BEHAVIORAL AND ECOLOGICAL CORRELATES OF INTERFERENCE COMPETITION AMONG SOME HAWAIIAN DREPANIDINAE

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ABSTRACT.—Interference interactions were studied on the island of Maui among four species of drepanidines that fed on canopy flowers of the ohia tree (*Metrosideros collina*). The birds had a size-related dominance hierarchy, with ranking (most to least dominant, by location in dominance matrix) as follows: Crested Honeycreeper (*Palmeria dolei*), Iiwi (*Vestiaria coccinea*), Apapane (*Himatione sanguinea*), and Common Amakihi (*Hemignathus virens*). Immatures were subordinate to conspecific adults. Crested Honeycreepers and Iiwis defended tree-canopy territories, Apapanes were nomadic flock foragers, and Common Amakihis were secretive foragers. Dominance by Iiwis was indicated by a lack of reversals in the dominance matrix. For the top-ranked Crested Honeycreeper dominance was also reflected in greater chase or greater resulting retreat distances or both. Age-related differences in interference behavior by dominants appeared to be due to inexperience, as indicated by shorter chase distances for immatures. Among subordinates both experience and plumage could be responsible for age differences in behavior. Immatures were chased equal distances (despite closer spacing) but less often than adults, and they chose safer retreat sites.

Apapanes fed in flocks in a dominant's tree. This increased a dominant's territorial costs, reduced chase frequencies, increased Apapane foraging times, and let Apapanes forage in trees from which they otherwise were excluded. Comparisons with the assemblage on the island of Hawaii suggested similar structure among the three species the two islands have in common. On Maui the bottom-ranked Common Amakihi may be more affected by interference competition, perhaps undergoing a niche shift toward greater insectivory because of an additional dominant. *Received 22 July 1985, accepted 17 February 1986.*

ALTHOUGH interference (vs. exploitation) is a major interaction that occurs among competing organisms (Schoener 1982, 1983), the few detailed studies of interspecific behavioral encounters in birds have dealt primarily with multispecies flocks (e.g. Morse 1970, 1976). Interference behavior has been invoked to explain parapatric distributions or joint occupancy of a single habitat through mutually exclusive territories (Orians and Willson 1964) or shifts in niche and foraging role (e.g. Murray 1971, 1981; Davis 1973; Feinsinger and Colwell 1978; Williams and Batzli 1979).

Nectar-feeding birds are known for their intra- and interspecific aggressiveness (Pitelka 1951, Carpenter 1978, Wolf 1978, Murray 1981), but details of the effectiveness and consequences of these agonistic behaviors are poorly known. This is particularly true for immature birds, especially if they occupy different habitats or utilize different food resources. When immatures form a major proportion of a population, however, their role in social dynamics and interspecific interactions can be important.

I studied interference interactions among three species of nectar-feeding Hawaiian drepanidines (Fringillidae) from the island of Maui: the Crested Honeycreeper (*Palmeria dolei*), the Apapane (*Himatione sanguinea*), and the Iiwi (*Vestiaria coccinea*). A fourth drepanidine, the Common Amakihi (*Hemignathus virens*), is discussed where data are available. The latter three species have been studied extensively on the island of Hawaii (e.g. Baldwin 1953; Carpenter 1976; Carpenter and MacMillen 1976a, b, 1980; van Riper et al. 1978; MacMillen and Carpenter 1980; Pimm and Pimm 1982; Scott et al. 1984; van Riper 1984; Mountainspring and Scott 1985). In contrast, there are few ecological accounts of those on Maui (Carothers 1982, 1986; Carothers et al. 1983).

I determined the basic social structures of the birds and the behavioral correlates of dominance relationships among them. Because im-

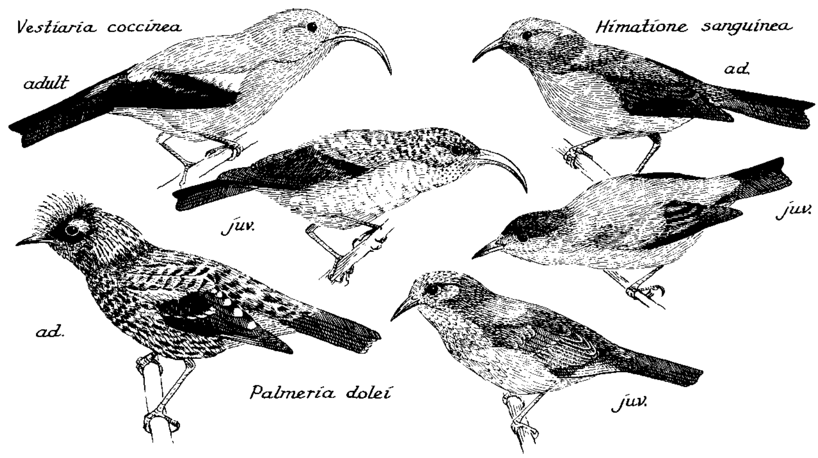

Fig. 1. Adult and immature plumages for the three main species of Hawaiian honeycreeper in this study.

matures sometimes outnumbered adults, age-related differences in behavior were of special concern. I attempted to establish whether birds of higher dominance rank, as determined by location in a dominance matrix, induced greater retreat responses and greater interindividual distances (herein termed spacing) in subordinates. This could result from increased chase frequency or increased chase distance by the more dominant birds. Alternatively, greater intimidation of subordinates also might result solely from plumage or size differences. Age should influence dominance status and general behavior because immatures are perhaps less aggressive and certainly less experienced than adults. Chase distances and the resulting retreat responses and spacing by subordinates were expected to be lower for immature than for adult dominants. For low-ranking immature subordinates (which should be more intimidated than conspecific adults), relatively farther retreats to safer retreat sites were expected. Their inexperience at avoiding aggression, however, might result in closer, not greater, spacing from dominants.

Because other studies (review in Murray 1981) showed that dominants alter resource use by subordinates and that subordinates attempt to ameliorate such effects, I investigated the behavioral and ecological consequences of joint resource use on interactions among the birds. The results of these behavioral and ecological studies of the Maui species were then compared with those on Hawaii. Because the Maui assemblage contains an extra species, I investigated whether the assemblage structure and the behavior of Maui birds differ much with the addition of an extra species. Such a comparison may give insight into the nature of the drepanidine assemblage before the extinction of part of its avifauna.

Methods

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 10–27 December 1981, and 28 December 1983 to 20 January 1984. Most observations were made at the same site, a segment of rain forest at 1,800 m, although some were from other locations at similar elevations. This forest is composed mainly of one tree species, the ohia (*Metrosideros collina*), which has a flattened dome-shaped flowering canopy and averages 10–13 m in height. It is a main food source (Baldwin 1953, Carpenter 1976) for rain-forest nectar-feeding drepanidines at all times of the year.

Although Common Amakihis are dichromatic, Apapanes, Iiwis, and Crested Honeycreepers are sexually monochromatic (Amadon 1950). Age differences for the latter three species are readily determined at a distance (Fig. 1). Because adult female and immature Common Amakihis are hard to distinguish, ages and sexes were combined for the analyses. Common Amakihis are the smallest of the four species [$\bar{x}$ mass (M) = 13.1 g, $\bar{x}$ wing length (WL) = 62.6 mm, $\bar{x}$ tarsus length (TL) = 25.4 mm; Pimm and Pimm 1982], Apapanes the next smallest ($\bar{x}$ M = 14.4 g, $\bar{x}$ WL = 70.9 mm, $\bar{x}$ TL = 26.6 mm; Pimm and Pimm 1982), Iiwis larger ($\bar{x}$ M = 17.1 g, $\bar{x}$ WL = 74.3 mm, $\bar{x}$

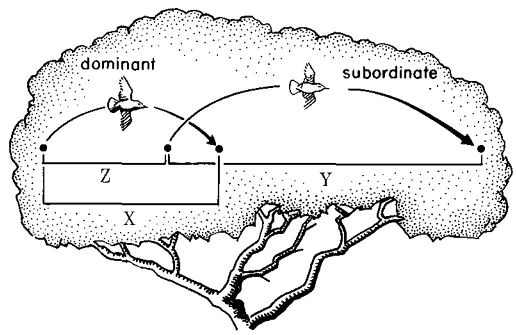

Fig. 2. Distance data used in the study. X = chase distance by a dominant, Y = distance retreated by a subordinate, and Z = distance between two individuals (interindividual distance).

TL = 27.5 mm; Pimm and Pimm 1982), and Crested Honeycreepers the largest (no mass data available; $\bar{x}$ WL = 94.4 mm, $\bar{x}$ TL = 31.7 mm; Amadon 1950).

Observations were made from the ground and by climbing trees to observe birds at relatively close range (usually 15-20 m) in nearby trees. I collected data on species, age, distances (described below), stratum to which retreated (if chased), and (for Apapanes) foraging times. Birds were timed from arrival in a tree until departure, and I noted whether individuals left trees spontaneously or were chased out to discern if foraging times were shortened due to chases. The presence or absence of conspecific adults also was recorded, to measure the effect of flock membership on foraging times. The retreat site selected was viewed as a continuum of sensitivity to chases, from low (neighboring canopy) through intermediate (subcanopy) to high (flying away). In this paper, when a species is discussed without reference to age class, both age classes are under consideration.

Chase frequencies (combining both age classes) were expressed as a percentage of the number of chases by a dominant out of the total number of times the subordinate co-occurred in a tree with the dominant. Two types of observations were excluded because they might decrease actual chase frequencies: when Apapane flock size was >4 and when a species of higher rank than the chasing species was also present. Although it was not always possible to record all co-occurring individuals (which inflated the frequency of chases), comparative chase frequencies still should provide accurate measures of the intensity of aggression. A possible exception was a visibility bias resulting from the greater crypticity of immatures (see Discussion). Larger flocks probably were underestimated as well because it sometimes was difficult to keep track of birds as flock size increased.

In conjunction with these data, distance measures (Fig. 2) were recorded as distance to (Z), and identity of, other birds in the canopy (if any), species chased (if any) and pursuit distance (X), and retreat distance (Y) of the chased bird. The intensity of interference interactions (as reflected in spacing, chase, and retreat distances) did not vary much with respect to location in canopy, perhaps because canopies were small (usually <12 m diameter) and all parts appeared of equal quality, and therefore location was not recorded.

Both chase and retreat responses were examined, because even if two species (or age classes) always chase a given species (or age class) the same distance, the fleeing species may respond differentially to the chasers. To detect such effects, I calculated "adjusted retreat distance" by subtracting the distance A chased B from the distance B retreated (Y − X; Fig. 2). This adjusts for differences in chase distances both within and between dominants.

Distances were estimated visually to the nearest meter, and because several observers collected data, each was trained and checked to ensure agreement and low variability in distance estimates. The hypotheses being tested were not explained to the observers, reducing the possibility of observer bias. Using relatively large (i.e. 1 m) intervals for distance measures may have obscured slight but significant differences, possibly resulting in a conservative bias in statistical comparisons. The Statistical Analysis System on the University of California, Berkeley IBM 4341 was used, and because all subsets of the distance data (chases, retreats, and interindividual distances) conformed to tests of normality, parametric tests were conducted.

RESULTS

Dominance relationships.—Both species identity and age class influenced dominance status. A species was considered dominant to another if it chased the second species more often than retreating from it (Table 1). A linear hierarchy existed. Crested Honeycreepers dominated Iiwis, which dominated Apapanes. All three were dominant over Common Amakihis. Adults dominated immature conspecifics (Table 1). The degree of dominance was complete (i.e. no reversals) in 18 of the 21 pairwise comparisons and ≥95% in the remaining three comparisons. Thus, outcomes were predictable with a probability error $P \leq 0.05$.

Chase frequencies, and chase and retreat distances.—Crested Honeycreepers chased adults more often than they chased immatures of subordinate species (Table 2). In contrast, Iiwis did not chase Apapane age classes differentially. Apapane adults chased conspecific adults more often than they chased immatures.

TABLE 1. Dominance matrix of degree of dominance as indicated by the number of chases directed toward or received from another species. Sample sizes (number of encounters) are given in parentheses.

	Subordinates					
	Crested Honeycreeper	Iiwi		Apapane		
Dominants	immature	Adult	Immature	Adult	Immature	Common Amakihi
Crested Honeycreeper adult	100% (23)	100% (40)	100% (14)	100% (118)	100% (37)	100% (3)
Crested Honeycreeper immature		100% (9)	100% (11)	99% (114)	99% (186)	100% (12)
Iiwi adult			100% (10)	100% (98)	100% (39)	100% (7)
Iiwi immature				100% (38)	100% (38)	100% (1)
Apapane adult					95% (19)	100% (12)
Apapane immature						100% (21)

There were significant differences among species in chase, retreat, and adjusted retreat distances ($P < 0.01$ in all cases, two-way ANOVAs; see Table 3). Chase distances increased with increasing dominance rank. Both Crested Honeycreeper age classes chased adult Apapanes farther than did either Iiwi age class, and the adults chased the Apapanes farther than did their immature conspecifics ($P < 0.05$ in all cases, Student-Newman-Keuls test). Crested Honeycreeper and Apapane adults chased adult Apapanes farther than they chased immature Apapanes ($P < 0.05$ in all cases, Student-Newman-Keuls test).

Adult and immature Apapanes responded differentially to chases by the two dominant species ($P < 0.01$ in all cases, two-way ANOVAs). Adult Apapanes (and adults and immatures combined) retreated farther from adult Crested Honeycreepers and Iiwis than from immatures, and retreated farther from adult Crested Honeycreepers than from adult Iiwis ($P < 0.05$ in all cases, Student-Newman-Keuls tests). Adult Apapanes retreated farther than did immatures when chased by adult Crested Honeycreepers and Apapanes ($P < 0.05$, Student-Newman-Keuls test). The adjusted-retreat data contained no significant differences.

Retreat sites.—Retreat-site selection by adult Apapanes depended on the age and species of the chasing bird. These Apapanes showed a greater retreat response (retreating to the sub-

TABLE 2. Chase frequencies of dominant birds (combined age classes) against adult and immature age classes of Iiwis and Apapanes compared using 2 × 2 tests of independence.

	Chasing species					
	Crested Honeycreeper		Iiwi		Adult Apapane	
Chased species	C[a]	n	C[a]	n	C[a]	n
Iiwi adult	25%	(87)				
Iiwi immature	28%	(54)				
	NS					
Apapane adult	40%	(315)	27%	(153)	7%	(1,256)
Apapane immature	21%	(169)	44%	(34)	12%	(274)
	$P < 0.001$, $G = 9.64$		NS		$P < 0.001$, $G = 7.07$	

[a] C = frequency of chases out of total number of times (n) birds co-occurred in a tree.

TABLE 3. Pairwise comparisons of differences in mean distances ($\bar{x} \pm 2$ SE) adult (A) vs. immature (I) Apapanes were chased by and retreated from dominants. See text for significant differences among comparisons.

Chaser	Apapane age class	n	Mean distances (m) Chase	Retreat	Adjusted retreat
Adult Crested Honeycreeper	A	38	7.0 (±3.4)	12.8 (±4.6)	5.8 (±2.7)
	I	28	3.1 (±1.2)	6.4 (±2.8)	3.3 (±2.2)
Immature Crested Honeycreeper	A	104	3.9 (±1.0)	7.3 (±1.4)	3.4 (±1.0)
	I	184	3.7 (±0.6)	7.5 (±0.8)	3.8 (±0.6)
Adult Iiwi	A	90	3.3 (±0.9)	7.6 (±1.5)	4.3 (±1.3)
	I	30	3.1 (±1.0)	6.2 (±1.2)	3.1 (±1.0)
Immature Iiwi	A	35	1.9 (±0.1)	4.0 (±0.8)	2.1 (±0.7)
	I	36	2.6 (±0.6)	3.8 (±0.9)	1.2 (±0.6)
Adult Apapane	A	83	3.9 (±1.2)	6.5 (±1.4)	2.7 (±1.4)
	I	174	2.3 (±0.3)	5.2 (±0.5)	3.0 (±0.6)

canopy or flying away to lessen exposure to further aggression) when chased by adult than by immature Crested Honeycreepers and Iiwis (Fig. 3). Adult Apapanes responded similarly to adults of both species, but more to immature Crested Honeycreepers than to immature Iiwis, and more strongly to other adult Apapanes than to immature Crested Honeycreepers or Iiwis (Figs. 3 and 4). Immature Apapanes responded more strongly than did adults to aggression by dominants (Fig. 4). Both Apapane age classes, however, chose similar retreat sites when chased by adult Apapanes (Fig. 4).

Interindividual distances.—Distances among pairs of species differed significantly ($P < 0.001$, two-way ANOVA). Distances between heterospecifics were much greater than those between conspecifics ($P < 0.01$, Student-Newman-Keuls test; Fig. 5). Immature Apapanes foraged closer than did adults to adult and immature Crested Honeycreepers and to adult Iiwis, and both adult and immature Apapanes foraged farther from adult than from immature Crested Honeycreepers, and farther from the latter than from adult Iiwis ($P < 0.05$ in all cases, Student-Newman-Keuls tests).

Social structures and foraging strategies.—Iiwis and Crested Honeycreepers were territorial, with a single adult or mated pair and perhaps one or more immature individuals (presumably offspring) foraging in a given tree. Pairs of Common Amakihis, generally secretive in nature, apparently occupied mutually exclusive territories. In contrast, Apapanes were nomadic, traveling and often foraging in small flocks. Typically, several birds fed in a tree, but individuals flew away and others entered the canopy at apparently random intervals, so flock cohesion appeared to be low. Sometimes seven or more Apapanes fed in a tree simultaneously, and a disproportionate number of large Apapane flocks occurred in trees containing dominant species (Table 4). Dominants had increasingly greater difficulty in chasing intruding Apapanes as the numbers of Apapanes increased (Fig. 6). The likelihood of an individual Apapane being chased from a tree occupied by a single Crested Honeycreeper decreased significantly with increasing Apapane flock size in the tree ($r = 0.893$, $P < 0.01$, one-tailed Spearman rank-order correlation).

Foraging times.—The time Apapane adults foraged on ohia canopy flowers in the presence of a dominant depended on whether the Apapanes were solitary or members of a flock (one-tailed t-test, $t = 5.1$, df $= 17$, $P < 0.001$). Apapanes in trees with a dominant fed longer when they were members of a flock (feeding time $\bar{x} = 2.96$ min) than when solitary (feeding time $\bar{x} = 0.23$ min). The shorter foraging time of solitary birds was associated with a greater frequency of chases by dominants.

DISCUSSION

Species dominance status and aggression.—Species dominance ranking was size related. Larger species dominated smaller species, and

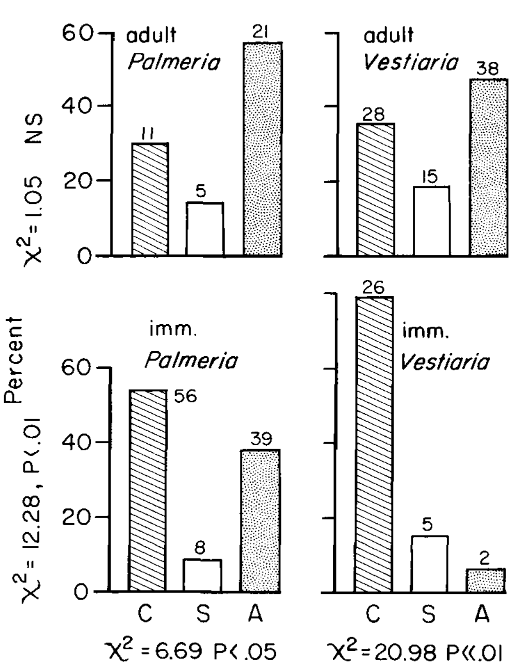

Fig. 3. Percentage use of retreat sites by adult Apapanes in response to chases by adult and immature dominants. C = retreat into neighboring canopy (hatched bar), S = retreat into subcanopy foliage (open bar), A = retreat into air (stippled bar).

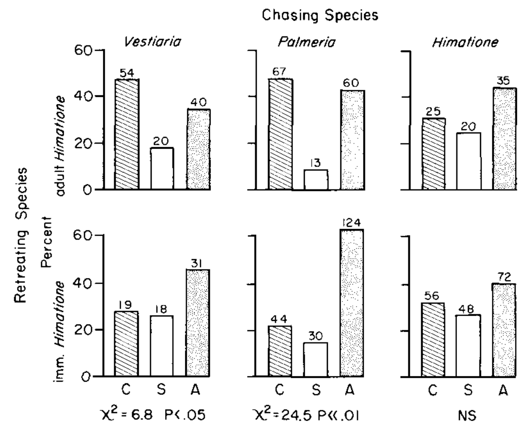

Fig. 4. Retreat-site selection of adult vs. immature Apapanes. See Fig. 3 for definition of symbols.

adults dominated immature conspecifics. Size was not the only indicator of dominance status. The Crested Honeycreeper's high rank also was reflected in the greatest chase and resulting retreat distances. Yet, data for adult Iiwis did not completely support this association: adult Iiwi chase distances did not differ from those of the bottom-ranking adult Apapanes, although unadjusted and adjusted retreat distances of adult Apapanes suggest greater sensitivity to adult Iiwi chases. Thus, while neither species showed reversals in the dominance matrix, the Iiwi's dominance is not as clearly reflected in chase and retreat distances as is the Crested Honeycreepers's dominance.

Dominants were often less tolerant of other dominants than of subordinants (given a lack of submissive behavior; Maynard Smith and Price 1973, Parker 1974). The two dominant species (Crested Honeycreepers and Iiwis) tended to be more distant from each other than from subordinates, but the difference was not significant.

Age and dominance.—The inexperience of immature birds explains some behavioral differences between age classes (e.g. Recher and Recher 1969, Searcy 1978, Berger and Gochfeld 1981) and was expected to be an important factor in aggression by immature dominants. Indeed, immature Crested Honeycreepers and Iiwis were less aggressive toward Apapanes than were adult dominants. Adult Apapanes were chased shorter distances by immatures than by adults, perhaps due to inexperience. Adjusted retreat distances of adult Apapanes were also shorter, showing that immature dominants were less effective than were adults in eliciting retreats. Such shorter retreats were partly due to shorter chase distances by immatures. Adult Apapanes were farther from adult than from immature dominants, however, indicating a greater intimidation by adult dominants. Because greater Apapane retreat response correlated with greater retreat distances, a causal relationship is likely: the higher the aggression (or the higher the disparity in dominance rank), the greater the retreat response and retreat distance. Although these differential responses to adult vs. immature dominants may be affected by plumage differences, differences in aggression levels by the two age classes indicate that experience may take precedence over plumage in determining dominance outcomes (see also Parsons and Baptista 1980). Experimental plumage manipulation (Rohwer 1977) would be required to differentiate these factors.

Adult Apapanes chased and retreated from each other farther than they chased immature

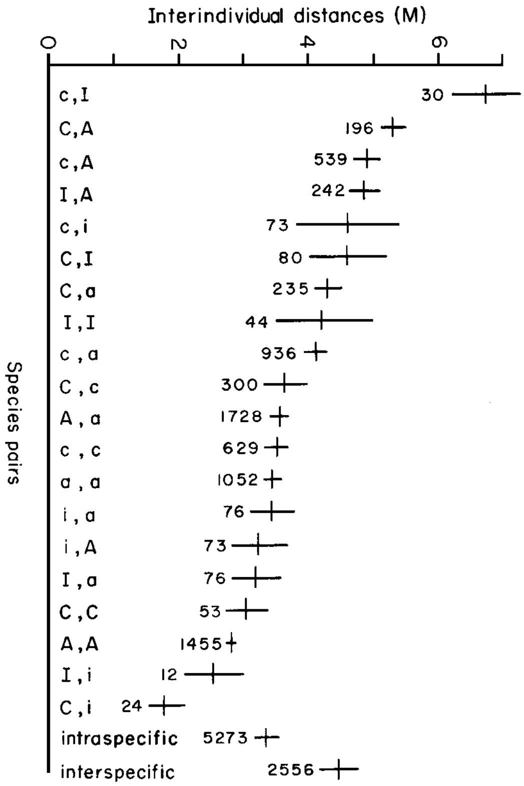

Fig. 5. Interindividual distances (in meters, $\bar{x} \pm 2$ SE) among pairs of species. C = Crested Honeycreeper, I = Iiwi, A = Apapane; upper-case letters denote adults, lower-case letters denote immatures.

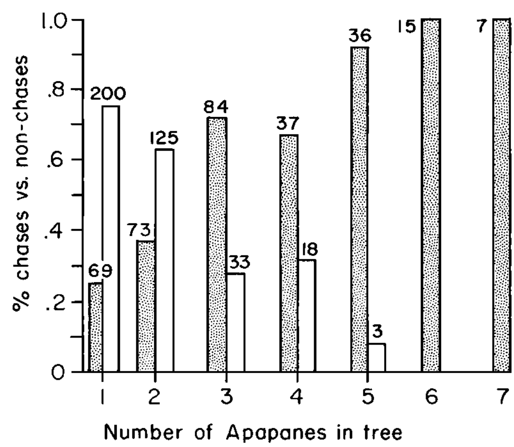

Fig. 6. Frequency with which Apapanes were chased (open bars) and not chased (stippled bars) in an ohia occupied by an Iiwi or Crested Honeycreeper as flock size increased.

conspecifics. This differential response to adult conspecifics is not unexpected. Aggression might be highest among individuals of the same age, because they show the greatest niche overlap (immatures feed on nectar less than adults do; Carothers pers. obs.), or because the closer two animals are in dominance status the more likely are altercations between them (Maynard Smith and Price 1973, Parker 1974). This effect also would explain higher aggression rates by Crested Honeycreepers toward adult than immature Apapanes, because the latter pose relatively less of a threat to the Crested Honeycreeper's status.

Adult Crested Honeycreepers and Iiwis usually have mutually exclusive territories, so that similar quantitative comparisons could not be made between them. The existence of these territories, however, reflects the occurrence of strong interspecific interference (see Murray 1971, 1981).

Age and subordinance.—Intraspecific plumage variation influences mating success (Payne 1982) and aggressive behavior competitors (Rohwer 1977, Balph et al. 1979, Ewald and Rohwer 1980). Because the two drepanidine age classes differed markedly in experience and plumage, behavioral differences between them were expected.

Apapanes and Iiwis showed differential spacing by age class. Immatures of both species occurred closer to dominants than did adults. This reduced spacing by immatures could result from (1) their drab plumage making them less visible, (2) lessened threat posed to a dominant, or (3) their inexperience in assessing potential threat from a dominant, perhaps partly resulting from lower chase frequencies. Immature Iiwis and Apapanes were chased less often than were adults, demonstrating that immatures could forage more easily in the presence of dominants. The plumage of an immature probably facilitates this apparent tolerance by dominants (e.g. Rohwer et al. 1980), but differences in visibility due to plumage differences cannot be ruled out.

I expected that the disparity in dominance status between two individuals should correlate with the subordinate's retreat distance and retreat-site selection. Apapane immatures chose safer retreat sites than did adults, although they retreated similar distances. Given the closer spacing to dominants, the greater retreat re-

TABLE 4. Percentages of Apapane flocks of various sizes in same tree as a function of the presence or absence of the dominant Iiwi or Crested Honeycreeper. Median flock sizes with dominants present differ significantly from those with dominants absent ($P < 0.01$, median tests).

Other residents (n)[a]	Apapane flock size					
	2	3	4	5	6	≥7
None (1,113)	63%	12%	12%	9%	4%	1%
Iiwis (549)	22%	56%	9%	2%	<1%	11%
Crested Honeycreepers (1,264)	41%	36%	20%	2%	1%	0%
Iiwis or Crested Honeycreepers (1,813)	35%	42%	16%	2%	<1%	4%

[a] Sample size.

sponse (despite similar or shorter chase distances) was not surprising. Although adult Apapanes had greater chase and retreat distances than did immatures, their retreat-site selection did not differ. Immatures were spaced farther from adults, however, which probably ameliorated the effects of chases. This difference in spacing also contributed to a lesser retreat-site response. Thus, as predicted, immatures reacted more to aggression than did adults, but this difference could have resulted from differential spacing rather than differential experience (reflected in greater intimidation).

Foraging strategies: territoriality and flocking.—Aggression by Crested Honeycreepers and Iiwis usually resulted in mutually exclusive territories, a situation observed in other studies (Murray 1971, 1981; Cody 1974; Catchpole 1978; Rice 1978). Common Amakihis were infrequent foragers in ohia canopies, and their secretive nature probably facilitated their use of trees occupied by dominants. In contrast, Apapanes formed flocks that flew from tree to tree and were only intraspecifically aggressive. The complete or nearly complete dominance among these species ensured highly predictable outcomes to all interspecific encounters. Predictability of outcomes may allow the development of specific behavioral tactics by subordinate species (e.g. Murray 1981) to deal with aggression by dominants, as discussed below.

As intruder density increases, a territory holder should modify or eventually abandon territoriality, reverting perhaps to dominance/subordinance relationships (Murray 1971, 1981; Wolf 1978; Myers et al. 1979). Apapanes apparently circumvent the territoriality of Iiwis and Crested Honeycreepers by entering defended trees in flocks, rendering defense of a tree too costly. This tactic has been observed in schools of reef fish invading a dominant species' territory (Robertson et al. 1976). Previously displaced Apapanes often re-entered trees while the defending dominant chased out other Apapanes (Carothers and Jaksić 1984). Thus, when avoidance alone was ineffective in minimizing aggression by a dominant, subordinates could also use flocks to overwhelm dominants.

Larger flock sizes associated with the presence of dominant species (Table 4) illustrate the tactic of flocking. Apapanes fed longer in the presence of a dominant when in a flock than when alone, and this difference was directly attributable to a difference in frequency of chases. The stepwise decline of chase frequency with increasing flock size clearly demonstrated the advantage of larger flocks. This decrease did not result from Crested Honeycreepers maintaining the same chase frequency in the face of increasing numbers of Apapane intruders. It represents an absolute decrease in the number of chases as flock size increased, as observed in other studies (e.g. Wolf 1978). The use by Apapanes of short-distance retreats into the concealing subcanopy made it difficult for dominants to evict them. This was another way Apapanes escalated the costs of territoriality to Crested Honeycreepers and Iiwis.

Because Apapane group size and the presence of dominants are positively associated with tree quality, flocking may partly result from clumped resources. That Apapanes frequently fly in loosely structured flocks (Baldwin 1953, Pimm and Pimm 1982, Carothers pers. obs.), however, shows that flocks exist away from as well as in the presence of clumped resources, which suggests that it is an adaptive behavioral tactic. In any event, its advantages are evident. Yet, ever-larger flocks are not better for flock members. Increasingly larger flock size is self-defeating, as it probably reduces the general level of nectar resources for all residents of a tree. Thus, a behavior that reduces interference may increase exploitation competition. Optimal flock size in a given ohia tree is then a compromise between the costs and benefits of these two forms of competition, and will vary among ohias depending on the tenacity of defense by the resident dominant, the food rewards available (including nectar renewal rates and number of inflorescences), and the availability of alternative food resources away from the tree.

Comparisons with the assemblage on Hawaii.— Maui and Hawaii have three drepanidine species in common, but Maui has an additional species, the Crested Honeycreeper. On Hawaii, Iiwis were generally territorial and chased Apapanes, which used a more mobile foraging strategy (Carpenter 1978, Pimm and Pimm 1982). Common Amakihis forage on the nectar of ohias and other plants solitarily or in pairs (van Riper 1984). These results agree with those of the present study. I tried to estimate what effect, if any, the addition of the dominant Crested Honeycreeper had on the interactions among the three species the two islands have in common. The Crested Honeycreeper dominated the other species. Similarly, the extinct nectar-feeding Hawaii Oo (*Moho nobilis*) dominated the extinct Hawaii Mamo (*Drepanis pacifica*), which dominated the Iiwi, Apapane, and Common Amakihi on Hawaii (Perkins 1903). On both islands the quality of nectar resources that a species used was correlated with its dominance status (Carpenter and MacMillen 1980, Pimm and Pimm 1982, Carothers pers. obs.). On Maui, the Crested Honeycreeper may cause the other three species to feed on trees of lower quality relative to the trees they use on Hawaii. The Common Amakihi was a very rare visitor to ohia flowers on Maui, hence the paucity of behavioral data. In contrast, studies on Hawaii indicate that Common Amakihis more frequently forage on flowers (van Riper 1984). On both islands this species appears to be more of a generalist feeder than the other species. Thus, a foraging shift as a consequence of interference interactions may have occurred on Maui. Unfortunately, the assemblage structure and interspecific behavioral interactions among the members of the original avifauna are unknowable because the number of species found today is a fraction of that existing before the mass extinctions resulting from the arrival of human populations (Olson and James 1982a, b).

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