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FORAGING ECOLOGY OF THE HAWAIIAN CROW, AN ENDANGERED GENERALIST[1]

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Abstract. The hypothesis that food was limiting the population of the endangered Hawaiian Crow (*Corvus hawaiiensis*) was investigated by observing its foraging habits. This crow was an omnivore, feeding on a wide variety of items including fruits, invertebrates, flower nectar, mammals, plant parts, and passerine eggs and nestlings. It was also an opportunistic feeder, shifting to readily available resources. The crow was adept at finding passerine nests, using this high protein diet of nestlings and eggs during the passerine breeding season. Oha kepau (*Clermontia* spp.) and olapa (*Cheirodendron trigynum*) comprised the bulk of the fruits taken. Arachnida and Isopoda were the predominant invertebrates found in droppings. Crows used the upper half of the canopy of mature trees, especially ohia (*Metrosideros collina*) and koa (*Acacia koa*), for their daily activities.

Although the sample size was small, in the study area food seemed to be reasonably plentiful, and the crows were adaptable. Therefore, other factors probably are restricting the population. Efforts to maintain present habitat of the Hawaiian Crow need to be increased, with emphasis on ensuring a temporally continuous source of food.

Key words: Hawaiian Crow; Corvus hawaiiensis; *Hawaii; feeding strategy.*

INTRODUCTION

The endangered Hawaiian Crow (*Corvus hawaiiensis*) is the largest member of the order Passeriformes in Hawaii and is endemic to the island of Hawaii. This medium sized (46 to 66 cm long), brownish-black, large-billed crow was once common in forests of the Kona and Kau districts (Perkins 1903). Crow numbers began declining in the early 1900s (Munro 1944), and by the end of our study in 1980, only isolated populations were found within its former range (Fig. 1). Population estimates range from 60 to 70 (Marshall 1975) to an estimate made in 1978 of 76 ± 18 (Scott et al., in press). Many hypotheses for the decline have been advanced. One is that limited food supply has disrupted rearing of nestlings and fledglings (Banko 1976).

Many species of crows are generalists, eating various foods as they become available, for example the Common Crow in central New York (Hering 1934); the Black Crow (*C. capensis*) in South Africa (Skead 1952); various Australian crows and ravens, *C. tasmanicus, C. mellori, C. orru,* and *C. bennetti* (Rowley and Vestjens 1973); and Carrion Crow (*C. corone*) in Britain (Holyoak 1968). Most of these crows, in addition to being generalists, are also relatively common in their ranges. Food generalists are not usually rare, because they can readily adapt to changing conditions.

Because the Hawaiian Crow is endangered, we hypothesized that if food were limiting the population, the bird would be a specialist concentrating on a single or few food sources. Fruits of the ieie (scientific names are found in Table 2) vine may have been the most important food source in the 1800s; adults fed their young fruits of ieie, and stomachs of adult crows also contained this fruit (Perkins 1903). In addition, crows fed on carrion, young birds, eggs, and various fruits. Crows have been reported foraging on fruits of introduced plants (Munro 1944), and—more recently—passerine nestlings, arthropods, and various fruits and flowers (Tomich 1971, Sakai and Ralph 1980, Giffin 1983).

This paper reports a study of the feeding habits of the Hawaiian Crow, to determine whether the food supply is limiting the population. Of particular interest were variety of foods, preference for feeding perches, and

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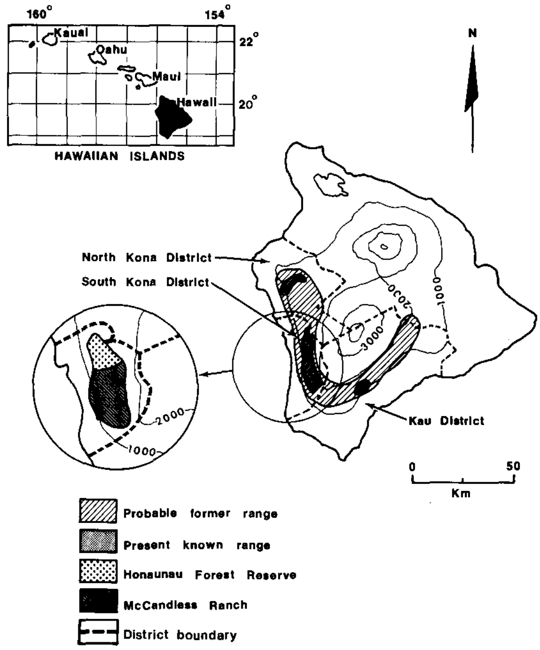


FIGURE 1. Former known range as of 1980 of the Hawaiian Crow; and study sites, Honaunau Forest Reserve and McCandless Ranch in the South Kona District, Island of Hawaii.

changes in feeding strategy between breeding and nonbreeding periods.

STUDY SITES

We studied the crow on the 4,000-ha Honaunau Forest Reserve (hereafter, "Forest Reserve") and the 24,000-ha McCandless Ranch (hereafter, "Ranch") in the South Kona District (Fig. 1). Both areas were extensively logged for koa from the mid 1920s to the late 1950s (Edward Ueda, pers. comm.). The Forest Reserve was grazed by feral cattle until 1959 (Bryan 1977), but has since remained essentially ungrazed. Wild cattle were introduced to the Ranch in the mid 1800s, and domestic cattle in the early 1900s; both are common there today. Compared with other known crow habitats, both study sites are relatively stable and are among the least disturbed crow habitats remaining.

Both sites are montane rain forests with a yearly average rainfall for the past ten years of about 120 to 140 cm, heaviest from July to October. Ohia is the dominant tree species, followed by koa (Table 1). The understory in the Forest Reserve is denser than on the Ranch. Common understory plants at both sites include tree fern, Hawaiian raspberry, pilo, ohelo, oha kepau, olapa, kolea, and mamaki.

MATERIALS AND METHODS

Four pairs of crows were studied in the Forest Reserve from May through June 1978, January through July 1979, and March to July 1980; and four pairs at the Ranch from March to July 1979. We divided observations into the nonbreeding period (January to mid-March) and the breeding period, including nest building through fledging (mid March to mid July).

We observed foraging crows by following them on foot, using binoculars, and tape-recording their activity. The length of various activities was later transcribed using a stopwatch. We classified feeding substrates as twigs (<1 cm in diameter), small branches (1 to 5 cm), medium branches (5 to 15 cm); large branches (>15 cm); and trunks (main support of a tree, with characteristic bark). Distances of hops and flights were measured by estimating the total distance traveled to the nearest 0.1 m. When a bird was foraging, we allowed 5 min to elapse between observations. A nonforaging bird was usually observed every 10 min. We used 1,537 observations of at least 10 sec, averaging 41 sec.

Because Hawaiian Crows seldom regurgitate

TABLE 1. Density, frequency, and height of 12 common tree species found in Honaunau Forest Reserve, Island of Hawaii.

Species	<3 m high <7.5 cm DBH Density (trees/ha)	<3 m high <7.5 cm DBH Frequency (%)	≥3–15 m high ≥7.5 cm DBH Density (trees/ha)	≥3–15 m high ≥7.5 cm DBH Frequency (%)	>15 m high Density (trees/ha)	>15 m high Frequency (%)	Average height (m)
Ohia	109.4	35.4	83.7	36.8	95.4	100.0	18.6
Koa	4.5	4.5	7.2	3.0	13.7	26.1	19.0
Kolea	24.7	14.8	22.9	19.9	2.7	7.9	8.0
Kawau	69.9	43.3	56.4	37.4	3.8	13.3	7.0
Pilo	51.4	25.6	66.3	41.1	0.8	3.1	7.0
Manono	23.7	18.1	7.5	6.6	0	0	5.0
Olapa	36.8	43.5	80.6	40.1	0	0	6.0
Mamaki	30.8	24.1	18.5	18.5	0	0	5.0
Kopiko	2.7	2.7	4.9	4.9	0	0	–
Alani	5.9	5.8	8.5	6.4	0	0	6.0
Oha kepau	19.0	12.6	2.2	2.2	0	0	4.0
Hoawa	8.1	7.2	–	–	0	0	7.0

TABLE 2. Percent[1] of plant species and food items on which Hawaiian Crows were observed foraging, between January and July.

	Substrate foraged upon							
Plant species	Fruit	Plant part	Flower part	Flower nectar	Sm. branch, and twig	Med. branch, lg. branch, and trunk	Bird nestling	Bird egg
Akala (*Rubus hawaiiensis*)	1.7	–	–	–	–	–	–	–
Aiea (*Nothocestrum longifolium*)	0.1	–	–	–	–	–	–	–
Alani (*Pelea* spp.)	0.4	–	–	–	–	0.1	–	–
German ivy (*Senecio mikanoides*)	–	0.1	–	–	–	–	–	–
Hai wale (*Cyrtandra* spp.)	0.1	–	–	–	–	–	–	–
Hoawa (*Pittosporum hosmeri*)	0.4	–	–	–	–	–	–	–
Hoi kuahiwi (*Smilax* spp.)	0.1	–	–	–	–	–	–	–
Ieie (*Freycinetia arborea*)	0.1	0.1	–	–	–	–	–	–
Kanawao (*Broussaisia arguta*)	0.1	–	–	–	–	–	0.1	–
Kawau (*Ilex anomala*)	0.3	–	–	–	0.7	2.1	–	–
Koa (*Acacia koa*)	0.1	–	0.1	–	4.7	10.6	1.8	–
Kolea (*Myrsine lessertiana*)	0.7	–	0.1	–	0.4	0.6	0.4	0.5
Kopiko (*Psychotria* spp.)	0.7	–	–	–	0.3	0.1	–	–
Mamaki (*Pipturus* spp.)	1.3	–	–	–	0.1	0.1	–	–
Mamane (*Sophora chrysophylla*)	0.1	–	0.1	–	–	0.1	–	–
Manono (*Gouldia terminalis*)	0.5	–	–	–	0.2	–	0.1	–
Ma oi oi (*Stenogyne* spp.)	0.1	–	–	–	–	–	–	–
Naio (*Myoporum sandwicense*)	0.1	–	–	–	–	0.2	–	–
Oha kepau (*Clermontia* spp.)	7.7	–	–	0.1	0.4	–	–	–
Oha (*Cyanea* spp.)	0.1	–	–	–	–	–	–	–
Ohe (*Tetraplasandra meiandra*)	0.1	–	–	–	0.1	0.1	–	–
Ohelo (*Vaccinium* spp.)	0.5	–	–	–	0.1	–	–	–
Ohia (*Metrosideros collina*)	–	–	0.1	6.7	9.4	22.8	3.2	0.3
Olapa (*Cheirodendron trigynum*)	12.6	–	–	–	0.6	0.7	–	–
Olomea (*Perrottetia sandwicensis*)	0.2	–	–	–	–	–	–	–
Painiu (*Astelia menziesiana*)	–	0.1	–	–	–	–	–	–
Pilo (*Coprosma* spp.)	1.4	–	–	–	0.2	0.1	0.1	–
Poha (*Physalis peruviana*)	0.1	–	–	–	–	–	–	–
Pukiawe (*Styphelia* spp.)	1.1	–	–	–	–	–	–	–
Purple poka (*Passiflora edulis*)	–	–	–	0.1	–	–	–	–
Southern pokeberry (*Phytolacca octandra*)	0.1	–	–	–	–	–	–	–
Thimbleberry (*Rubus rosaefolius*)	0.2	–	–	–	–	–	–	–
Tree fern (*Cibotium glaucum*)	–	0.1	–	–	–	0.2	0.1	–

[1] Calculated as: 100 × number of observations ÷ total observations.

pellets and rarely roost communally like some other corvids, we analyzed adult and nestling crow droppings to assess their food habits (Ralph et al. 1985). Droppings were collected from foraging birds immediately after adults defecated. We also gathered droppings, which were most likely all from the young, from below nests. Indigestible materials in the droppings of Common Crow (*C. brachyrhynchos*) consisted of virtually the same kinds of invertebrates and mammals as found in pellets (Platt 1955).

We assessed the seasonal availability of fruits and flowers on a monthly basis by counting all flowers and fruits of ten flagged plants of each species, spaced 60 m apart along a transect in the Forest Reserve. We used a sugar refractometer to analyze nectar sugar content once a week (40 measures per month) of ten ohia flowers, each on a separate tree.

We used the point quarter method (Mueller-Dombois and Ellenberg 1974:110ff) to estimate tree density. Sampling stations were located 10 m apart on both sides of a north-south grid line, at right angles to the line. The distances of the stations from the grid line were determined using randomized numbers up to 50. From each station we measured distances to the closest tree for each quarter of the circle.

RESULTS

FOOD ITEMS

Hawaiian Crows were omnivorous, eating a wide variety of plant species and other food items (Table 2). Foods ranged from plant parts to nestling birds (Fig. 2).

Foraging on trunks, branches, and foliage, probably for invertebrates, occupied 55% of their feeding activity. Crows consumed isopods (mainly pillbugs) and land snails while they foraged in foliage or while they fed woodpecker-fashion, flaking bark and moss from trunks or branches to expose hidden insects. Most of the foraging on trunks, branches, and foliage was in ohia (61%) and koa (29%). These species were the tallest and the most dominant trees in both study areas (Table 1). Crows spent

TABLE 3. Frequency of occurrence (%) of food items in Hawaiian Crow droppings, by prenesting and nesting periods.

Species	Prenesting Jan. to Mar.	Nesting Apr.	May	June	July
Total droppings sampled	10	19	72	100	57
Fruit					
Akala	0	21	19	29	44
Aiea	0	0	0	2	33
Hoawa	0	0	0	0	7
Ieie	0	0	32	22	4
Kanawao	0	0	0	1	0
Mamaki	10	5	7	38	28
Manono	0	5	3	11	28
Oha kepau	50	47	39	89	84
Ohelo	0	5	3	9	14
Olapa	20	5	57	84	79
Pilo	40	16	0	0	0
Poha	0	0	0	0	9
Pukiawe	30	0	0	1	0
Flower					
Plant unknown	20	0	0	4	0
Seed					
Koa	0	0	1	0	4
Bird part					
Passerine	20	11	45	82	55
Mammal					
House mouse	0	0	0	3	5
Invertebrate					
Arachnida	20	16	50	59	26
Isopoda	80	5	19	45	81
Diplopoda	0	0	0	3	5
Gastropoda	0	0	6	5	2
Psyllidae	0	0	10	13	2
Delphacidae	0	0	8	0	2
Lepidoptera	0	0	40	37	26
Nabidae	0	5	29	45	9
Coleoptera	0	5	14	42	38
Curculionidae	0	0	0	2	0
Carabidae	0	0	0	1	0
Diptera	0	5	5	23	23
Hymenoptera	10	0	14	23	12
Hemiptera	0	0	6	4	2
Cixiidae	0	0	0	5	0
Cicadellidae	0	0	0	3	2
Neuroptera	0	5	8	11	0
Psocoptera	10	0	1	1	0
Unknown insect	0	21	18	3	11

two thirds or more of their time foraging for invertebrates on trunks and on medium and large branches. The remainder of the time was spent foraging on small branches or twigs (Table 2).

Analyses of droppings substantiated their diverse feeding habits (Table 3). Isopoda were the predominant (61%) invertebrates during January through July; next were Arachnida (32%). Frequency of most invertebrate groups increased during the prenesting and nesting seasons, but the prenesting sample size was relatively small.

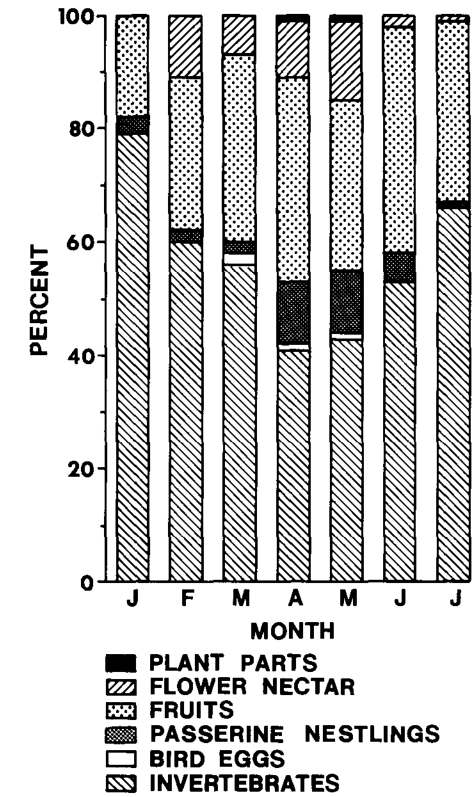


FIGURE 2. Items foraged by Hawaiian Crows, and the percent occurrence of various food items, January to July 1978–1980.

Fruits were consumed in 31% of the foraging observations and ranked second only to invertebrates as a food item (Fig. 2). The crows generally shifted their attention to the various fruits as they became available. This flexibility further demonstrates that the species is opportunistic in its feeding (Fig. 3). Most foraging was either on olapa (42%) or oha kepau (26%). Analysis of droppings (Table 3) confirmed this, as the occurrence of both olapa (59%) and oha kepau (56%) seeds was high. As would be expected, peak occurrence of oha kepau and olapa seeds in droppings (Table 3) coincided with the peak of crows feeding on these fruit (Fig. 3). During the incubation and brooding period (May to June), crows often cached oha kepau and olapa fruit clusters in the crotch of branches or twigs of ohia, koa, and kolea trees. These cached fruits were consumed mostly by the incubating or brooding bird, although the other bird of the pair occasionally ate some. The incubating or brooding bird either left the nest to feed on the cached fruits or was fed at the nest.

Passerine nestlings and eggs were taken most

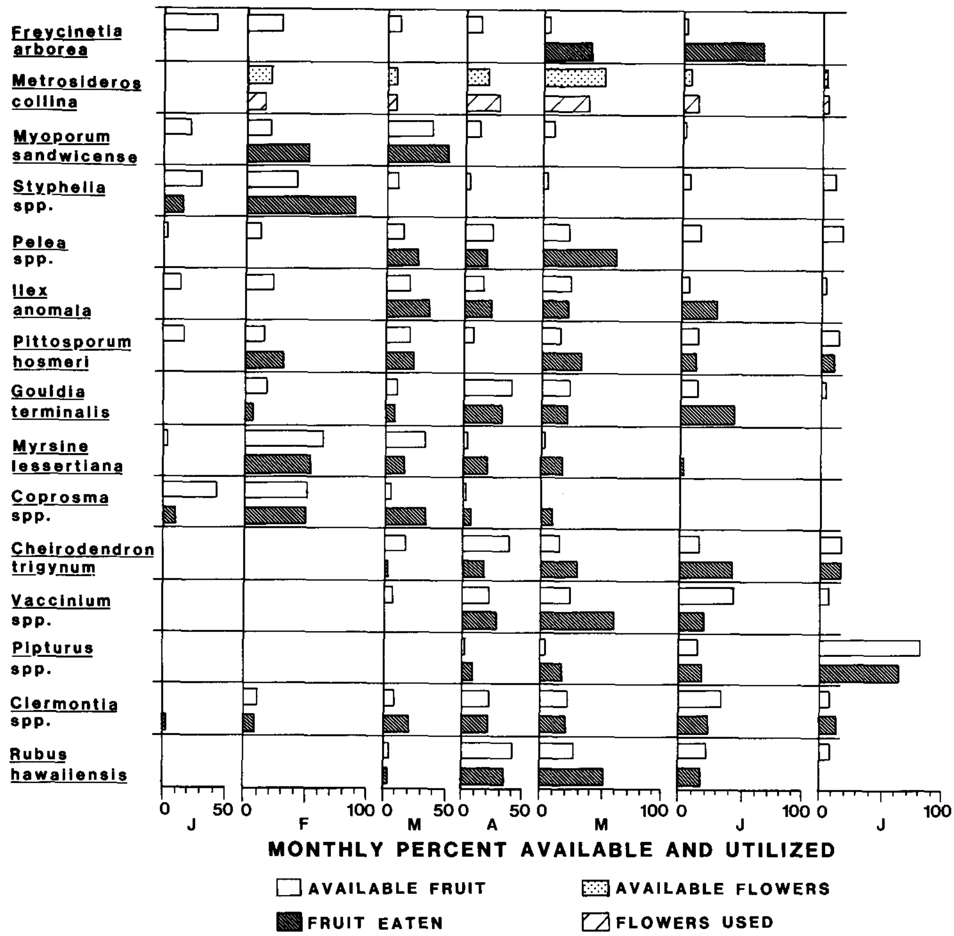


FIGURE 3. Monthly availability and the observed use by Hawaiian Crows (as the percent of the maximum observed by species) of selected fruiting and flowering plants.

frequently during April and May (Fig. 2), the breeding season of both the passerine species and the crow (Berger 1981). We observed crows preying on nestlings of several species. They included the introduced Red-billed Leiothrix, *Leiothrix lutea* (6 observations) and Japanese White-eye, *Zosterops japonicus* (11 observations) as well as four native species, Common Amakihi, *Hemignathus virens* (7 observations); Iiwi, *Vestiaria coccinea* (2 observations); Elepaio, *Chasiempsis sandwichensis* (1 observation); and Apapane, *Himatione sanguinea* (10 observations). We identified the nestlings by observing the passerine adults as they were frightened from nests by an approaching crow. Hawaiian Crows were adept at nest finding and, like Australian Crows (Rowley and Vestjens 1973), appeared to spend much time searching for nests. Crows often did not return directly to their nest, but would cache nestlings in the crotch of large branches of koa, ohia, and kolea or in twigs of kanawao, manono, pilo, and tree fern. Although no crows were observed capturing or eating house mice (*Mus musculus*), droppings in 3 of 100 samples in June contained mouse hairs, and in 3 of 57 samples in July. The incidence of small passerine bones as well as mouse bones and hairs in droppings increased from March through July, and bird feathers were common in the droppings during June. Egg shells were fairly common in the droppings between May and July. Some shell fragments may have been from their own eggs that failed to hatch. We saw an adult crow pecking at eggs of Japanese White-eye and Apapane (1 observation each) and then eating the contents.

Crows commonly foraged on flowers, presumably for nectar (Fig. 2), especially from February through May. Ohia was used most frequently. We assumed that crows were eating nectar when they tipped their heads back after probing into flowers (156 observations). The sugar content of ohia nectar remained relatively stable throughout the sampled months (Table 4) except in March, when little rain preceded sampling. The use of ohia flower nectar increased in May, when crows were feeding

TABLE 4. Mean sugar content (%) of ohia (*Metrosideros collina*) nectar, and monthly use by Hawaiian Crow.

Month	Sugar mean content (Standard deviation)	Crow use (%)
January	12 (5.0)	0
February	14 (4.2)	19
March	48 (8.8)	8
April	18 (6.7)	19
May	15 (4.3)	48
June	10 (4.1)	5
July	10 (1.3)	1
		100

week-old young. Giffin (1983) assumed that nectar was also regularly fed to young. Crows also occasionally obtained nectar from oha kepau and purple poka during the nesting period (Table 2).

Crows also foraged on various plant parts including flower petals of kolea, koa, and mamane. The Palila (*Psittirostra bailleui*) is the only other bird in Hawaii known to eat flower petals (van Riper 1980), although other cor-

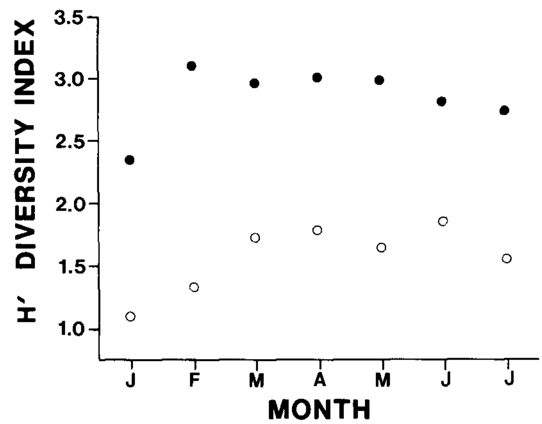


FIGURE 4. Changes in diversity of plant species used and all food items eaten by Hawaiian Crows, January to July.

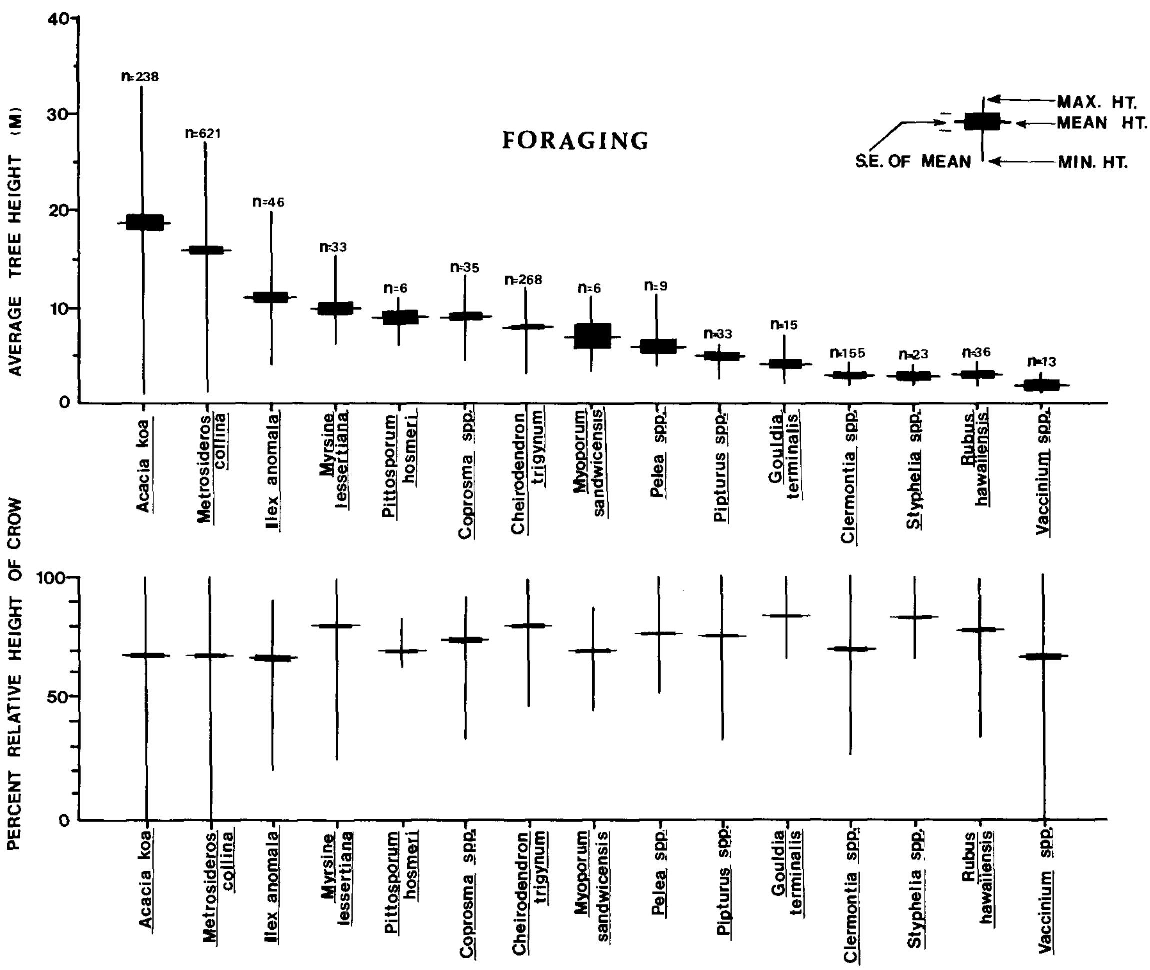
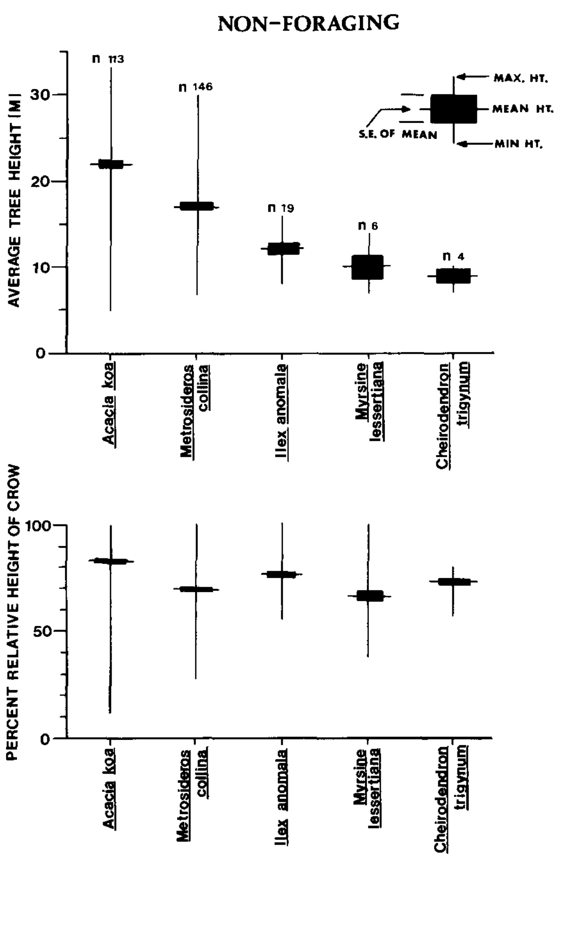


FIGURE 5. Average height of plants used by foraging (A) and nonforaging (B) Hawaiian Crows, and the relative height at which crows were seen in the plants.

vids commonly do so (Rowley and Vestjens 1973, Platt 1955). We found flower petals in 2 of 10 droppings sampled from January to March, and in 4 of 100 droppings sampled during June (Table 3). Crows stripped the basal portions of painiu plants of their fibrous outer covering and ate the inner fleshy pulp. They also fed on tree-fern stipe hair and dried German ivy vine. Mature koa and mamane pods were taken, apparently for their seeds. Crows always grasped the pod with a foot and then pecked and stripped the pod open to extract the seeds. The seeds may also have contained insects. We cannot explain crows foraging on tree-fern stipe hair, dried German ivy vine, or ohia bark stripped from twigs and small branches for reasons other than to supplement roughage. This behavior is similar to that in the Eurasian Rook (*C. frugilegus*), which habitually strips bark off lime trees (Shore 1928).

Fruits were an important food source. Although hoawa and alani fruits have hard outer coverings, and prying them open requires much energy, crows foraged on them quite regularly (Table 2). Fifteen observations of crows feeding on these fruits showed some wastefulness, which may indicate that the crows were not wanting for food. They usually ate only one seed per alani fruit, which normally contain four to eight seeds (Rock 1974). By contrast, in 80% of all hoawa capsules examined by Rock (1974), almost the entire seed content had been eaten by crows. In capsules we examined, only between 33% and 50% of all seeds had been eaten.

The diversity (H'; Shannon and Weaver 1949) of plant species eaten by crows was low in January, possibly due to fewer available fruiting plants (Fig. 4). It increased thereafter, but varied little before February to March, during April to June and after July nesting (Fig. 3).



PREFERRED PERCHES

Hawaiian Crows fed extensively in mature trees and spent over two thirds of their time in the upper half of the canopy for both their foraging and nonforaging activities (Fig. 5). The crows spent limited time on the ground, most likely as a defensive measure against ground predators. This is in contrast to many other corvids.

Mature trees with sturdier branches were favored over younger trees. Adult crows attempted to perch on small, single-stemmed pilo and Hawaiian raspberry plants to feed (7 observations) but were unsuccessful. Crows perched on more supportive parts of adjacent trees (41 observations) to feed on fruits of Hawaiian raspberry, ohelo, oha kepau, pilo, olapa, and ma oi oi. Crows used medium to large perches (21 observations) as they removed the outer covering from fruits of oha kepau, hoawa, and alani. Crows occasionally foraged on the ground for invertebrate larvae (6 observations), for fallen fruits of olapa (3 observations) and ohelo (2 observations), or to pluck fruit from thimbleberry and poha. Thimbleberry and poha shrubs grow only to a meter in height and have weak branches.

FEEDING STRATEGY

In order to assay possible food stress during the nestling period, we determined changes in the type of food and rates of feeding from those at other times of the year. If food resources were limited, we would expect crows to work harder during the nestling period. Of the seven known nests, six either contained infertile eggs or the nestlings suffered from disease or suspected predation, so we confined our observations to a single nest.

Changes in the diversity of food items eaten (Fig. 4) by all the crows that we observed fluc-

TABLE 5. Mean number and rates of foraging motions of a successful nesting pair of Hawaiian Crows.

	Prenesting period	Nesting period		
		Nest building	Incubating-brooding	Post-brooding
	Number of motions			
Observations	287	96	190	66
Mean foraging motions/min	19.6	24.7	30.9	37.6
Standard error	0.90	2.07	1.21	1.17
Z-value between periods		2.26	2.59*	3.98*
	Rates of motions			
Hops				
Observations	473	255	913	199
Mean speed, m/min	5.7	7.8	11.4	14.9
Standard error	0.3	0.6	0.3	1.0
Z-value between periods		2.96*	5.13*	3.32*
Flights				
Observations	473	254	904	181
Mean speed, m/min	55.7	18.7	33.4	3.3
Standard error	6.3	5.8	2.3	0.6
Z-value between periods		4.30*	2.35	12.75*

* Bonferroni Z-value significant, $P \leq -5$.

tuated little between February and July, but less use of plants was evident in both January and July. This can be attributed to increased feeding on invertebrates (Fig. 2).

Numbers of feeding motions defined as probes, plucks, pecks, and other feeding motions (Table 5) did not differ significantly ($P >$ 0.05; Bonferroni Z-test) between the prenesting and nesting periods. However, during the nesting period, the rate of feeding motions did increase between nest building and incubating and brooding, and between incubating and brooding and postbrooding ($P \leq 0.05$). This increase presumably could be attributed to crows providing food for their own physiological needs and for their young.

The mean speed of movements (Table 5) revealed that the average distance hopped per min of foraging was larger ($P \leq 0.05$) during the nesting season, including postbrooding, presumably in search of invertebrates, nestlings, and eggs (Fig. 2). However, the average distance flown per minute of foraging decreased irregularly during the breeding season ($P \leq 0.05$), as more fruiting and flowering plants became available (Fig. 3).

DISCUSSION

If food were limiting, the Hawaiian Crow would probably be a specialist, not flexible in its feeding habits. However, we found that the crow was flexible. We believe that in our study areas they were not food-stressed during our study. This conclusion is suggested by four lines of evidence, none of them unequivocal, but each suggestive. First, our analysis of the feeding strategy at one nest, the food items available vs. those eaten (Table 2), and the wide variety of food in their droppings (Table 3), all indicate the Hawaiian Crow is a true generalist capable of taking virtually any kind of food available. Second, the propensity for shifting the diet to foods that are most available further suggests a plasticity and nonselectivity. This flexibility is further supported by the change in feeding habits since earlier observations (Perkins 1903) when ieie was abundant and an important food for nestlings. We found it to be scarce and not important; other foods apparently have replaced ieie. Third, when feeding upon certain fruits, the crows were much more wasteful than they were observed to be when their numbers were greater. And finally, the 1.56 average value of H' (Fig. 4), representing diversity of food items taken throughout the nesting season, was fairly consistent and indicated lack of specific food requirements. In addition, the species is apparently quite flexible in choosing its nest sites (Giffin 1983; Jenkins and Sakai, unpubl. data). We believe that the small population of Hawaiian Crows can be attributed to other factors, e.g., disease or infertile eggs (Jenkins and Sakai, unpubl. data), or illegal hunting.

Hawaiian Crows were rarely seen in areas other than intact native forests. This suggests that they favored undisturbed areas. Since food resources in undisturbed areas are more abundant than in disturbed areas, we feel that some areas that are presently disturbed should be allocated to uses compatible with the growth and regeneration of native forests if the crow is to survive as a viable, wild species.

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