOVA, overall $F_{4,39}$ = 33.66, P < 0.0001 in undisturbed habitat, $F_{4,41}$ = 47.04, P < 0.0001 in disturbed habitat. See Table 1 for partitioning of F -values).

COMPARISON OF HABITATS

Broad scale tree and shrub densities were higher in undisturbed habitat at both use and random points (Table 1). Overall intermediate scale foliage density was higher in undisturbed habitat at use points and random points, but in comparisons of individual height categories, only understory and upper canopy foliage densities were higher in undisturbed habitat (MANOVA, over-

TABLE 2. Proportions of tree species use (U) and availability (A) in undisturbed and disturbed habitat. Availability (calculated from total basal area) and use are averages of proportions from all individuals. Slope is the slope of the regression line, SE is the standard error of the slope, and *t* is student's *t*, which indicates whether the slope of the regression line is different from one. Slopes > 1 indicate use is greater than availability, *P*-values < 0.05 indicate slopes significantly different from 1.

Tree sp.	Avail.	Use	Slope	SE	<i>t</i>	<i>P</i> -value	Conclusion
Undisturbed habitat (<i>n</i> = 22)							
<i>Metrosideros</i>	0.690	0.883	1.19	0.069	7.21	0.014	U > A
<i>Acacia</i>	0.265	0.071	0.29	0.024	896.34	0.00001	U < A
Dead	0.018	0.00	0.0	—	—	—	
<i>Cheirodendron</i>	0.011	0.019	0.92	0.66	0.016	0.90	U = A
<i>Myrsine</i>	0.009	0.012	1.22	0.76	0.083	0.78	U = A
<i>Coprosma</i>	0.005	0.005	1.22	0.22	1.03	0.32	U = A
<i>Ilex</i>	0.004	0.011	3.23	0.42	27.85	0.00003	U > A
Disturbed habitat (<i>n</i> = 23)							
<i>Metrosideros</i>	0.801	0.934	1.12	0.049	6.13	0.021	U > A
<i>Acacia</i>	0.179	0.050	0.24	0.051	217.95	0.00001	U < A
Dead	0.012	0.00	0.0	—	—	—	
<i>Myrsine</i>	0.006	0.006	0.74	0.35	0.56	0.46	U = A
<i>Cheirodendron</i>	0.001	0.00	0.0	—	—	—	
<i>Ilex</i>	0.001	0.010	12.28	2.93	14.86	0.0009	U > A

all $F_{1,43} = 30.81, 32.21, P < 0.001$ at use and random points, respectively. See Table 1 for partitioning of *F*-values). At a fine scale, foliage density was higher in undisturbed habitat at random points, but did not differ at use points. Bark surface did not differ between habitats at use or random points (Table 1). Overall numbers of perches (trunks, large branches, small branches, and twigs) did not differ between habitats at use or random points, and none of the individual size-class comparisons was significant (Table 1, MANOVAs, $F_{4,40} = 1.34, 1.38, P = 0.27, 0.25$ at use and random points, respectively).

DISCUSSION

CRITERIA FOR HABITAT SELECTION

At a broad scale, 'Elepaio did not appear to be selective in their use of their habitat. They did not choose foraging sites based on tree or shrub densities, neither of which differed between random points and use points. Within the broad scale, tree species did affect choice of foraging sites. 'Elepaio preferred to forage in 'Ohia, and preferred not to forage in Koa. These preferences may be related to the physical structure of these tree species and its effect on the foraging techniques required to capture prey in each

TABLE 3. Proportions of height category use (U) and availability (A) in undisturbed and disturbed habitats. Availability (calculated as proportion of overall foliage height profile) and use are averages of proportions from all individuals. Slope is the slope of the regression line, SE is the standard error of the slope, and *t* is student's *t*, which indicates whether the slope is different from one. Slopes > 1 indicate use is greater than availability, *P*-values < 0.05 indicate slopes significantly different from 1.

Height	Avail.	Use	Slope	SE	<i>t</i>	<i>P</i> -value	Conclusion
Undisturbed habitat (<i>n</i> = 22)							
Understory	0.156	0.122	0.83	0.20	0.73	0.40	U = A
Low canopy	0.116	0.079	0.80	0.11	3.45	0.078	U = A
Mid canopy	0.320	0.468	1.50	0.10	23.24	0.00009	U > A
Upper canopy	0.409	0.329	0.85	0.10	2.45	0.13	U = A
Disturbed habitat (<i>n</i> = 23)							
Understory	0.066	0.092	1.34	0.25	1.80	0.19	U = A
Low canopy	0.190	0.138	0.74	0.13	4.20	0.053	U = A
Mid canopy	0.372	0.397	1.08	0.076	1.04	0.32	U = A
Upper canopy	0.374	0.372	1.02	0.088	0.06	0.81	U = A

TABLE 4. Proportions of groundcover category use (U) and availability (A) in undisturbed and disturbed habitats. Availability and use are averages of proportions from all individuals. Slope is the slope of the regression line, SE is the standard error of the slope, and t is student's t , which indicates whether the slope is different from one. Slopes > 1 indicate use is greater than availability, P -values < 0.05 indicate slopes significantly different from 1.

Category	Avail.	Use	Slope	SE	t	P -value	Conclusion
Undisturbed habitat ($n = 22$)							
Native	0.549	0.803	1.34	0.087	15.13	0.0008	U > A
Exotic grass	0.292	0.142	0.49	0.069	54.14	0.00001	U < A
Pig damage	0.122	0.045	0.35	0.040	269.22	0.00001	U < A
Bare	0.036	0.011	0.25	0.10	51.74	0.00001	U < A
Disturbed habitat ($n = 23$)							
Native	0.076	0.143	1.27	0.20	1.78	0.20	U = A
Exotic grass	0.817	0.777	0.94	0.038	2.56	0.12	U = A
Pig damage	0.079	0.060	0.87	0.095	1.86	0.19	U = A
Bare	0.027	0.020	0.28	0.14	27.29	0.00003	U < A

(VanderWerf, unpubl. manuscript). In 'Ohia, 'Elepaio more often attacked prey by perch-gleaning, which is relatively simple and energetically inexpensive. In Koa, they used hanging and flight-gleaning more often, which are more difficult and require more energy.

In other studies, Szaro and Balda (1979) found that timber removal in a ponderosa pine forest affected tree species selection in 13 out of 15 bird species, and Franzreb (1983) found that logging affected tree species and tree height selection in five out of five species. Robinson and Holmes (1984) found that foraging success of some bird species was higher in certain tree species or at certain heights. They hypothesized this was due to differences in foliage structure that made certain maneuvers or search tactics more efficient, and that these in turn affected microhabitat selection. Indeed, I found that 'Elepaio in both undisturbed and disturbed habitats preferred to forage in tree species that allowed them to use easier foraging maneuvers.

At an intermediate scale, 'Elepaio in both habitats foraged at sites with higher than average (random) foliage density, regardless of height. Foliage density indexes in all four height categories of both habitats were higher at use points than at random points, and only one height category in either habitat was used disproportionately. 'Elepaio selected foraging sites based on foliage density, and they used sites at any height as long as they had dense foliage. Others have reported that 'Elepaio foraged at all heights (Perkins 1903, MacCaughy 1919), but Conant (1977) observed them foraging most often in the un-

derstory in a forest of exotic trees. Szaro and Balda (1979) found that use of available foliage at different heights varied considerably among bird species, but that foliage-height use of all species combined closely followed availability.

Groundcover damage by feral pigs is a serious threat to native habitats in Hawaii and is thought to be a major cause of declines in native forest bird populations (Stone and Scott 1985, Scott et al. 1986, Mountainspring 1987). I found that areas in undisturbed habitat with feral pig damage or exotic grasses were not much better than those with bare ground as foraging sites for 'Elepaio since all were underused relative to availability. Furthermore, the isolated patches of native ground cover remaining in disturbed habitat were not significantly favored by 'Elepaio, suggesting that after a certain level of disturbance even native ground cover was not useful for foraging. Birds in disturbed habitat did not prefer any type of ground cover relative to availability and did not seem to use ground cover in selecting foraging sites. This is not surprising since 'Elepaio foraged on the ground very rarely in disturbed habitat, but did so commonly in undisturbed habitat (VanderWerf, unpubl. manuscript). Areas with bare rock and soil were avoided in both habitats, possibly because they often had little or no vegetation of any kind, even above them.

At a fine scale, 'Elepaio in both habitats selected foraging sites with higher than average foliage density and bark surface area. These sites may have been preferred because their denser structure facilitated searching for and capturing prey (VanderWerf, unpubl. manuscript), because

they harbored more prey, or because they provided 'Elepaio with more cover from predators (Lima 1985). Numbers of large branches, small branches, and twigs appeared to be criteria for choosing foraging sites, but number of trunks was less important. The relative importance of these size classes as selection criteria reflect the frequency with which 'Elepaio used them as foraging substrates. Twigs and small branches were used very often, large branches were used less often, and trunks were used infrequently (VanderWerf, unpubl. manuscript).

SCALE OF HABITAT SELECTION

'Elepaio exhibited varying degrees of selectivity and used different sets of selection criteria at different spatial scales. Information from these habitat parameters that appear to serve as selection criteria may be relied on to a greater or lesser extent in making choices about foraging sites. At a fine scale, 'Elepaio chose a location from which to make a single foraging attempt based on information such as density of foliage to be searched and numbers and sizes of available perches. At an intermediate scale, the area chosen provided foraging opportunities not only for the present search, but also the next one or several searches. Height was unimportant, as long as the site had dense foliage. Finally, areas chosen at a broader scale presumably provide foraging success over a large number of foraging movements. 'Elepaio chose to forage in tree species that allowed greater efficiency, but did not appear to exhibit selectivity based on tree or shrub density and used all areas equally at this level. In a similar study of hierarchical nest site selection in Western Kingbirds, Bergin (1992) also found differential selectivity and criteria at different spatial scales. Moreover, the scales at which 'Elepaio showed selectivity of foraging sites were smaller than those at which kingbirds showed selectivity of nest sites, perhaps indicating that information used to make choices about foraging sites is perceived, or acted upon, at a finer level than that used to select territories or nest trees.

COMPARISON OF SELECTION BETWEEN HABITATS

To determine if 'Elepaio were restricted in their use of disturbed areas, I compared patterns of selection between habitats. At a fine scale, 'Elepaio preferred sites with higher than average foliage density in both habitats, but they were more

selective, or "hyperselective," toward high-density sites in disturbed habitat. Foliage density at random points was lower in disturbed habitat, but foliage density at use points did not differ between habitats. In effect, the greater selectivity in disturbed habitat compensated for the lower average foliage density available, resulting in equal densities at use points.

Although intermediate scale patterns of foliage density use differed among height categories, similar patterns occurred at random points, indicating 'Elepaio were using foliage at each height in proportion to its availability. The apparent differences in use of height categories between habitats simply reflected corresponding differences at random points. Variation in distribution of foliage among height strata at random points was caused by differences in tree crown shape. Crowns tended to be dome shaped in disturbed habitat, while foliage was concentrated in the upper canopy in undisturbed habitat (Table 3).

At a broad scale, 'Elepaio did not select foraging sites based on tree or shrub densities, and tree and shrub densities at both random and use points were lower in disturbed habitat. Thus, lower broad scale tree and shrub densities meant birds in disturbed habitat had to move farther or more often to find sites with high fine scale density.

CONCLUSIONS

'Elepaio select foraging sites based on a variety of habitat variables, including tree species, foliage density, bark surface area, numbers of perches, and, in undisturbed habitat, ground cover. They either do not respond to broad scale tree and shrub densities or cannot afford to select only certain areas and must use their entire territory. The diversity of criteria used by 'Elepaio may reflect their ability to use a wide variety of foraging maneuvers and substrates (VanderWerf, unpubl. manuscript).

Foraging site preferences within habitats were apparent at both fine and intermediate scales, but differences in patterns of selection between habitats occurred only at a fine scale, between areas only 0.75 m in radius. Moreover, the broad scale, which encompassed an area similar to that recommended as a standard size for measuring avian habitats (0.04 ha circles with a radius of 11.3 m, James and Shugart 1970, Noon 1981), did not detect patterns of foraging site selection. Such a scale is appropriate for describing habitat

around nest sites and song perches (Bergin 1992, Sedgwick and Knopf 1992), but a finer scale may be necessary to determine foraging site preferences, particularly for forest birds.

'Elepaio appear to be somewhat limited in their use of disturbed habitat at Hakalau Forest N.W.R. in the sense that they must be more selective in order to forage in preferred high-density sites and may have to move farther or more often to do so. However, disturbance like that at the Hakalau site obviously does not prevent them from using an area. Instead, limitation might be manifested in other forms, such as larger territory sizes, lower population density, or differences in time and energy budgets in disturbed habitat. Preliminary evidence indicates population density is lower in disturbed habitat (VanderWerf, unpubl. data), but measurement of territory size would provide more rigorous support.

ACKNOWLEDGMENTS

I thank Dick Wass, refuge manager, for permission to work at Hakalau Forest National Wildlife Refuge and Bill Andrade for access to adjacent areas of Pua Akala ranch. Leonard Freed generously allowed me to use University of Hawaii facilities at the study site, and I thank him for his hospitality. Jack Jeffrey and Jaan Lepson helped me identify plants. I thank my committee members, Peter Feinsinger, Carmine Lanciani, and especially my advisor, Doug Levey, who provided many helpful comments and criticisms at various stages of the work. Scot Fretz and two anonymous reviewers commented on the manuscript and provided several insights. This study was supported by a Grinter Graduate Fellowship from the University of Florida.

LITERATURE CITED

- BERGER, A. J. 1981. Hawaiian birdlife, second edition. University of Hawaii Press, Honolulu, HI.
- BERGIN, T. M. 1992. Habitat selection by the Western Kingbird in western Nebraska: a hierarchical analysis. *Condor* 94:903-911.
- BROWN, J. H. 1984. On the relationships between abundance and distribution of species. *Am. Nat.* 124:255-279.
- CODY, M. L. [ED.]. 1985. *Habitat selection in birds*. Academic Press, New York.
- CONANT, S. 1977. The breeding biology of the Oahu 'Elepaio. *Wilson Bull.* 89:193-210.
- COTTAM, G., AND J. T. CURTIS. 1956. The use of distance measures in phytological sampling. *Ecology* 37:451-460.
- DODGE, K. M., R. C. WHITMORE, AND E. J. HARNER. 1990. Analyzing foraging use versus availability using regression techniques, p. 318-324. *In* M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. [eds.], *Avian foraging: theory, methodology, and applications*. *Stud. Avian Biol.* No. 13.
- FRANZREB, K. E. 1983. A comparison of avian foraging behavior in unlogged and logged mixed-coniferous forest. *Wilson Bull.* 95:60-76.
- HILDÉN, O. 1965. Habitat selection in birds. *Ann. Zool. Fenn.* 2:53-75.
- HOLMES, R. T. 1981. Theoretical aspects of habitat uses by birds, p. 33-37. *In* D. E. Capen [ed.], *The use of multivariate statistics in studies of wildlife habitat*. U.S.D.A. Forest Service General Technical Report RM-87.
- HOLMES, R. T., AND J. C. SCHULTZ. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. *Can. J. Zool.* 66:720-728.
- JAMES, F. C., AND H. H. SHUGART. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- KIRCH, P. V. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. *Pac. Sci.* 36:1-14.
- KIRCH, P. V. 1983. Man's role in modifying tropical and subtropical polynesian ecosystems. *Archaeol. Oceania* 13:26-31.
- KOLASA, J., AND S.T.A. PICKETT. 1991. *Ecological heterogeneity*. Springer-Verlag, New York.
- KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.
- LIMA, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a tradeoff in the Black-capped Chickadee. *Oecologia* 66:60-67.
- MACCAUGHEY, V. 1919. The Hawaiian Elepaio. *Auk* 36:22-35.
- MARTIN, T. E. 1986. Competition in breeding birds: on the importance of considering processes at the level of the individual. *Current Ornithology* 4:181-210.
- MAURER, B. A. 1985. Avian community dynamics in desert grassland: observational scale and hierarchical structure. *Ecol. Monogr.* 55:295-312.
- MORRIS, D. 1987. Ecological scale and habitat use. *Ecology* 68:362-369.
- MOSER, E. B., W. C. BARROW, JR., AND R. B. HAMILTON. 1990. An exploratory use of correspondence analysis to study relationships between avian foraging behavior and habitat, p. 309-317. *In* M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. [eds.], *Avian foraging: theory, methodology, and applications*. *Stud. Avian Biol.* No. 13.
- MOUNTAINSPRING, S. R. 1987. Ecology, behavior, and conservation of the Maui Parrotbill. *Condor* 89:24-39.
- MUNRO, G. C. 1960. *Birds of Hawaii*. Tuttle, Rutland, VT.
- NOON, B. R. 1981. Techniques for sampling avian habitats, p. 42-52. *In* D. E. Capen [ed.], *The use of multivariate statistics in studies of wildlife habitat*. U.S.D.A. Forest Service General Technical Report RM-87.
- OLSON, S. L., AND H. F. JAMES. 1984. The role of polynesians in the extinction of the avifauna of the Hawaiian Islands, p. 768-780. *In* P. S. Martin

- and R. G. Klein [eds.], Quaternary extinctions. Univ. of Arizona Press, Tucson, AZ.
- ORIAN, G., AND J. WITTENBERGER. 1991. Spatial and temporal scales and habitat selection. *Am. Nat.* 137(S):S29-S49.
- PERKINS, R.C.L. 1903. *Vertebrata (Aves)*, p. 368-465. In D. Sharp [ed.], *Fauna hawaiiensis*. Cambridge Univ. Press, Cambridge, England.
- PRATT, H. D. 1980. Intra-island variation in the 'Elepaio on the island of Hawai'i. *Condor* 82:449-458.
- REMSEN, J. V., JR. 1985. Community organization and ecology of birds of high elevation humid forest of the Bolivian Andes. *Ornithol. Monogr.* 36:733-756.
- ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918-1931.
- ROBINSON, S. K., AND R. T. HOLMES. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk* 101:672-684.
- ROTENBERRY, J. T. 1981. Why measure bird habitat?, p. 29-32. In D. E. Capen [ed.], *The use of multivariate statistics in studies of wildlife habitat*. U.S.D.A. Forest Service General Technical Report RM-87.
- SAKAI, H. F. 1988. Avian response to mechanical clearing of a native rainforest in Hawaii. *Condor* 90:339-348.
- SCOTT, J. M., S. MOUNTAINSPRING, F. L. RAMSEY, AND C. B. KEPLER. 1986. Forest bird communities of the Hawaiian islands: their dynamics, ecology, and conservation. *Stud. Avian Biol.* No. 9.
- SEDGWICK, J. A., AND F. L. KNOPF. 1992. Describing Willow Flycatcher habitats: scale perspectives and gender differences. *Condor* 94:720-733.
- SHERRY, T. W., AND R. T. HOLMES. 1985. Dispersion patterns and habitat responses of birds in northern hardwood forests, p. 283-309. In M. L. Cody [ed.], *Habitat selection in birds*. Academic Press, New York.
- STONE, C. P., AND J. M. SCOTT. 1985. Hawaii's terrestrial ecosystems: preservation and management. Cooperative National Park Resources Studies Unit and University of Hawaii, Honolulu, HI.
- SZARO, R. C., AND R. P. BALDA. 1979. Bird community dynamics in a ponderosa pine forest. *Stud. Avian Biol.* No. 3.
- WIENS, J. A., AND J. T. ROTENBERRY. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds, p. 154-172. In J. Diamond and T. J. Case [eds.], *Community ecology*. Harper & Row, New York.
- WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1987a. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* 48:132-147.
- WIENS, J. A., B. VAN HORNE, AND J. T. ROTENBERRY. 1987b. Temporal and spatial variations in the behavior of shrubsteppe birds. *Oecologia* 73:60-70.