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INTRASPECIFIC VARIATION IN ELEPAIO FORAGING BEHAVIOR IN HAWAIIAN FORESTS OF DIFFERENT STRUCTURE

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ABSTRACT.—I studied intraspecific variation in foraging behavior of an endemic, insectivorous bird, the Elepaio (*Chasiempis sandwichensis*), in two Hawaiian forests that differed in degree of human modification. The undisturbed forest had a closed canopy, a dense understory, and a groundcover of native plants. The disturbed forest had much lower tree and shrub densities, and a ground cover of alien grasses. Search-and-attack rates, proportions of attack maneuvers, and proportional substrate use differed between habitats. Birds in disturbed habitat attacked prey two-thirds as often as birds in undisturbed habitat, hopped less frequently, and flew farther and more often. They also did less perch-gleaning and chasing, did more flight-gleaning and hawking, used small branches and the ground less often, and used leaves and the air more often than birds in undisturbed habitat. Disturbed areas may be lower-quality foraging habitat because they require more difficult foraging methods. Age was associated with variation in search-and-attack rates and proportions of attack maneuvers, but sex was not. Subadult Elepaio attacked prey less often than adults, searched more slowly, and used simpler maneuvers more often, possibly to compensate for their lower proficiency. Log-linear analysis showed that attack maneuver was related to substrate and to tree species. Birds perch-gleaned more often on twigs and in ohia (*Metrosideros polymorpha*), hung more often on bark and in koa (*Acacia koa*), and flight-gleaned more often on leaves. Elepaio showed much flexibility in foraging behavior and used more-diverse attack maneuvers and substrates than related continental species, which may allow Elepaio to exploit disturbed habitats successfully. *Received 2 August 1993, accepted 11 January 1994.*

STUDIES OF AVIAN foraging behavior traditionally have focused on niche partitioning and community structure and, hence, have emphasized differences among species (e.g. MacArthur 1958, Holmes et al. 1979, Szaro and Balda 1979, Wiens and Rotenberry 1981, Alatalo 1982). Species may be separated by one or more of several niche components, including plant species, substrate, height, horizontal position, foraging technique, and foraging speed (reviewed in Airola and Barrett 1985, Martin 1986, Schoener 1986).

This emphasis on interspecific variation often obscured differences in foraging within a species (but see, for example, Partridge 1976, Holmes et al. 1978, Gustafsson 1988). Moreover, models of community structure based on niche partitioning and species overlap assume that all individuals of a species forage identically, which may not be valid (Martin 1986, Grubb and Woodrey 1990, Martin and Karr 1990). Recognition of the importance of intraspecific variation has led to the discovery that foraging by an individual bird is influenced by numerous biotic and abiotic factors: age (reviewed in Wunderle 1991); sex (Selander 1966, Peters and Grubb 1983, Petit et al. 1990); morphology (Fitzpatrick 1985, Sherry 1985, Gustafsson 1988, Moermond 1990); intraspecific dominance (Hogstad 1988, Grubb and Woodrey 1990); habitat structure (Maurer and Whitmore 1981, Robinson and Holmes 1982, Sabo and Holmes 1983); food distribution and abundance (Holmes and Schultz 1988); season and stage of breeding cycle (Robinson 1986, Hejl and Verner 1990, Sakai and Noon 1990); weather (Grubb 1978); and time of day (Verbeek 1972).

Most studies of intraspecific variation in avian foraging have concentrated on one or two of the above factors, but a foraging bird responds simultaneously to a complex and dynamic set of stimuli. Ideally, one should examine all factors and their interactions at once, but this is difficult and often impractical (Grubb

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1979). A reasonable compromise is to examine a subset consisting of several factors that may interact. For insectivorous forest birds, habitat structure is perhaps the most important determinant of foraging behavior (Robinson and Holmes 1982), and several habitat variables constitute such a subset of related factors.

Habitat structure affects the abundance, distribution, and perceptibility of prey, and also which search-and-attack methods birds can employ to capture prey (Fitzpatrick 1980, Robinson and Holmes 1982, Holmes and Schultz 1988). Aspects of habitat structure known to affect foraging of insectivorous forest birds include: plant species (Holmes and Robinson 1981, Franzreb 1983, Morrison et al. 1985); substrate (Jackson 1979, Fitzpatrick 1980, Greenberg and Gradwohl 1980); structural characteristics of vegetation (Robinson and Holmes 1984, Whelan 1989); and foliage density (Maurer and Whitmore 1981, Sabo and Holmes 1983). Valuable insights on the effect of habitat structure on foraging patterns may be gained by comparing the behavior of a single species in two habitats that differ in structure (Robinson and Holmes 1982). Understanding effects of habitat structure on foraging may be particularly useful in the conservation of species with restricted habitat or specialized habitat requirements and in making management decisions that will alter habitat structure.

In Hawaii, human alteration of native habitats by physical disturbance, introduction of alien species, and loss of native species diversity has been extensive (Kirch 1983, Stone and Scott 1985, Cuddihy and Stone 1990). Native Hawaiian birds appear to be especially sensitive to disturbance (Olson and James 1984, Sakai 1988), and many species have restricted ranges or are less abundant in disturbed areas (Scott et al. 1986). The Elepaio (*Chasiempis sandwichensis*) is an insectivorous bird endemic to the Hawaiian Islands that inhabits forests of varying structure and degree of human modification.

The goals of my study were to: (1) compare foraging methods used by Elepaio in undisturbed and human-modified forests to understand how they forage and whether human disturbance affects their ability to exploit a habitat; (2) investigate diversity and degree of intraspecific variation in Elepaio foraging behavior; (3) simultaneously examine effects of several habitat variables on foraging to evaluate possible interactions between factors.

METHODS

Study site.—I conducted work from February through July 1991 at Hakalau Forest National Wildlife Refuge on the island of Hawaii. The site lies at approximately 1,900 m elevation on the east side of Mauna Kea and is characterized by sloping terrain, heavy rainfall (3 m/year), and daytime temperatures rarely above 20°C. The natural vegetation type is montane rain forest. For a detailed description of the region, see Scott et al. (1986).

Although the site is now protected, parts of the forest have been extensively modified by human activities during the last 100 years. Timber was harvested in some areas and large tracts were cleared for cattle ranching, resulting in a patchwork of highly disturbed and relatively undisturbed forest. The boundary between these habitats is not sharp, and even the "undisturbed" forest has been somewhat modified by the same activities. The undisturbed habitat consisted of closed-canopy forest with a moderately dense understory and a ground cover primarily of native forbs and ferns. The disturbed habitat was a shorter, open-canopy woodland with almost no understory and a ground cover of alien grasses introduced for cattle grazing.

I selected three plots totaling 11.4 ha in undisturbed habitat and three totaling 10.6 ha in disturbed habitat that represented extremes of the continuum from undisturbed to disturbed. I chose plots in both habitats that were as close to each other as possible and at similar elevations (within 100 m) without including areas that were intermediate in structure.

Study species.—The Elepaio is placed in a monotypic genus endemic to the Hawaiian Islands; its closest relatives are the monarchine flycatchers of Australasia and Oceania (Boles 1979, Pratt et al. 1987, Sibley and Ahlquist 1990). Elepaio are common permanent residents of both habitats at the study site, although population density is higher in undisturbed habitat (unpubl. data). They are monogamous and nonmigratory, remaining paired and territorial throughout the year (MacCaughey 1919, Conant 1977, Berger 1981). Elepaio are insectivorous (Munro 1960, Conant 1977, VanderWerf unpubl. data), although nectarivory has been reported (MacCaughey 1919).

I was able to sex and age Elepaio by plumage differences (MacCaughey 1919, Pratt 1980). Males have black throat feathers narrowly tipped with white, whereas females have broader white tips that often make the throat appear almost completely white. Subadult birds of both sexes retain a uniformly drab gray-brown plumage for at least one year. All subadult Elepaio I observed were second-year birds and were no longer being fed by adults.

I used four methods to identify 48 individual Elepaio in the study plots: a unique combination of colored leg bands ($n = 17$); distinctive plumage ($n = 5$); being paired with a color-banded or distinctivelyplumaged bird ($n = 10$); and known territory boundaries ($n = 16$). Based on observations of banded birds, it was unusual to find a bird in a territory that was not its own, and such an occurrence quickly provoked an attack by the territory owner. If I observed a bird at a territory boundary or if I was unsure whether a bird was the territory owner, I followed the bird until I could conclusively determine its identity. I compiled data separately for each individual.

Data collection.—For characterization of habitats, I used a stratified random design to select 15 points in plots of each habitat and used the method of James and Shugart (1970) as modified by Noon (1981) to quantify differences in habitat structure. This method is based on 0.04-ha circles in which the species and diameter of all trees are recorded, and maximum canopy height is estimated. Shrub density, percent of groundcover in specified categories, and foliage density at various heights are measured at 2-m intervals along north-south and east-west diameters.

To evaluate foraging in Elepaio, I collected data from March through July 1991 by regularly traversing study plots and searching for birds. I followed each bird for as long as possible, recording the following information during each observation sequence: age, sex, and individual identity of bird, hops, flights, distances flown, prey-attacking maneuvers, substrates of attacks, tree species, height, and duration of sequence. I recorded data on a portable cassette recorder and transcribed them later while using a stopwatch. Most sequences were less than 1 min long, but a few were over 2 min.

I employed five variables to evaluate rates at which Elepaio searched for and attacked prey. Hop, flight, and attack intervals were the average times between hops, flights, and attacks, respectively. Flight distance was the average length of flights between perches. Attack radius was the average distance flown during attack maneuvers that involved flying. I usually could not determine if an attack was successful, so attack rate refers only to the rate at which prey was attacked, not captured.

Elepaio used attack maneuvers that I classified into five mutually exclusive categories defined below, with equivalent terms from other authors. Perch-glean included all maneuvers in which prey were taken from a solid substrate while perched. This is equivalent to "glean" (Eckhardt 1979, Robinson and Holmes 1982), "pluck" (Emlen 1977, Mountainspring 1987), and "pick" (Remsen 1985); it includes both "simple perching" and "landing and perching" (Fitzpatrick 1980). Hang occurred when a bird clung upside-down by its feet to examine a substrate that could not be reached while perching. Flight-glean I defined as taking prey from a solid substrate while flying. I did not distinguish whether the maneuver was directed outward or upward from a perch, if the prey was on the upper or lower leaf surface, or if the bird hovered while flying. Therefore, this includes "upward" and "outward hover-glean" and "strike" (Fitzpatrick 1980), "hover," and "snatch" (Robinson and Holmes 1982, Recher et al. 1985, Sherry 1985). Hawk indicates that a bird flew out from a perch to capture prey that was in the air. This is synonymous with "sally" (Eckhardt 1979), "aerial hawk" (Fitzpatrick 1980), and "flycatch" (Maurer and Whitmore 1981). Chase occurred when a bird chased prey that had been flushed, often in a downward flight. Other terms used for this maneuver include "flush-chase" (Robinson and Holmes 1982), "pursue" (Sherry 1985), "tumble" (Root 1967), "flutter-chase" and "flush-pursue" (Remsen and Robinson 1990).

Attack maneuvers were directed at a variety of substrates that I classified into seven categories: ground, trunk (including branches >20 cm in diameter), large branch (>5–20 cm), small branch (1–5 cm), twig (<1 cm), leaf, and air.

Analyses.—For continuous variables, including search-and-attack rates, proportions of attack maneuvers, and proportional substrate use, I calculated average values for each individual from all sequences combined, and used individuals as independent data points. Another commonly used method is to calculate rates for each sequence and average values from all sequences (e.g. Robinson and Holmes 1982). The method I used provides information on variability at the individual level and is not biased by short observation sequences, but does not allow examination of temporal variation.

In the strict sense, treating individuals sampled at the same site as independent is a form of pseudoreplication (Hurlbert 1984). However, for a territorial species in a heterogeneous environment, one would not expect all individuals to forage in the same way because they have access to different sets of resources (Dodge et al. 1990). If the species is behaviorally plastic, individuals may respond differently. The alternative of lumping observations from all individuals at a site may be more statistically justifiable, but may cause serious loss of biological information. Viewed from another perspective, I tested differences in the way Elepaio forage in different territories in two habitats.

I performed six multivariate analyses of variance (MANOVA; Sokal and Rohlf 1981), one each with search-and-attack-rate variables, proportions of attack maneuvers, or proportional substrate use as dependent variables, and habitat with either sex or age as independent variables. I analyzed variation associated with sex separately from age because subadult birds could not be sexed. Values presented for habitat are those from analyses with age, not sex, because sample sizes for analyses with sex were smaller. I required at least 20 attack maneuvers and 300 s of observation per individual for inclusion in analyses (see Dodge et al. 1990, Martin and Karr 1990).

In studies of proportions of attack maneuvers and foraging substrates, authors disagree whether it is

TABLE 1. Contingency table of Elepaio foraging observations classified by habitat, tree species, substrate, and attack maneuver. Cells containing a dash are impossible classifications that were treated as structural zeros (see Methods).

		Maneuver			
Tree species	Substrate	Perch-glean	Flight-glean	Hang	Aerial
	Undisturbed habitat				
Ohia	Bark	28	3	19	—
	Twig	118	25	19	—
	Leaf	19	21	1	—
	Ground	—	—	—	—
	Air	—	—	—	22
Koa	Bark	5	0	4	—
	Twig	4	2	1	—
	Leaf	0	2	0	—
	Ground	—	—	—	—
	Air	—	—	—	1
Other	Bark	4	0	0	—
	Twig	15	6	0	—
	Leaf	2	7	0	—
	Ground	10	0	—	—
	Air	—	—	—	1
	Disturbed habitat				
Ohia	Bark	16	8	11	—
	Twig	85	73	17	—
	Leaf	18	58	0	—
	Ground	—	—	—	—
	Air	—	—	—	38
Koa	Bark	0	1	2	—
	Twig	5	0	2	—
	Leaf	0	4	0	—
	Ground	—	—	—	—
	Air	—	—	—	2
Other	Bark	3	2	0	—
	Twig	4	1	0	—
	Leaf	0	0	0	—
	Ground	2	0	—	—
	Air	—	—	—	1

better to use all observations in a sequence or only the initial observation or a certain subset of each sequence. Using sequential observations allows faster data collection and more information can be gathered from each bird, which may be important for species that are rare or hard to locate (Morrison 1984, Recher and Gebski 1990). Nevertheless, sequential observations may not be independent and, thus, may violate assumptions of many statistical tests (Morrison 1984, Bell et al. 1990, Hejl et al. 1990). Alternatively, initial observations may be biased toward conspicuous maneuvers, particularly for birds foraging in dense foliage where observation sequences typically are short (Holmes et al. 1979, Bradley 1985). To avoid oversampling from a few individuals, some authors recommend truncating sequential observations after either a certain length of time (e.g. Wagner 1981, Morrison 1984) or a specified number of observations (e.g. Peters and Grubb 1983, Martin and Karr 1990). I used all observations in a sequence because Elepaio often were difficult to locate in dense foliage and because I wanted information about search-and-attack rates, which may be biased if only one observation is used (Fitzpatrick 1980).

I calculated diversity of foraging maneuvers and substrates using the Shannon-Weaver index,

$$H' = -SP_i(\log P_i), \tag{1}$$

where P_i is the proportional use of category i (Shannon and Weaver 1949). To facilitate comparison of diversity indexes with studies that used different categories or natural logarithms, I lumped categories not recognized by other authors or by me and scaled diversity as the equitability index,

$$J' = H'/H'_{\max}, \tag{2}$$

where $H'_{\max}$ is the case where use of all categories is equal (Pielou 1966).

I investigated interaction of categorical variables using log-linear analysis of a multidimensional contingency table (Fienberg 1981). This type of analysis is advantageous because it allows simultaneous examination of all interactions between categorical variables (Schoener 1970). In log-linear analyses, observations must be independent because the purpose is to look for dependency among variables. Therefore, I used only the initial observation from each sequence. I cross-classified each of 691 foraging observations using four categorical variables; habitat, attack maneuver, substrate, and tree species. In practice, it was necessary to collapse the data by combining some categories to reduce the number of empty or sparse cells, and because a larger number of categories resulted in fewer degrees of freedom, making it impossible to evaluate models with many parameters. I combined "hawk" and "chase" as "aerial" maneuvers, and all but the two most common tree species as "other." I lumped "trunk" and "large branch" substrates as "bark" and grouped "small branch" with "twig." The latter two lumpings probably did not cause loss of information because substrate interacted only with maneuver in the final model and these pairs of substrate categories may have similar effects on maneuver (Bishop 1971). The results was a 2 × 3 × 4 × 5 contingency table (Table 1).

Table 1 is "incomplete" because some cross-classifications are not possible (Fienberg 1972). For example, "aerial" could never be classified with "leaf" because by definition "aerial" is directed at "air." I treated cells representing impossible classifications as structural zeroes. Expected cell frequencies are not calculated for structural zeroes. They do not contribute to goodness-of-fit statistics, and degrees of freedom are decremented by one for each (Fienberg 1972).

The objective of multidimensional contingency-table analysis is to find the simplest model that adequately explains the data. I determined if a model was adequate with a goodness-of-fit test based on the *G*-statistic (Sokal and Rohlf 1981). I found expected cell frequencies using an iterative fitting algorithm (Fienberg 1970) calculated with SYSTAT (Wilkinson 1987). I rejected any model where the probability of fit was less than 0.05. To find the simplest adequate model, I used a stepwise procedure outlined by Goodman (1971). I started by evaluating models that contained all interactions of a given order of complexity (full models). The final model could be reached by forward or backward selection from a full model; I tried both methods. Forward selection started with the highest-order full model that did not fit the data and involved adding the most-significant terms of the next-highest order that did not cause the overall significance to be lower than 0.05. Backward selection involved deleting the least-significant terms from the lowest-order full model that did fit the data. I calculated significance of a term using a conditional log-likelihood ratio test (Fienberg 1981). Any term whose conditional log-likelihood ratio had a probability of less than 0.05 was a significant component of the model. The final model was reached when no terms could be added or deleted.

I used the following notation to refer to variables used in models: (H) habitat; (M) maneuver; (S) substrate; and (T) tree species. Interactions between variables were represented by terms with symbols for each variable (e.g. HM represents an interaction between H and M). Higher-order interactions implicitly contained all lower-order interactions that were combinations of the same variables (e.g. HMS includes HM, HS, MS, H, M, and S).

RESULTS

Habitat quantification.—Ohia (*Metrosideros polymorpha*) was the dominant tree species in each habitat (79.5% of total basal area in undisturbed habitat, 74.3% in disturbed), and koa (*Acacia koa*) was also common (15.0% in undisturbed, 25.2% in disturbed). Other trees were sparsely distributed and were more common in undisturbed habitat: kolea (*Myrsine lessertiana;* 2.1 vs. 0.4%), olapa (*Cheirodendron trigynum;* 0.4 vs. < 0.1%), kawau (*Ilex anomola;* 0.5 vs. < 0.1%), pilo (*Coprosma* sp.; 0.2 vs. <0.1%), and standing dead trees of all species (2.2 vs. 0.1%). Common understory plants in both habitats included akala (*Rubus sandwicensis*), ohelo (*Vaccinium calycinum*), pukiawe (*Styphelia tameiameiae*), blackberry (*Rubus argutus*), and saplings of tree species listed above. Tree and shrub densities were higher in undisturbed habitat (868 vs. 198 trees/ha, and 1,633 vs.150 shrubs/ha). Canopy height was higher in undisturbed habitat (18.1 vs. 13.6 m), foliage density was higher in all height categories, and tree crown shape differed between habitats (Fig. 1). Trees in undisturbed habitat had foliage concentrated toward their tops, whereas trees in disturbed habitat had rounded crowns with more foliage distributed toward their middle. Ground cover in the undisturbed habitat was primarily native forbs and ferns (65%), with small patches of exotic grasses (14%), particularly Kikuyu grass (*Pennisetum clandestinum*), velvet grass (*Holcus lanatus*), meadow ricegrass (*Microlaena stipoides*), and sweet vernalgrass (*Anthoxanthum odoratum*). In disturbed habitat, these exotic grasses were much more common than native forbs (87 vs. 7.7%). Both habitats also suffered ground-cover damage by feral pigs and had areas of bare rock or soil without groundcover.

Variation in foraging associated with habitat, age, and sex.—Habitat was a significant factor in explaining variation in search-and-attack rates (MANOVA, $n = 46$, $F_{5,39} = 25.14$, $P < 0.0001$). Four of five search-and-attack variables differed between habitats (Table 2). On average, birds in disturbed habitat hopped less frequently, flew farther and more frequently, and attacked prey two-thirds as often as birds in undisturbed habitat. Only the attack radius was the same in both habitats. Age also was an overall factor in determining search-and-attack rates (MANOVA, $n = 46$, $F_{5,39} = 3.68$, $P < 0.005$), but only two variables differed between birds of the two age categories (Table 2). Subadult birds hopped less frequently and attacked prey 25% less often than did adults.

Habitat and age also were significant factors in explaining overall variation in proportion of attack maneuvers (MANOVA, $n = 46$, $F_{5,39} =$ 25.80 and 2.87, $P < 0.001$ and 0.02, respectively). In comparisons of individual attack maneuvers, birds in disturbed habitat did less perch-gleaning and chasing, and more flight-gleaning and hawking. Subadult birds did more perch-gleaning, and less hanging and hawking (Table 2).

Habitat was a significant predictor of substrate use, but age was not, although the significance levels of these factors were not that different (MANOVA, $n = 46$, $F_{7,37} = 2.37$ and 2.11, $P = 0.04$ and 0.06, respectively). Small branches and the ground were used more in undisturbed habitat, while leaves and the air were used more in disturbed habitat. Only leaf use differed between ages, with subadults using them more often (Table 2).

Sex did not have a significant overall effect on search-and-attack rates (MANOVA, $n = 42$, $F_{5,35} = 1.99$, $P = 0.10$), proportions of attack maneuvers ($n = 41$, $F_{5,34} = 1.13$, $P = 0.36$), or proportional substrate use ($n = 41$, $F_{7,32} = 1.97$, $P = 0.09$). Only 3 of 17 foraging variables differed between sexes (Table 2). Males flew less often, hung more often, and used large branches more often than females.

Diversity of foraging behavior and individual variation.—Diversity of attack maneuvers for the species as a whole measured as H'/H'_{max} was 0.86, and diversity of substrate use for the species was 0.67. There was considerable individual variation in proportions of attack maneuvers and substrates used, and their relative proportions varied among individuals, even within a habitat (Figs. 2 and 3). Diversity of attack maneuvers for individual birds measured as H'/H'_{max} ranged from 0.48 to 0.98 ($\bar{x} = 0.77 \pm$ SD of 0.12) and was greater in disturbed habitat ($n = 46$, $t = 2.04$, $P = 0.048$). Diversity of substrate use for individual birds ranged from 0.29 to 0.91 ($\bar{x} = 0.57 \pm 0.14$) and did not differ between habitats ($n = 46$, $t = 1.39$, $P = 0.11$). Differences in proportions of attack maneuvers between habitats found in previous analyses were corroborated by data from two birds for which I had sufficient observations in both habitats (Fig. 2; WABG and GAWB). In both individuals perch-gleaning was the most common maneuver in undisturbed habitat, and flight-gleaning the most common in disturbed habitat. Both birds also chased in undisturbed habitat but did not hawk, and hawked but did not chase in disturbed habitat.

Interaction of categorical variables using log-linear analysis.—HM + HT + MS + MT was the simplest model that adequately explained the observed data (Table 3). The full second-order model did not quite fit the data, so forward selection started with the full second-order model. Backward selection was not possible because the full third-order model contained so many parameters that degrees of freedom fell to zero. There were significant interactions between each pair of variables in the final model, and no third-order interactions were necessary to explain the data.

I interpret the model in the following way: The presence of the HM term indicates that attack maneuver depended on habitat, as found in the previous analysis. The HT term indicates tree-species use was related to habitat, primarily because "other" trees were used almost four times more often in undisturbed habitat (13.0 vs. 3.7%; Table 1). This is not surprising since species other than ohia and koa were rare in disturbed habitat. The interaction of maneuver and substrate (MS) indicates an association of certain maneuvers with particular substrates. Specifically, birds on bark were more likely to perch-glean (53%) or hang (34%) than flight-glean (13%). While on twigs, birds were more likely to perch-glean (61%) than flight-glean (10%). Conversely, flight-gleaning was more common than perch-gleaning on leaves (70 vs. 30%). Certain maneuvers were also used more frequently on different tree species (MT). Perch-glean was used more on ohia (47%) than on koa (40%), and hang was more common on koa (26%) than on ohia (11%).

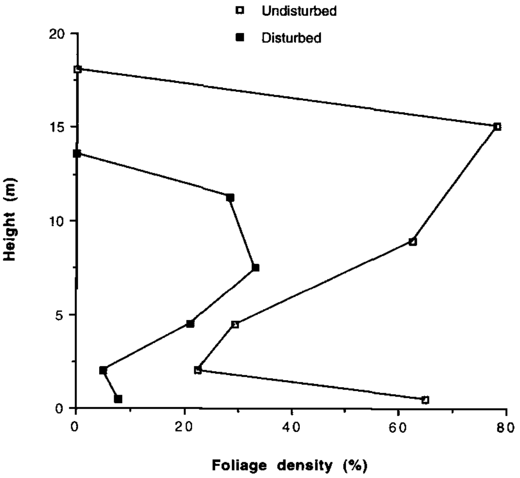

Fig. 1. Foliage-height profile showing percent area in each height category covered by leaves in each habitat.

DISCUSSION

Effects of habitat.—Elepaio in disturbed habitat attacked prey only two-thirds as often as those in undisturbed habitat, suggesting that prey are less abundant in disturbed habitat, harder to search for and detect, or both. Data from Peck (1993) indicate that arthropod biomass per dry mass of vegetation actually is higher in disturbed habitat. Search patterns of Elepaio suggest that the second explanation is true. Birds in disturbed habitat flew farther and more often while searching for prey, which presumably re-

TABLE 2. Analyses of variation in search-and-attack rates, proportions of attack maneuvers, and proportions of substrates used between habitats, ages, and sexes. Sex analyzed separately from age because subadult birds were not sexable. Values for habitat are from analyses with age because sample sizes were larger. Values are $\bar{x} \pm$ SD based on all individuals in given group. See text for overall *F*- and *P*-statistics.

	Habitat			Age			Sex		
Variable	Undisturbed	Disturbed	*F*	Adult	Subadult	*F*	Male	Female	*F*
				Search-and-attack rate					
n	22	24		42	4		23	19	
Hop interval (s)	4.23 ± 0.43	4.60 ± 0.76	4.49*	4.36 ± 0.47	5.05 ± 1.60	4.87*	4.35 ± 0.49	4.37 ± 0.47	0.003
Flight interval (s)	14.11 ± 1.75	11.81 ± 1.82	18.07**	12.93 ± 2.15	12.94 ± 1.90	0.001	13.62 ± 2.09	12.14 ± 1.99	6.82*
Flight distance (m)	0.56 ± 0.09	0.77 ± 0.11	49.48**	0.67 ± 0.14	0.64 ± 0.19	0.28	0.65 ± 0.13	0.70 ± 0.16	1.70
Attack interval (s)	22.72 ± 4.66	34.28 ± 5.99	61.81**	28.12 ± 7.85	35.34 ± 5.81	8.19**	27.43 ± 7.95	28.96 ± 7.86	0.05
Attack radius (m)	0.42 ± 0.10	0.45 ± 0.16	0.71	0.43 ± 0.11	0.41 ± 0.18	0.75	0.46 ± 0.12	0.41 ± 0.13	1.22
				Attack maneuver					
n	23	23		41	5		23	18	
Perch-glean	0.60 ± 0.09	0.37 ± 0.10	73.67**	0.47 ± 0.15	0.64 ± 0.16	12.30**	0.48 ± 0.14	0.45 ± 0.16	0.17
Flight-glean	0.20 ± 0.08	0.41 ± 0.11	54.89**	0.30 ± 0.14	0.29 ± 0.12	0.04	0.27 ± 0.13	0.34 ± 0.15	3.23
Hang	0.13 ± 0.10	0.09 ± 0.08	2.47	0.12 ± 0.09	0.03 ± 0.08	4.45*	0.14 ± 0.10	0.08 ± 0.06	5.16*
Hawk	0.02 ± 0.03	0.12 ± 0.09	25.86**	0.08 ± 0.08	0.0 ± 0.0	4.81*	0.07 ± 0.08	0.09 ± 0.09	0.18
Chase	0.06 ± 0.04	0.02 ± 0.04	8.57**	0.04 ± 0.05	0.03 ± 0.03	0.16	0.04 ± 0.04	0.04 ± 0.05	0.48
				Substrate					
n	23	23		41	5		23	18	
Trunk	0.06 ± 0.09	0.05 ± 0.06	0.82	0.06 ± 0.08	0.05 ± 0.08	0.05	0.08 ± 0.09	0.03 ± 0.05	4.06
Large branch	0.11 ± 0.11	0.06 ± 0.08	2.82	0.09 ± 0.10	0.05 ± 0.04	1.17	0.12 ± 0.11	0.05 ± 0.05	5.91*
Small branch	0.19 ± 0.09	0.13 ± 0.10	4.52*	0.16 ± 0.10	0.17 ± 0.06	0.001	0.18 ± 0.11	0.15 ± 0.09	0.81
Twig	0.38 ± 0.12	0.39 ± 0.13	0.21	0.38 ± 0.13	0.33 ± 0.19	0.73	0.35 ± 0.13	0.42 ± 0.11	2.78
Leaf	0.17 ± 0.10	0.23 ± 0.12	4.57*	0.18 ± 0.10	0.32 ± 0.14	8.59**	0.16 ± 0.10	0.22 ± 0.10	4.01
Air	0.08 ± 0.05	0.14 ± 0.10	6.54*	0.11 ± 0.09	0.03 ± 0.03	3.86	0.11 ± 0.08	0.13 ± 0.10	0.43
Ground	0.01 ± 0.03	0.001 ± 0.001	4.94*	0.01 ± 0.02	0.05 ± 0.11	3.06	0.01 ± 0.02	0.01 ± 0.02	0.002

*, $P < 0.05$; **, $P < 0.01$; others not significant ($P > 0.05$).

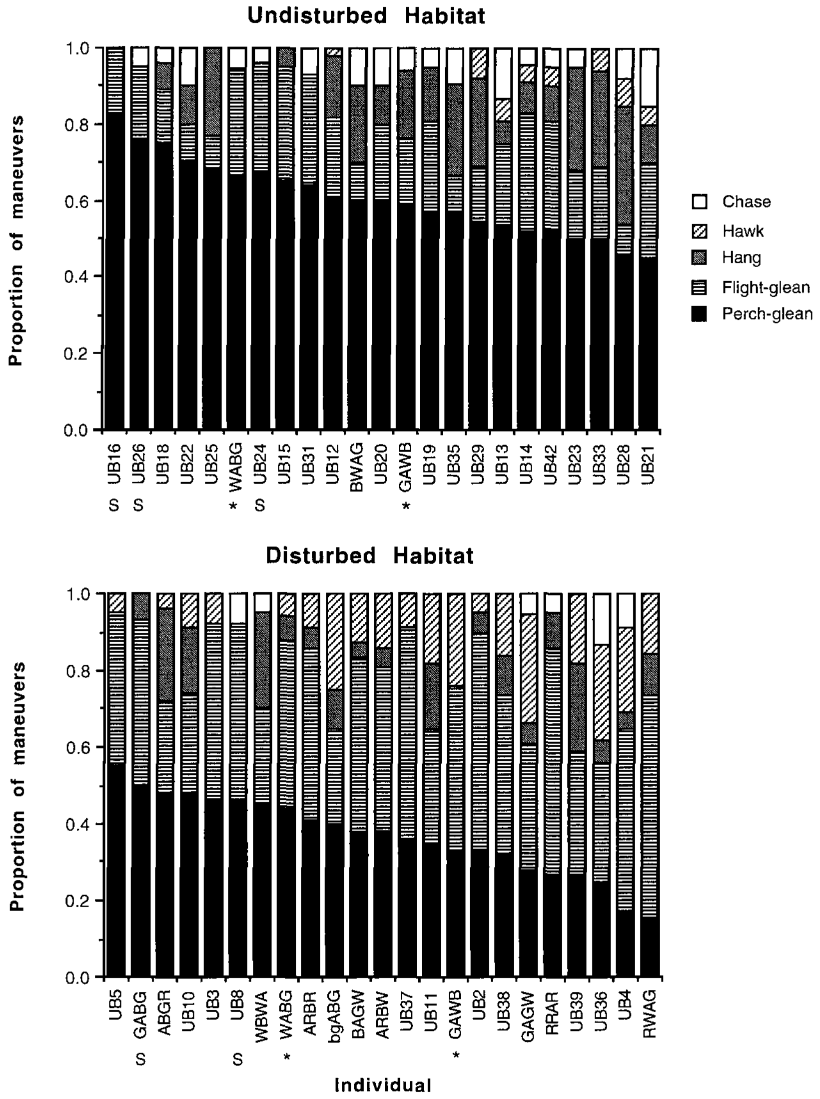

Fig. 2. Individual variation in proportions of attack maneuvers in different habitats. Symbols for each individual are color-band codes or "UB" for unbanded birds. Individuals found in both habitats marked with asterisk (*); subadults marked with "S."

quired more time and energy. The more-open structure and lower foliage density of disturbed habitat may have caused fewer perches to be within hopping range of each other, necessitating more and longer flights between perches. Moreover, the attack radius did not differ between habitats, suggesting there may be an effective prey-detection distance determined by perceptual ability, beyond which searching is inefficient (Fitzpatrick 1981). This is consistent with my earlier findings (VanderWerf 1993) in which Elepaio selected foraging sites at a fine scale based on habitat cues within 0.75 m. The combination of lower foliage density, longer distances between perches, and an upper limit to attack radius likely caused birds in disturbed habitat to search less substrate from a given perch (Robinson and Holmes 1984). Because birds in disturbed habitat searched less substrate from each perch and spent more time

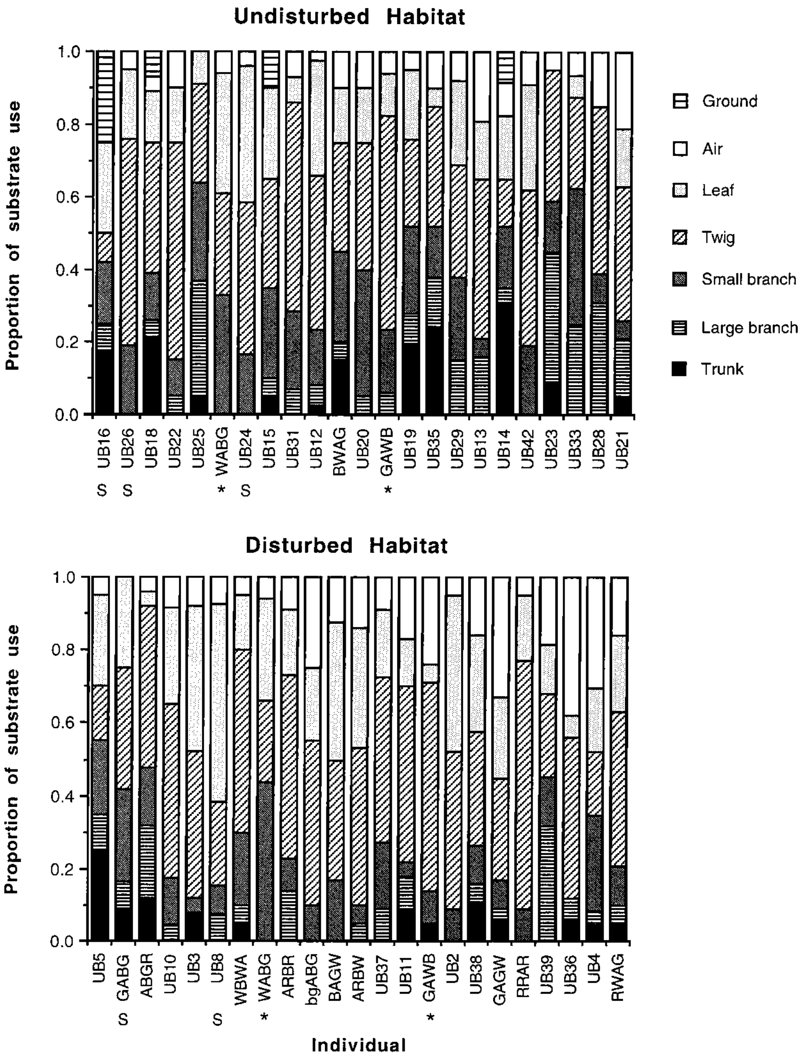

Fig. 3. Individual variation in proportional substrate use in different habitats. Symbols given for each bird are color-band codes, or "UB" for unbanded birds. Individuals found in both habitats marked with asterisk (*); subadults marked with "S."

TABLE 3. Steps in reaching final log-linear model by forward selection (H = habitat, M = maneuver, S = substrate, T = tree species). Terms with symbols for more than one variable represent interactions between those variables. $P > 0.05$ indicates adequate fit to observed data. Asterisk (*) indicates model whose conditional log-likelihood ratio not significant ($P < 0.05$), meaning model is not statistically different from previous one, and term added or deleted not necessary to explain observed data.

Model	G^2	df	P	Conditional log-likelihood
H + M + S + T	248.37	53	<0.0001	—
HM + HS + HT + MS + MT + ST	31.96	18	0.022	—
HST + HM + MS + MT	20.54	10	0.025	11.42*
HM + HT + MS + MT + ST	32.60	22	0.068	0.64*
HM + HT + MS + MT	41.35	30	0.081	8.75*

moving between perches, they may have encountered fewer prey.

Differences in habitat structure also affected proportions of attack maneuvers. More frequent use of perch-gleaning in undisturbed habitat may be explained by higher foliage density. In disturbed habitat, lower foliage density and more-distant perches may have resulted in more prey being out of reach, causing birds to use flight-gleaning more often (Maurer and Whitmore 1981, Sabo and Holmes 1983). Birds in disturbed habitat also attacked more prey in the air by hawking, perhaps because the open structure of disturbed habitat made flying prey more visible (Seidel and Whitmore 1982). The chase maneuver was used to capture prey that flushed and attempted to escape, such as homopterans (Sherry 1985) and geometrid moths (pers. obs.). The fact that chase was used less in disturbed habitat suggests that prey of this type was less abundant or harder to flush (or perhaps easier to capture) in disturbed habitat.

Flight-gleaning and hawking presumably are more energetically expensive methods of capturing prey than perch-gleaning, and birds may employ these techniques to increase food intake (Morse 1973, Bennett 1980). Martin and Karr (1990) found shifts in proportions of attack maneuvers at different seasons and hypothesized that changes in foraging patterns toward energetically expensive maneuvers reflected periods of demanding environmental conditions and food limitation. Increased use of energetically expensive maneuvers by Elepaio in disturbed habitat likewise may indicate greater food limitation. Disturbed areas at the study site may be lower-quality habitat for Elepaio because they provide a more-difficult foraging environment, which could account for the lower population density of Elepaio in disturbed habitat (unpubl. data).

In other studies comparing foraging between habitats, Szaro and Balda (1979) found that foraging methods (maneuvers) of species comprising the bird community in ponderosa pine (*Pinus ponderosa*) forests did not change with forest structure, and that only 5 of 15 species changed proportions of maneuvers. Maurer and Whitmore (1981) found that of five species, only American Redstarts (*Setophaga ruticilla*) changed foraging maneuvers between forests with different structure, and that other birds instead changed tree species, substrates, or height.

Diversity and variation in foraging methods.—Martin and Karr (1990) found that proportions of attack maneuvers used by species changed seasonally, but the relative rank of each maneuver did not change. They suggested species were plastic only within certain limits determined by their evolutionary histories. Because attack maneuvers used by a species may be constrained by morphology, birds may be more likely to change other aspects of foraging, such as height or plant species (Hutto 1981, Fitzpatrick 1985, Sherry 1985, Martin and Karr 1990, Moermond 1990). This was not true for the Elepaio; several aspects of foraging behavior, including attack maneuver, were plastic. Relative proportions of attack maneuvers and substrates used differed between habitats for the species as a whole, varied among individuals within a habitat, and even changed within individuals whose territories overlapped both habitats.

The differences in degree of flexibility found in my study compared to the previous studies may reflect that bird species on small islands with relatively depauperate avifaunas often show much variation in foraging methods (Selander 1966). Morse (1971, 1977) found that species of wood-warblers that foraged opportunistically were more likely to inhabit small islands. Abbott et al. (1977) found that diet breadth of Galapagos ground finches (*Geospiza* spp.) was correlated with number of islands occupied. Feinsinger and Swarm (1982) showed that during periods of food scarcity a species of hummingbird had a broader feeding niche on Tobago, where there were only two other nectarivores, than on Trinidad, where there were many. The Bonin Islands Honeyeater (*Apalopteron familiare*) also has been reported to have diverse foraging methods compared to related species in Japan (Higuchi et al. 1984, pers. comm.). An unusual example was reported by Werner and Sherry (1987) for the Cocos Island Finch (*Pinaroloxias inornata*), in which individuals were highly specialized even though the species as a whole showed a wide range of behaviors.

The Elepaio also appears to use more-diverse foraging maneuvers and substrates than related species found on continents and large islands. After conversion to categories equivalent to those in my study and expressed as H'/H'_{max}, data from Croxall (1974) for 14 species in three genera of monarchine flycatchers from New Guinea showed that diversity of foraging maneuvers ranged from 0.16 to 0.69 ($\bar{x} = 0.47 \pm$

0.16). Data from Bell (1984) showed that, for eight of the same species in New Guinea, diversity of foraging maneuvers ranged from 0.05 to 0.84 ($\bar{x}$ = 0.47 ± 0.32) and diversity of substrates used from 0.31 to 0.79 ($\bar{x}$ = 0.53 ± 0.16). Data from Recher et al. (1985) for two fantails (*Rhipidura*) and a monarch (*Monarcha*) in Australia showed foraging maneuver diversity ranging from 0.48 to 0.68 ($\bar{x}$ = 0.57 ± 0.10) and substrate diversity from 0.47 to 0.67 ($\bar{x}$ = 0.58 ± 0.10). Thus, the Elepaio appears to use more-diverse foraging maneuvers than its relatives on large islands and continents, and has among the highest diversities of substrate use. The diversity of foraging maneuvers used by Elepaio (0.86) is similar to the 0.88 reported for the Cocos Island Flycatcher (*Nesotriccus ridgwayii*; Sherry 1985), which also inhabits a small oceanic island.

Effects of age.—As found in numerous studies of age-specific foraging (see Wunderle 1991), subadult Elepaio had lower foraging proficiency than adults. The interval between attacks on prey was 25% longer in subadults. Subadult Elepaio also hopped less frequently than adults, suggesting the lower foraging proficiency of subadults was caused by a slower search rate. Given that flight interval and flight distance of subadult Elepaio were no different than those of adults, subadults do not perceive as many prey items, search incompletely before flying to a new perch, or both. Similar results were obtained by Richardson and Verbeek (1987), who found that juvenile Northwestern Crows (*Corvus caurinus*) had lower success, searched more slowly, and spent more time searching than adults. In contrast, Gochfeld and Burger (1984) found that juvenile American Robins (*Turdus migratorius*) searched faster than adults, but still had lower success. Subadult birds may not be as skilled at perceiving prey or may not have developed an appropriate search image (Wunderle 1991). The increase in foraging efficiency with age could be due to learning or to elimination of inefficient birds from the population (Groves 1978).

In the ontogeny of foraging behavior, maneuvers that require more coordination, particularly those involving flight, often develop later (Davies and Green 1976, Moreno 1984, Breitwisch et al. 1987). Both attack maneuvers used less by subadult Elepaio than by adults (i.e. hang and hawk) are relatively complex and presumably require more skill and coordination than perch-gleaning. Subadults may use simpler and energetically less expensive maneuvers more often to compensate for their lower proficiency (Davies and Green 1976).

Interaction of variables in log-linear model.—Birds are thought to use different maneuvers to capture different types of prey (Rabenold 1978). In my study, interaction of maneuver and substrate in the log-linear model indicates Elepaio also use different maneuvers to capture prey on different substrates. Perch-gleaning was more common on bark and twigs, perhaps because these substrates could support the mass of a perched bird, allowing birds the option of using the easiest maneuver. Most leaves probably could not support a perched bird, and may have been out of reach of birds perched on bark or twigs, therefore explaining why leaves were used more in conjunction with flight-gleaning. Hang was used more on bark, possibly because the diameter of trunks and large branches was too large to allow a bird to reach all parts of the substrate while perched.

Structural differences between tree species affect which maneuvers birds can use to capture prey (Robinson and Holmes 1984). More frequent use of perch-gleaning on ohia may be explained by its relatively dense crown with many twigs and small leaves on short petioles (Jackson 1979). Birds easily could reach many leaves while perched on twigs or small branches. In contrast, the primary photosynthetic surfaces of koa are phyllodes (elongate, flattened petioles) that are too thin to support the mass of a perched bird and may be too distant for birds to reach while perched. Birds on koa were forced to use flight-gleaning more often. Hang may have been used more on koa because they typically reach much larger sizes than ohia, and their thicker trunks and branches required hanging more often. This effect of vegetation structure on foraging behavior of insectivorous birds is analogous to fruit-accessibility and preference patterns of frugivorous birds (Denslow and Moermond 1982, Levey et al. 1984).

Similar comparisons can be made among several studies of foraging methods of insectivorous bird communities at sites dominated by tree species with differing vegetation structure. Airola and Barrett (1985) and Alatalo (1982) found that perch-gleaning was more common than flight-gleaning at their study sites, which were dominated by coniferous trees that had foliage on short petioles distributed continuously along twigs. Robinson and Holmes (1982) found that flight-gleaning was more common, and most trees at their site were deciduous and had foliage on long petioles concentrated at branch tips. At an Australian site consisting of *Eucalyptus* spp. trees with widely spaced branches and leaves, search-and-attack flights were longer than in the above studies (Holmes and Recher 1986). Overall foraging methods at each site were related to physical structure of the dominant tree species. I found similar patterns of attack maneuvers for the Elepaio between tree species at one site.

There are several possible alternative explanations for the differences in foraging between habitats. The risk of predation may affect how long birds forage or which foraging sites they choose (Lima 1985). Suhonen (1993) found that birds foraged in more protected sites toward the centers of trees in a year when predation risk was higher. At my study site, one might expect the risk of predation to be higher in the more open disturbed habitat because birds would be more visible to predators. However, the maneuvers (hawk and flight-glean) and substrates (air and leaves) used more in disturbed habitat would seem to increase vulnerability to predators. Unless the benefits of increased prey capture outweigh the predation risk, it is unlikely that predation risk is responsible. The primary predator on the Elepaio at my site may be the Hawaiian Hawk (*Buteo solitarius*). I frequently observed hawks hunting in both habitats, and I observed a hawk prey on a fledgling Elepaio once (in disturbed habitat).

Interspecific competition also can alter foraging behavior (Morse 1967, Alatalo 1981, Carothers 1986). Some competition may occur between the Elepaio and other insectivorous birds, particularly the introduced Japanese White-eye (*Zosterops japonicus;* Mountainspring and Scott 1985). However, since similar changes in foraging were found even within individuals between habitats, and species composition of the insectivorous bird guild was the same in both habitats, it seems unlikely that the differences in foraging behavior between habitats were caused by competition.

Finally, arthropod abundance and diversity undoubtedly affect foraging behavior of insectivorous birds (Holmes and Schultz 1988). At my study site, arthropod abundance is higher in disturbed habitat and diversity of most arthropod taxa does not differ between habitats (Peck 1993), which cannot explain the use of more difficult foraging methods in disturbed habitat.

Summary and conclusions.—Open-canopy disturbed habitat may be of lower quality for the Elepaio because searching for and capturing prey is more difficult. Birds in disturbed habitat flew farther and more often while searching, used energetically expensive attack maneuvers more often, and encountered prey less often. Subadult Elepaio had lower foraging proficiency that may be explained by a slower search rate. Subadults may compensate for their lower proficiency by using simpler, less-expensive maneuvers more often. Few differences in foraging were found between sexes. Foraging behavior of the Elepaio was very plastic and was more diverse than that reported in the literature for related species on continents and large islands. Proportions of attack maneuvers and substrates used differed between habitats, varied among individuals within a habitat, and even changed within individuals between habitats. Elepaio were more likely to use specific maneuvers on different tree species and on different substrates, perhaps because of the physical structure of these surfaces.

Habitat alteration by humans at Hakalau Forest National Wildlife Refuge may have made some areas more demanding as foraging sites for Elepaio, but their behavioral flexibility and diverse repertoire of foraging techniques allow Elepaio to successfully exploit arthropod resources in disturbed habitat. Population density is slightly lower in disturbed habitat, and it is possible that habitat alteration affects the Elepaio in other ways. In the future I hope to test whether disturbance influences territory size, population structure, time budgets, and ptilochronology.

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