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AGE-RELATED DIET DIFFERENCES IN TWO NECTAR-FEEDING DREPANIDINES: THE ʻĀKOHEKOHE AND THE ʻAPAPANE

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Abstract. Nectar-feeding birds face special dietary demands because the amino acid content of nectar is very low. I studied foraging ecology of two Hawaiian drepanidines, the ʻApapane (*Himatione sanguinea*) and the ʻĀkohekohe (*Palmeria dolei*), to see how differential growth demands of immatures and adults might be reflected in diet choice. Interference interactions affect foraging, but when this effect was factored out immatures still appeared to favor arthropod prey more than adults did. Diet differences were significant for three-month-old immatures but were indistinguishable for those nine months of age, as they are probably at adult mass. This difference in diet could be explained by the lower mass of immatures and their growth needs for attaining adult mass. These observations suggest that growing juveniles may have higher protein/calorie requirements than adults, causing differences in their foraging ecology. Differential diet demands on breeding adults were controlled, but breeding and other factors besides growth are also expected to influence diet choice.

Key Words: age and diet; ʻĀkohekohe; ʻApapane; Drepanidinae; *Himatione sanguinea*; insectivory; nectar feeder; *Palmeria dolei*.

Foraging differences between adult and immature birds have been observed for a variety of species and may result from three different age-related factors: inexperience at foraging, behavioral interference by adults, or differences in dietary requirements. Inexperience is particularly relevant when prey items require skilled detection and active pursuit and capture of prey (Amadon 1964, Recher and Recher 1969, Buckley and Buckley 1974, Searcy 1978, Porter and Sealy 1982), whereas interference interactions are important for socially interacting species which feed at a common food source (reviews in Murray 1971, 1981; Collins et al. 1990). Dietary preferences would differ among individuals facing differing metabolic demands (e.g., Sedinger 1997).

In this study, I examine which factors cause differences in the foraging behavior of adults and immatures in two nectar-feeding Hawaiian drepanidine species. These birds primarily feed upon the nectar of a single tree species (Berlin et al. *this volume*), although they also forage upon arthropods. Because of their manner of foraging and the nature of the food they consume, inexperience is unlikely to play an important role in the types of food they consume and hence unlikely to cause any differences observed. As with other nectar-feeding species (Wolf 1978, Murray 1981, Collins et al. 1990), interference interactions within and among these species are high and have an important affect upon their foraging behavior (Carothers 1986a,b; Mountainspring and Scott 1985; Scott et al. 1986). Immature Hawaiian drepanidines are subordinate to adults in the dominance hierarchy, and thus they are often excluded from nectar by defending adults (Carothers 1986a,b). Amino acid and protein levels are low in nectar (Baker and Baker 1973, 1975), but they are significant diet components and they play major roles in foraging decisions (Pulliam 1975, Gass and Montgomerie 1981). Nectar feeders certainly need protein (e.g., Brice and Gray 1991, Brice 1992). Various authors have suggested that ontogenetic diet shifts occur in birds because of differing physiological needs of immatures undergoing growth to adulthood; immatures progressing toward the attainment of adult body mass have higher protein requirements than adults (Ricklefs 1968, Fisher 1972, Morton 1973, Foster 1978, Pyke 1980, O'Connor 1984). Although it is a general observation that nestlings are fed arthropods by their parents (O'Connor 1984), there are almost no studies comparing diets of immature (postfledgling) and adult nectar-feeding birds. This paper investigates if ontogenetic diet differences occur in two species of Hawaiian drepanidines, and whether such differences can be more likely attributed to interference behavior or to differing dietary demands.

METHODS

STUDY AREA

Birds were observed in the Koʻolau Forest Reserve, on the north slopes of Haleakalā volcano on the island of Maui, Hawaiʻi, for three periods: 15 May to 25 July 1980 (Summer 1), 10 July to 10 August (Summer 2), and 10 to 27 December 1981 (Winter 1). This rain forest habitat is mainly composed of one tree species, the ʻōhiʻa (*Metrosideros polymorpha*), which has a flowering canopy and is a main food source for the nectar-feeding Hawaiian honeycreepers at all times of the year (Baldwin 1953, Carpenter 1978; Carothers 1986a,b; Berlin et al. *this volume*). The forest contains a diversity of smaller trees and shrubs that provide other locations for foraging for arthropods and as minor nectar sources.

THE BIRDS

The two species I studied are the ‘Apapane (*Himatione sanguinea*) and the ‘Ākohekohe (*Palmeria dolei*). Although both are sexually monochromatic, adults have brightly colored plumages whereas immatures are cryptically colored, allowing one to readily distinguish the two age classes (Carothers 1986a, Fancy et al. 1993a). Weight data on tags of museum specimens in University of California, Berkeley's Museum of Vertebrate Zoology collected by Baldwin (1953) on the island of Hawai‘i provide evidence that adult male ‘Apapanes ($\bar{x}$ = 16.35 g, SE = 0.17, n = 34) are heavier than immatures (14.85 g, SE = 0.32, n = 10; t-test, $P < 0.01$). ‘Ākohekohe specimens were not available, but the trend occurs in the closely-related ‘I‘iwi (*Vestiaria coccinea*) as well: adult males ($\bar{x}$ = 20.96 g, SE = 0.18, n = 13) had a higher average mass than immature males ($\bar{x}$ = 16.62 g, SE = 0.64, n = 6; t-test, $P < 0.01$). Because drepanidines are sexually dimorphic in size (Amadon 1950) we used data from males only.

‘Ākohekohes are territorial, with a single adult or mated pair and perhaps one or more immature individuals (presumably offspring) foraging in a given tree (Carothers 1986a). In contrast, ‘Apapanes are nomadic, flying about and often foraging in small flocks (Carpenter 1978, Carothers 1986a). ‘Ākohekohes of either age class dominate ‘Apapanes, and within each species adults dominate immatures (Carothers 1986a). Another nectar-feeding drepanidine that occurs in the Maui rain forests, the ‘I‘iwi, also dominates ‘Apapanes, but too few data on the diets of immature ‘I‘iwi were available to include this species in the comparative analyses.

OBSERVATIONS

Observations were conducted both from the ground and by climbing trees to observe birds at relatively close range (usually 15–20 m) in nearby trees. The following data were recorded for each individual observation: date, time, species, age of individual (by plumage), plant species occupied, stratum occupied, foraging site, and presence and identity of co-occurring birds. The presence or absence of others was recorded in order to determine the effects of dominants upon the foraging behavior of subordinates.

FORAGING COMPARISONS

There were yearly and seasonal variations in both resource availability and relative abundances of the two age classes of both bird species, necessitating the subdivision of all comparisons. Because sufficient sample sizes for immatures were not available for all three field seasons, data for each species were only analyzed for two seasons. Two types of analyses were performed. In the first, the general foraging behaviors of immature and adult conspecifics were compared to see if the two age classes differed. These analyses compared plant species foraged upon and food items selected to establish if basic differences in foraging ecology occurred between age classes.

The second set of analyses focused specifically on foraging behavior in ‘ōhi‘a trees (their main foraging site). Here I compared stratum occupied, foraging site, and food item of adult and immature conspecifics. To investigate differences in dietary preference on foraging behavior in ‘ōhi‘a trees, I needed to eliminate the effect of interference interactions by dominant individuals. Dominants defend nectar resources, inhibiting immatures from use of nectar; this should bias subordinates towards insectivory (Carothers 1986a). To control for the effect of interference interactions upon feeding preference, comparisons were made with a data set in which observations with a dominant present in the same tree were excluded. (Experimental removal of dominants, the "ideal" way of testing this hypothesis, is not feasible, as ‘Ākohekohes are on the U.S. Endangered Species List). Because adult ‘Ākohekohes dominate all others, no observations of their foraging behaviors needed to be excluded. For immature ‘Ākohekohes, observations were excluded if adults were present. Foraging observations of ‘Apapane adults were excluded if ‘Ākohekohes or ‘I‘iwis were present; for immature ‘Apapanes, observations with any co-occurring ‘Ākohekohes, ‘I‘iwis, or adult ‘Apapanes were excluded. As noted above, comparisons were made within a given season. Contingency table analyses with G-tests were used to compare frequencies of use of plant species, strata occupied, foraging sites, and food items taken. Raw frequency data (not percentage of use) were used in all tests. When a single cell size was < 5, Yate's correction was employed. Where both cell sizes were < 5, the cells were excluded from the analysis.

RESULTS

Adults and immatures of both species differ in their use of plant species (Table 1). Except for comparisons of ‘Ākohekohes during the winter season, immatures fed less frequently from the nectar producing ‘ōhi‘a trees than adults did. This demonstrates a lesser reliance upon ‘ōhi‘a nectar by immatures, as reflected in the generally lower levels of nectar foraging (Table 1).

Comparisons of foraging characteristics in ‘ōhi‘a trees in the absence of dominants show significant differences between age classes in stratum of tree occupied, foraging site, and food items taken (Table 2). In these comparisons, immatures fed less often in the flower-filled canopy. Sites occupied by arthropods (leaf buds and axils, branches and twigs) were favored foraging sites, with the result that arthropods were taken more often than was nectar. These results held for all but the winter ‘Ākohekohe adult and immature comparisons, which showed no differences.

Insects occupy flower clusters and could be taken while birds are visiting flowers for nectar. However, my observations indicate that such a behavior is not prominent: when foraging on flowers, birds displayed little evidence of doing anything other than feeding on nectar. In either case, such behavior does not change the fact that

TABLE 1. PERCENTAGES OF USE OF PLANT SPECIES AND OF ARTHROPODS AND NECTAR BY IMMATURE AND ADULT ‘APAPANE AND ‘ĀKOHEKOHE (SAMPLE SIZES IN PARENTHESES)

	‘APAPANE				‘ĀKOHEKOHE			
	Summer 1		Summer 2		Summer 2		Winter 1	
	Immature (71)	Adult (246)	Immature (2284)	Adult (1884)	Immature (1613)	Adult (458)	Immature (42)	Adult (458)
PLANT SPECIES								
Acacia koa	0	0	0.26	0	0	0	0	0.44
Broussaisia arguta[a]	1.41	4.47	0	0	0.06	0	0	0
Cheirodendron trigynum	8.45	2.08	0.79	0	0.31	0	0	3.72
Coprosma sp.	0	0	0.18	0	0.12	0	0	0
Gouldia sp.	0	0	0	0	0.06	0	0	0
Ilex anomola	0	0	0	0	0.06	0.22	0	0
Metrosideros polymorpha[a]	78.87	90.24	95.53	99.29	93.49	98.03	100	37.55
Myrsine lessertiana	0	0	0	0	1.80	1.09	0	0.44
Rubus hawaiiensis[a]	1.41	1.22	0	0	0	0	0	0
Pelea clusiaefolia	1.41	0	0.61	0.11	3.35	0.66	0	1.75
Stenogyne sp.[a]	0	0	0	0	0.37	0	0	1.75
Styphelia sp.	4.23	1.22	0.61	0	0.06	0	0	0.44
Vaccinium calycinum	4.23	0.81	0.88	0	0.31	0	0	53.93
G[b]	7.47**		63.57**		14.77*		65.65**	
FOOD ITEM								
Arthropods	57.8	24.2	10.4	2.1	21.9	12.3	29.5	23.3
Nectar	42.3	75.8	89.6	97.9	78.1	87.7	70.5	77.0
G[b]	27.15**		131.22**		22.95**		0.91	

[a] Mainly a nectar source.
[b] G-test compairing distribution of observations between immature and adults.
* denotes $P < 0.05$
** denotes $P < 0.01$

juveniles preferentially foraged on strata bearing insects.

DISCUSSION

Differences in body mass between immature and adult drepanidines are consistent with the expectation that immatures are still growing and have not yet attained adult body mass. Thus, any age-related differences in use of forage plant species and use of arthropods or nectar as a food source can be attributed at least in part to the metabolic demands of immatures for continued growth. While such considerations do not mean that this is necessarily an actual cause of diet differences, they are important for considering this hypothesis.

The few data available on other passerines (e.g., Ricklefs 1975, Austin and Ricklefs 1977) are evidence that the greatest increase in body mass of birds occurs before fledging, with more modest increases continuing into adulthood. During this postfledging period body lipid mass appears to stay constant or decrease, while protein containing components of body tissue (measured by lean dry weight) continue to increase. Thus protein/calorie considerations, while not as influential as during the prefledging period, may well be important in diet selection of immatures after fledging.

Foraging characteristics of adults and immatures reveal that they differ significantly in diet, with immatures foraging less often on flowers of ‘ōhi‘a trees (the main nectar source) than adults. These results also demonstrate that immatures feed on arthropods more often than adults. Interference competition by dominants keeping out subordinates from ‘ōhi‘a flowers is an expected cause of at least part of this bias (Carothers 1986a,b). However, the data on comparative foraging in ‘ōhi‘a trees presented here suggests the importance of dietary requirements in the foraging of immatures. In these comparisons, which statistically controlled for effects of interference interactions, immatures foraged in places where they are more likely to encounter arthropod prey items; this decreased the proportion of nectar in their diet. These results indicate that immatures indeed preferentially feed on arthropods compared to adults, despite the effect that interference interactions has in determining the foraging behavior of immatures, primarily immature ‘Apapanes.

For ‘Ākohekohe immatures, the presence of adults likely does not have an important influence on food selection. A difference between immatures of the two species is expected, given the comparatively higher levels of interference interactions directed against immature ‘Apapa-

TABLE 2. PERCENTAGES OF USE AMONG DIFFERENT FORAGING CATEGORIES IN ʻŌHIʻA TREES BY IMMATURE AND ADULT ʻAPAPANE AND ʻĀKOHEKOHE (SAMPLE SIZES IN PARENTHESES)

	ʻAPAPANE				ʻĀKOHEKOHE			
	Summer 1		Summer 2		Summer 2		Winter 1	
	Immature (36)	Adult (36)	Immature (849)	Adult (1233)	Immature (447)	Adult (1355)	Immature (172)	Adult (42)
STRATUM								
Canopy	58.3	86.3	94.1	98.6	94.4	91.0	95.2	94.1
Subcanopy	41.7	13.7	4.4	1.2	4.4	8.3	4.8	5.9
Branches	0	0	1.5	0.2	1.2	0.7	0	0
G[a]	13.1**		32.2**		9.7**		0.05	
FORAGING SITE								
Flower	54.3	80.6	83.8	98.4	83.9	90.2	73.8	71.5
Leaf Bud	8.6	5.3	6.6	0.5	5.2	0	21.4	11.6
Leaf Axil	0	0	5.7	0.6	7.5	1.3	4.8	11.1
Twig	0	0	1.5	0.2	0.7	6.5	0	0
Branch	37.1	14.1	2.5	0.6	2.6	2.0	0	5.8
G[a]	10.8**		160.4**		107.8**		5.0	
FOOD ITEM								
Arthropod	47.2	79.7	16.3	1.6	16.1	9.8	26.2	28.5
Nectar	52.8	20.3	83.7	98.4	83.9	90.2	73.8	71.5
G[a]	10.4**		160.3**		11.1**		0.09	

[a] G-test comparing distribution of observations between immatures and adults.
** denotes $P < 0.01$.

nes, which are at the bottom of the dominance hierarchy (Carothers 1986a). Immature ʻĀkohekohes are dominated only by conspecific adults, and because the adults with which they co-occur in trees are probably their parents, the levels of interference interactions are quite low (Carothers 1986a). Thus, interference interactions are unlikely to influence foraging choices of immature ʻĀkohekohes. Hence, the observed dietary preferences probably resulting from differing physiological requirements are the main factor responsible for the observed age-related foraging differences. For ʻApapanes, both diet preference and interference interactions play roles in the foraging ecology difference between adults and immatures.

One group of data did not fit the predictions of differing diet, those for immature and adult ʻĀkohekohes during the winter. Here no significant differences existed between the age classes; yet what at first seems to contradict the predictions actually supports them. With all other comparisons being of newly fledged summer immatures (approximately three months old), the immature ʻĀkohekohes observed in the winter were a full six months. Thus, they were very likely at adult body mass despite the lack of attainment of adult plumage. Accordingly, with their body growth phase completed, their metabolic demands for protein, and resulting dietary preferences and ecology, should have been and was similar to those of adults. (Data for corroboration were unavailable on ʻApapanes during this same period). In another study of nectar-feeding birds, Thomas (1980) found that for two meliphagid species that emphasized nectar, immatures also ate more arthropods but shifted to more nectar as the season progressed. Some studies (Young 1971, Hainsworth 1977, Thomas 1980) have partly attributed seasonal differences in diet to differences in nectar availability. However, because adult-immature comparisons in this study are made within seasons, any differences between the age classes cannot be attributed to differing availabilities.

A factor not addressed in this paper that may seasonally obscure diet differences based upon differing physiological requirements is the effect of reproduction. It is expected that adult females during the breeding season would eat more arthropods while they are forming eggs (Ricklefs 1974, Montgomerie and Redsell 1980, O'Connor 1984). Both adult male and female nectar feeders may increase the proportions of arthropods they capture when they are feeding young in the nest (for trochilids see Wagner 1946, Hainsworth 1977, Carpenter 1976a, Gass and Montgomerie 1981, Stiles 1995; for meliphagids see Halse 1978, Thomas 1980). These breeding effects would confound the detection of differing diet preferences of adults and immatures. However, the birds in this study were observed both before and after, but not during, the spring breeding season. In this way, diet differences that may have resulted from these breeding affects were eliminated. Future studies on the possible influence of reproduction (and molting) on diet choice in these and other nectar-feeding birds should prove rewarding, and more work on the diets of adult and immatures in other species of nectar-feeding or fruit-eating (Morton 1973, Foster 1978) birds, which also have lower than average protein contents in their diets is needed.

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