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THE EFFECT OF RETREAT SITE QUALITY ON INTERFERENCE-RELATED BEHAVIOR AMONG HAWAIIAN HONEYCREEPERS[1]

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Abstract. Four species of Hawaiian honeycreepers feeding on canopy flowers of the Ohia, *Metrosideros collina,* used canopy foliage as a retreat site from interference interactions. Concealment value of canopy foliage varied with its density. In open-canopied trees, birds were more widely spaced, flew away from chases more often, and chased and retreated for greater distances than in closed-canopied trees. Greater spacing seemed to be due to lower concealment value, which in turn resulted in greater chase distances. While greater retreat distances may have resulted from greater chase distances or lower retreat site quality, corrections for differential chase distances suggest that greater retreat distances are a response to decreased canopy density. Adult dominants evoked greater retreat responses in subordinates than did immature dominants. Unlike adult subordinates, immature subordinates were not spaced more widely nor did they retreat more frequently in open than in closed canopy. These results indicate that birds modify agonistic behaviors and responses with respect to retreat site quality and interference, and that sometimes age-related effects determined the responses evoked.

Key words: Hawaiian honeycreepers; interference competition; nectar feeders; aggression; Hawaii; behavior; interspecific competition.

INTRODUCTION

Interference interactions often result when individuals use a common resource at the same time. In order to reduce such interactions, subordinates should avoid dominants (Cody 1973), perhaps through the asynchronous use of the resource (Carothers and Jaksić 1984). The probability of avoidance increases when food rewards are low or when foraging rates in the presence of dominants are reduced (Morse 1977a, b). However, when food rewards are high, individuals may still profit from using a resource despite interference behavior from a dominant resident. Such encroachment by subordinates is facilitated by structurally complex habitats that provide nearby refuges for avoiding interference interactions (Brown 1971, Dow 1977, Ebersole 1985).

The intra- and interspecific aggressiveness of nectar-feeding birds is well-known (Pitelka 1951, Carpenter 1978, Wolf 1978) and resulting because nectar is generally a high reward, defendable resource. This study investigates interference interactions with respect to variation in retreat site quality among four species of Hawaiian honeycreepers feeding on the canopy flowers of the numerically dominant rainforest tree in Hawaii. The honeycreeper species of highest dominance rank territorially defends a given tree canopy, but the high turnover rate of subordinates within a given tree promotes frequent interactions (Carothers 1986). When chased, these subordinates often use the canopy foliage as a concealing retreat site. Although temporarily interrupting feeding behavior, this tactic saves the subordinate from having to completely abandon feeding and go off in search of other foraging areas (Carothers 1986). Variation in the density of a canopy influences its concealment quality, and hence its quality as a retreat site. The potential thus exists for variation in behaviors of both dominants and subordinates in response to variation in canopy density. Do the subordinates modify their retreat responses when occupying trees that differ in concealment value? Do the dominants in turn modify their own behavior to compensate for changes in subordinates behavior and/or the canopy density?

To ascertain how dominants and subordinates occupying the same trees respond to differences in canopy foliage density (and hence its quality as a retreat site), the following questions were addressed: 1) Given that birds select specific retreat sites from a variety of possible choices (Carothers 1986), do they select safer retreat sites when density of the canopy foliage is lower? I predict that birds should use the canopy foliage less and fly away more when canopy density is low. 2) If spacing patterns are adjusted to differences in threat potential posed in open- vs. closed-canopied trees, what is the dispersion of birds with respect to canopy density? I suggest that as canopy density decreases (lowering its effectiveness as a retreat site), inter-individual distances will increase. 3) If there are no differences in inter-individual distances, are chase distances (the distance a

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dominant travels when chasing a subordinate) equivalent? I suggest that dominants may not need to chase subordinates as far in open (vs. closed) canopied trees to enforce their dominance, because there is reduced opportunity for subordinates to take advantage of readily accessible shelter from such chases. 4) When chase distances are equivalent in canopies of different density, are retreat distances (the distance a subordinate retreats from its original position to where it stops) equivalent? I hypothesize that retreat distances will be greater for subordinates in low-density canopies, for the same reason that chase distances might be shorter. 5) What are some consequences of age in the patterns observed? I expect immature, and hence inexperienced, individuals to be less effective as dominants and less sophisticated in responses to aggression than subordinates.

MATERIALS AND METHODS

THE STUDY AREA

Birds were observed in the Koolau Forest Reserve on the north slopes of Haleakala volcano on the island of Maui, Hawaii, from 15 May to 25 July 1980, 10 July to 10 August and 10 to 27 December 1981, and 28 December 1983 to 20 January 1984. Most observations were made at a segment of rainforest at 1,800 m, though some were made at other locations at similar elevations. This forest is composed predominantly of one species of tree, the ohia (*Metrosideros collina*), which has a broad, flattened, dome-shaped, flowering canopy varying greatly in density, and averages 12 to 15 m in height in the study area. It is the main food source (Baldwin 1953, Carpenter 1976, Pimm and Pimm 1982) for nectar-feeding Hawaiian Honeycreepers (Fringillidae: Drepanidinae).

THE BIRDS

The four species I studied, in increasing order of behavioral dominance, are the Common Amakihi (*Hemignathus virens*), the Apapane (*Himatione sanguinea*), the Iiwi (*Vestiaria coccinea*), and the Crested Honeycreeper (*Palmeria dolei*). Adults of all species dominate immature conspecifics (Carothers 1986.). The Common Amakihi is olive drab in color, although males have a yellow breast and face. Common Amakihis are secretive, occurring singly or in pairs in Ohia trees. The latter three species are sexually monomorphic, although adults are more brightly colored than are immatures. Both Iiwis and Crested Honeycreepers are territorial, with a single adult or mated pair and perhaps one or more immature individuals (presumably offspring) foraging in a given tree (Carothers 1986). In contrast, Apapanes are nomadic, flying about and often foraging in small flocks. Typically, several Apapanes feed in a tree, with individuals flying away and others entering the canopy at apparently random intervals (Carothers 1986). As a result, flock cohesion of Apapanes appears low, with variable membership.

OBSERVATIONS

Observations were made both from the ground and by ascending trees to observe birds in neighboring trees, from distances of 5 to 20 m using 8× binoculars. The following data were collected for each bird observed foraging in a tree canopy: species; age (by plumage); approach level to tree; entry site into tree canopy; location in tree; density of the canopy foliage of the tree; distance to and indentity of other birds in the canopy (if any); species chased (if any) and distance of chase; retreat distance and stratum to which retreated (if chased).

Level of approach (high/low) and entry site in tree (top/bottom) are designated with respect to the level of the canopy of the individual tree occupied, and were recorded to see if birds use different strategies to detect residents of the tree approached. A high approach level would allow the detection of birds feeding on flowers in the canopy. Entering the canopy from below would facilitate chasing of individuals which have hidden in the canopy foliage. Canopy density refers to the openness of the canopy foliage, and is related to the degree to which a bird is concealed by the canopy foliage. Two density categories are used: closed (75 to 100% cover) and open (<75% cover). Chase and retreat distances were visually estimated to the nearest meter. The retreat strata are ranked to reflect the degree of intimidation of the chasee by the chaser, in increasing order of response: neighboring section of canopy, the concealing subcanopy (underlying branches of canopy), and flying away from the tree. Because several observers collected data, each was checked to ensure low inter-observer variability in distance estimates. Periods of observation were highly variable in length of observation session, tree (and number of individuals) under observation, time of day of observation, and season of observation.

Because age classes are herein considered separately, individuals are not referred to by species. Instead I use the terms subordinate, dominant, or bird to refer to the species-age classes. The only exception is the Amakihi, for which observations of both sexes and age classes are lumped in the same analyses. I had too few chase and retreat data for this species, so only spacing data are presented. The Statistical Analysis System on the U.C. Berkeley

IBM 4341 was used, and because all subsets of the distance data (chases, retreats, and inter-individual distances) conformed to tests of normality, parametric tests were conducted.

RESULTS

APPROACH AND ENTRY CHARACTERISTICS

Canopy approach levels did not differ among adult and immature Apapanes and adult Crested Honeycreepers (65% of these being low for each species and age class). However, they all differ ($P < 0.01$ in all cases, χ^2 tests) from immature Crested Honeycreepers and adult Iiwis, which usually (90%) approach canopies from lower levels. In 77% of the cases, both Apapane age classes usually enter the canopy from above, while both age classes of Crested Honeycreepers and adult Iiwis enter mostly (63%) from below ($P \ll 0.01$ in all cases, χ^2 tests).

INTER-INDIVIDUAL DISTANCES

There was a significant trend for subordinates to be spaced farther from dominants in trees with less dense canopies, with 11 of the 13 pairwise comparisons showing an increase in inter-individual distance in open as compared to closed crowns ($\chi^2 = 4.92$, $\nu = 1$, $P < 0.05$, with Yates correction). Eight had significantly ($P < 0.01$) greater inter-individual distances (Table 1), while none showed significantly shorter inter-individual distances.

CHASES AND RETREATS

Canopy density (open vs. closed) had a significant effect on the selection of retreat strata. Adult and immature Apapanes responded to reduced canopy coverage by flying away, rather than staying in the tree ($\chi^2 = 6.22$, $P < 0.05$). Mean chase distances of adult Apapanes, adult Iiwis, and adult and immature Crested Honeycreepers were inversely related to canopy density: chase distances were greater in open-canopy trees (Figs. 1a, b). Differences were significant in two individual cases (adult Iiwis and Apapanes) and when the data from the four cases were combined (Fig. 1b). The data were then broken down into seven pairwise comparisons (not counting combined species) of chases against adult and immature Apapanes (Fig. 2a, b). In all such comparisons, chase distances were greater in more open canopies ($\chi^2 = 5.14$, $\nu = 1$, $P < 0.05$, with Yates correction), although in only one pairwise comparison was the difference statistically significant.

In pairwise comparisons of retreat distances, adult and immature Apapanes retreated farther when canopy density was low in all cases

TABLE 1. Average inter-individual distances in closed (C) and open (O) canopies Ohias.

	Canopy density	Adult Akohekohes	Immature Akohekohes	Adult Iiwis	Immature Iiwis	Adult Apapanes	Immature Apapanes
Immature Akohekohes	C	1.84 ± 0.30 (103)					
	O	3.18 ± 0.48 (125)**					
Immature Iiwis	C		2.75 ± 0.82 (8)				
	O		6.85 ± 0.32 (54)**				
Adult Apapanes	C	2.19 ± 0.33 (16)	5.10 ± 0.47 (102)	5.28 ± 0.58 (56)	3.02 ± 0.02 (55)		
	O	6.76 ± 0.36 (191)**	5.42 ± 0.30 (143)	5.22 ± 0.59 (37)	4.00 ± 0.00 (4)**		
Immature Apapanes	C	4.21 ± 0.28 (213)	3.92 ± 0.18 (410)	2.83 ± 0.52 (55)		3.53 ± 0.14 (738)	
	O	4.59 ± 0.40 (119)	4.67 ± 0.20 (600)**	3.13 ± 0.28 (22)		4.62 ± 0.14 (1,365)**	
All Amakihis	C		4.85 ± 0.84 (20)			3.41 ± 0.74 (17)	4.03 ± 0.38 (132)
	O		4.35 ± 0.38 (34)			5.95 ± 0.30 (282)**	5.97 ± 0.50 (110)**

Distances shown are followed by ±2 SE with sample sizes in parentheses. Missing comparisons resulted from low sample size.
* Significant difference between retreat distances at $P < 0.05$, t-tests.
** Significant difference between retreat distances at $P < 0.01$, t-tests.

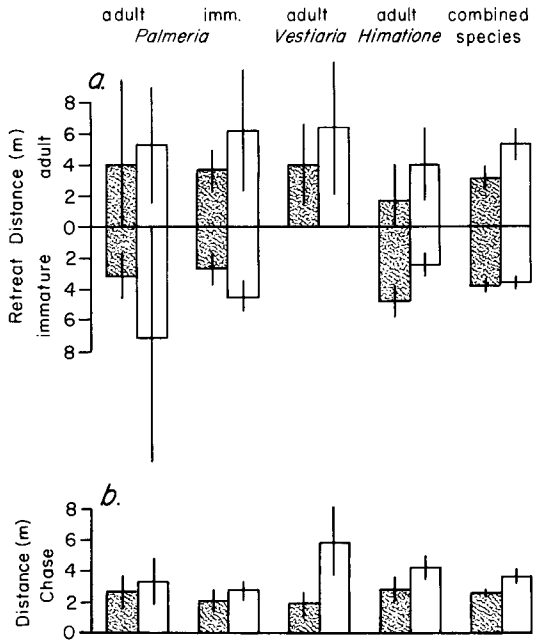

FIGURE 1a, b. The upper figure (a) shows the corrected retreat distances (retreat distance minus chase distance) of Apapane adult (above the axis) and immatures (below the axis) in open-canopied and closed-canopied trees. The lower figure (b) shows average chase distances ($\bar{x} \pm 2$ SE) of each bird species in trees that are open-canopied (open bars) or closed-canopied (closed bars).

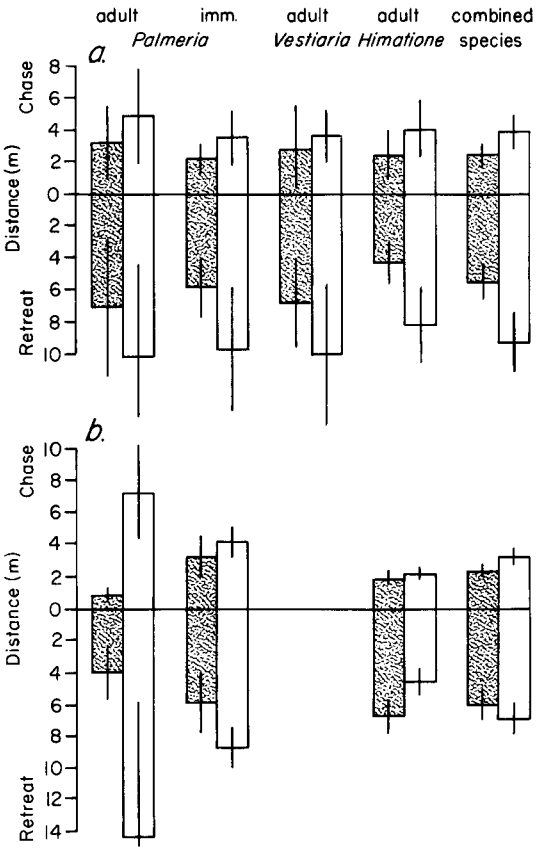

FIGURE 2a, b. Average distances ($\bar{x} \pm 2$ SE) adult (a) and immature (b) Apapanes were chased (above the axis) and corresponding average distances they retreated (below the axis) in open-canopied (open bars) and closed-canopied (closed bars) trees.

except chases of immature Apapanes by adult conspecifics (Fig. 2a, b). The combined retreat distance data for adult (but not immature) Apapanes showed a significant increase (Fig. 2a).

A measure of response to chases can be made by subtracting chase distances from retreat distances in the pairwise comparisons. Correcting retreat distances against chase distances in this manner should eliminate any biases due to longer chases in canopies of either density. The results from this parallel those of the uncorrected retreat distances above: corrected retreat distances were greater with lower canopy density in all cases except that of adult Apapanes chasing immature conspecifics (Fig. 1a). Furthermore, combined corrected retreat distance data showed a significant increase for adult but not immature Apapanes (Fig. 1a).

DISCUSSION

CANOPY APPROACH AND ENTRY, AND RETREAT SITE SELECTION

The structural complexity of a habitat has been suggested to play an important role in predator avoidance (e.g., Rosenzweig and Winakur 1969; Stamps 1983a, b). A similar shelter role is seen in Hawaiian Honeycreepers with respect to avoidance of interspecific interference interactions. Canopies are used as sites of retreat from interference (Carothers 1986). Thus, its value as a retreat site is expected to vary with its density: with greater openness the utility of subcanopy retreats to avoid aggression decreases and a shift to aerial retreats is expected. Interspecific aggressive displacement related to variation in vegetation density has also been observed among some birds (Dow 1977), chipmunks (Brown 1971, Meredith 1977), and fishes (Ebersole 1985), resulting in altitudinal zonation or exclusive occupancy of certain habitats (review in Murray 1981). Coexistence of Hawaiian Honeycreepers in favored areas still occurs, but it is clear that the opportunity to avoid agonistic interactions varies with varying canopy density. This variation apparently determines the behaviors used by the component species.

As noted above, Apapanes tended to retreat into the subcanopy when under threat, a behavior effective in avoiding chases while reducing retreat costs (Carothers 1986). However, they compensated for the reduced concealment value of open-canopied trees by flying

away more frequently (vs. retreating into the subcanopy) when chased in open- (vs. closed-) canopied trees. In a study of two chipmunk species (*Eutamius* spp.), Brown (1971) found a similar result: interference interactions were less effective in areas of greater vegetation density. Apapane's use of subcanopy as a retreat site also occurs upon the aerial approach of Crested Honeycreepers, making it more difficult for Crested Honeycreepers to chase them out of the canopy. However, both Iiwis and Crested Honeycreepers countered this ploy by entering the canopy from below (63% of total), chasing out Apapanes that had sought shelter in the subcanopy upon the dominant's approach. Entering from below allowed dominants to more readily discern and chase out birds in hiding. By usually entering the canopy from the top (77%), Apapanes should be able to observe the locations of resident dominants and land elsewhere in the canopy (or avoid the tree entirely). Differential canopy entrance as a strategy is supported by the fact that Apapanes and Crested Honeycreepers approached the canopy from the same angle before diverging in their site of canopy entrance. The large bias by Iiwis of low approaches (90%) reflected its tendency to feed from understory vegetation (Carothers 1986).

Theoretical models have discussed how animals differing in status should use different behavioral tactics in aggressive encounters (Maynard Smith and Price 1973; Maynard Smith and Parker 1976; Murray 1981). Apapanes use flock swamping to overcome a territorial dominant (Carothers 1986). These results indicate that Hawaiian honeycreepers use specific tactics to both avoid aggression from dominants and to enforce aggression against subordinates.

SPACING, CHASE, AND RETREAT DISTANCES

Because the subcanopy's value as a retreat site is positively associated with its density, birds should decrease spacing to take advantage of the greater refuge from interference interactions. Brown (1971) suggested that intruder density increased with greater vegetational structural complexity. This effect is indeed observed, with a marked reduction in inter-individual distances when canopy density is greater.

Due to differences in experience, immatures should perhaps behave in ways less sophisticated than adults (e.g., Moynihan 1959), although this need not always be the case (Stamps 1978). While for hummingbirds, adults normally dominate immature conspecifics (e.g., Ewald and Rohwer 1980), the more complex issues of interspecific dominance among age classes is very poorly known. I have found (Carothers 1986) that Hawaiian Honeycreeper age influences both its own behavior and responses of others. Immature Apapanes do not differ as much as do adults in retreat distances relative to canopy density, even though chase distances in either canopy class tend to be the same. Age-related inexperience of a dominant influences the degree to which they can intimidate subordinates (as reflected in retreat site selection or retreat distances of subordinates—Carothers 1986). Thus, the fact that adult Crested Honeycreepers and Iiwis cause greater retreat site responses in adult Apapanes than do immatures of these dominant birds is expected. However, this is the only case in which age-dominance differences appear; no trends emerge when examining spacing, chase, and retreat distance relative to canopy density.

Contrary to predictions, chase distances are greater, not lower, in more open canopy cover, showing that dominants do not benefit from the reduced retreat opportunity afforded subordinates in open-canopied trees. However, the prediction does not take into account the greater spacing of the birds in the open-canopied trees, which necessitates the greater chase distances. Although it is possible that differences in dominance rank might result in differences in chase distances with respect to the two canopy densities, no such patterns are evident.

As inferred from above, dominants do not realize a savings in their requisite chase distances of subordinates in open-canopied trees. However, subordinates incur a greater cost, as their retreat distances were greater. While this is a predicted effect of the reduced value of the subcanopy as a retreat site, differential spacing and chasing might bias retreat distance results. Although birds show greater spacing and hence greater chase distances in open canopied trees, the corrected retreat distances (adjusting for these differences) support the contention that the birds do respond to density differences as predicted. Thus, chase behavior of dominants appears more effective in open-canopied trees even though they do not actually have a shorter chase distance as predicted.

These results indicate that dominant birds cannot reduce their per-chase costs by choosing among trees of the two canopy density types. However, subordinates incur higher costs per chase in the more open trees, and are able to reduce these costs (retreat distances) by foraging in the closed-canopied trees.

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