

ASPECTS OF THE LIFE HISTORY AND FORAGING ECOLOGY OF THE ENDANGERED AKIAPOLAAU¹

C. JOHN RALPH AND STEVEN G. FANCY

U.S.D.A. Forest Service, Redwood Sciences Laboratory,
1700 Bayview Dr., Arcata, CA 95521 and
National Biological Service, Pacific Islands Science Center,
P.O. Box 44, Hawaii National Park, HI 96718

Abstract. Relative abundance, breeding ecology, annual survival, home range, and foraging ecology of Akiapolaau (*Hemignathus munroi*), an endangered Hawaiian honeycreeper, were studied on the island of Hawaii. The species is a specialist: Akiapolaau used koa (*Acacia koa*) for foraging much more than expected based on koa availability, and most Akiapolaau occurred in old-growth koa and ohia (*Metrosideros polymorpha*) forests. Male Akiapolaau most often foraged on the trunks and large branches of koa, whereas females used small branches and twigs. The longer bill of males is apparently adapted to the greater bark thickness of larger branches. Lichen-covered and dead branches were preferred feeding sites. Akiapolaau showed serial monogamy and had a relatively low reproductive rate of 0.86 young pair⁻¹ year⁻¹, with a long parental dependency period. Home range sizes averaged 10.7 ha and did not differ between males and females. Annual survival for adults was 0.71. Avian diseases appear to restrict Akiapolaau to higher elevation forests where mosquitoes are rare. Protection of remaining old-growth koa and ohia forests above the mosquito zone are critical to the survival of the species.

Key words: *Akiapolaau*; *Hemignathus munroi*; *demography*; *survival*; *home range*; *foraging ecology*; *Hawaii*.

INTRODUCTION

Hawaiian honeycreepers (Fringillidae: Drepanidinae) are a showcase example of adaptive radiation and speciation on a remote island chain. This endemic subfamily, thought to be derived from a single colonization by a cardueline finch from North America (Johnson et al. 1989), has evolved into a diverse group of species that includes the sickle-billed, nectarivorous Iiwi (*Vestiaria coccinea*), the cross-billed, insectivorous Akepa (*Loxops coccineus*), and the stout-billed, seed-eating Palila (*Loxioides bailleui*) (Scott et al. 1986, 1988; Freed et al. 1987). Even among such an assemblage, the bill and feeding motions of the Akiapolaau (*Hemignathus munroi*) are bizarre. The maxilla is long (21–29 mm; Amadon 1950, Pratt et al. 1994) and decurved. By contrast, the mandible is straight and robust, and only half the length of the maxilla (Pratt et al. 1994). The utility of the beak is realized in the species' woodpecker-like foraging motions and its ability to extract insects from beneath the bark of trees as well as to probe and pry insects from surface deformities and glean them from twigs

and leaves (Perkins 1903, this study). The Akiapolaau is the only surviving species on the island of Hawaii to exploit this woodpecker niche, and yet it is rare and restricted in its range despite the apparent lack of competition.

Akiapolaau are found only on the island of Hawaii, where they occur in four disjunct populations totaling fewer than 1,500 birds (Scott et al. 1986, Fancy et al. 1996). Their distribution ranges from 1,300 to 2,100 m elevation in mesic and wet ohia (*Metrosideros polymorpha*) and koa (*Acacia koa*) forests in the Kau, Hamakua, and Kona districts of Hawaii (Fig. 1) and from 1,900 to 2,900 m elevation in dry mamane (*Sophora chrysophylla*) and naio (*Myoporum sandwichense*) forests on Mauna Kea. Total population size in the dry, high-elevation forest is probably now less than 15 birds, and the dry forest population may become extinct within the next five years (Fancy et al. 1996).

The species' foraging methods are well described (Perkins 1903, Berger 1981), as are its eggs and nest (Banko and Williams 1993). Methods to sex and age Akiapolaau were developed by Pratt et al. (1994). However, the species' rarity and the inaccessibility of its habitat have prevented any previous detailed study of its foraging

¹ Received 13 June 1995. Accepted 26 February 1996.

ecology or life history. We report here on the relative abundance, breeding ecology, annual survival, home range, and foraging ecology of Akiapolaau. This information was obtained during a larger study of the demography and foraging ecology of Hawaiian forest birds at five study sites on Hawaii.

STUDY AREAS AND METHODS

We studied Akiapolaau between November 1976 and January 1982 at five study areas on Hawaii: Keauhou Ranch (19°31'N, 155°20'W; 1,740 m elevation), Kilauea Forest (19°31'N, 155°19'W; 1,630 m), Hamakua (19°47'N, 155°20'W; 1,770 m), Kau Forest (19°13'N, 155°39'W; 1,750 m), and a Dry Forest site (19°49'N, 155°33'W; 1,865–2,800 m). The vegetation and level of disturbance to each of the first four, wet forest, study areas is described in Ralph and Fancy (1994a). The Kau Forest study area is dominated by ohia and lacked koa and naio, and we never found any Akiapolaau at that site. The Dry Forest site is a 4.3 km belt transect on the southwest slope of Mauna Kea dominated by mamane and naio and ranges from 1,865 m to tree line at 2,800 m.

We surveyed 25–162 stations each month at each study site using the variable circular-plot method with 8-min counts (Scott et al. 1986) to obtain indices of Akiapolaau abundance. We were unable to obtain accurate densities by this method because of the species' rarity and large differences in detectability among months; therefore, we used the mean number of Akiapolaau detected per station as an index of abundance. We excluded birds detected >100 m from the station to reduce the effects on the abundance index of using different observers and counting the same bird from multiple stations. Relative abundance among study sites and months was compared by two-way ANOVA and Tukey's test using survey data for 1979–1980, when all three study sites were sampled. We used Type-IV sum of squares to compare differences because of missing data for some months at the Hamakua site.

We captured birds in mist nets at the Keauhou Ranch ($n = 62,006$ net hours, November 1976 to January 1982) and Kilauea Forest ($n = 16,958$ net hours, April 1978 to November 1979) study areas, and processed birds as described by Ralph and Fancy (1994b). Fecal samples from cloth bags in which the birds were placed were preserved and analyzed as described in Ralph et al.

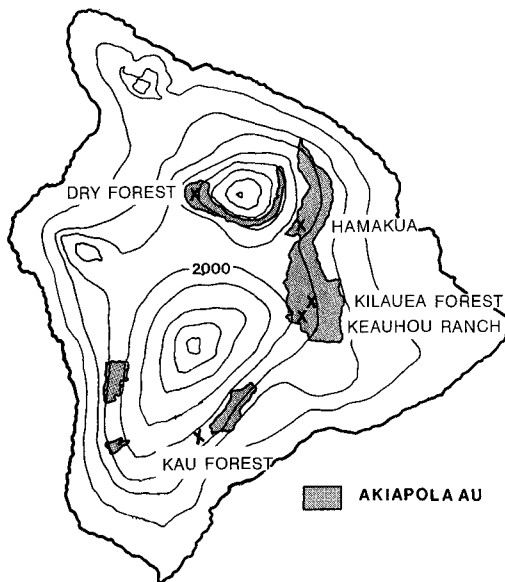


FIGURE 1. Location of study areas (X) and distribution of Akiapolaau on the island of Hawaii during the 1970s.

(1985) to determine food habits. Sex was determined by presence of a brood patch or cloacal protuberance (Ralph et al. 1993), by plumage characteristics (Pratt et al. 1994) in the case of a few adult males, or by observations of nesting birds. We identified juvenile birds on the basis of plumage characteristics, skull ossification (Pyle et al. 1987), calls, and behavior.

We conducted a discriminant analysis of culmen length, wing length, and body mass of known-sex, adult (AHY) Akiapolaau to develop additional methods for sexing Akiapolaau from measurements. Wing length (chord) was measured to the nearest millimeter with a metal rule, from the bend to the tip of the longest primary of the unflattened, folded wing. Exposed culmen was measured with a flexible rule along the upper surface of the maxilla from the tip to the start of the feathered area at the base of the maxilla. We classified each specimen by sex using linear discriminant functions, and we produced unbiased error rates by classifying individuals by a jack-knife procedure.

We estimated annual survival of adult Akiapolaau at the Keauhou Ranch site with a Jolly-Seber model (Pollock et al. 1990) from capture-recapture and resighting records for 20 color-banded birds. We excluded juvenile (hatching year) birds from this analysis because of small

sample sizes. We selected a four-month sampling period each year from September through December, 1976–1980, based on goodness-of-fit tests from preliminary runs. Birds captured or resighted during the eight-month period from January through August were coded as resightings and used to calculate survival probabilities (Model AX of JOLLY; Pollock et al. 1990:85). The complement of survival probability that we report here includes both mortality and permanent emigration.

Home ranges of 17 Akiapolaau were determined from locations of birds captured in nets or resighted during weekly surveys throughout a 600 × 600 m site at Keauhou Ranch, following methods described in Ralph and Fancy (1994b). Individuals with fewer than ten locations were excluded. Home range size was correlated with the number of locations; therefore, we compared minimum convex polygon size between males and females by analysis of covariance using the number of locations as a covariate.

We quantified foraging activities and use of different foraging substrates during weekly surveys at the Keauhou Ranch site. During each survey, we walked throughout the entire grid and recorded activities, locations, and band combinations of Akiapolaau; we attempted to obtain at least 35 sampling bouts during each survey. Each bird was observed for a mean of 24.8 ± 0.32 SE seconds (range 3–161 seconds), and usually fewer than three activity budgets were taken on an individual during each survey. Each time that a bird was observed foraging, we recorded the foraging activity (probe, glean, peck, or pry), height of the bird above the ground, height of the tree, species of tree, size (diameter) of branch that the bird was on (twig = < 1 cm; small branch = 1–5 cm; medium branch = 5–15 cm; large branch = > 15 cm; and trunk), whether the bird was foraging on live or dead wood, and whether or not the bird was foraging on bark with > 10% coverage by the epiphytic, fruticose lichen *Usnea* spp. We compared foraging heights between males and females using analysis of covariance with tree height as a covariate, and we compared heights of trees used by each sex using a *t*-test. Differences in the percentage of time spent by males versus females on different tree species (koa, ohia, and naio) and branch sizes were compared by Tukey's test to control for Type-I errors.

We developed indices of foliage volume and bark surface area at each site to compare the

availability of ohia, koa, and naio with their use by Akiapolaau for foraging. Foliage volume was measured at each of the bird census stations on each study area following methods of MacArthur and MacArthur (1961) and Anderson et al. (1983). Bark surface area was derived from the point quarter method (Mueller-Dombois and Ellenberg 1974:110) and measurements of the total length of the trunk and of small, medium, and large branches of sampled trees. Surface area was calculated from length measurements and the formula for the surface area of a cylinder.

Values presented are means \pm SE.

RESULTS

RELATIVE ABUNDANCE

The number of Akiapolaau detected per station each month was highly variable, with peak numbers usually detected during August–November each year (Fig. 2). Abundance indices of Akiapolaau at Keauhou Ranch and Kilauea Forest were highly correlated ($r = 0.52$, $n = 27$, $P = 0.005$). During 1979 and 1980, when we conducted variable circular-plot surveys at Keauhou Ranch, Kilauea Forest, and Hamakua, we found significant variation in Akiapolaau abundance among study sites ($F_{2,19} = 4.21$, $P = 0.03$) and among months ($F_{11,19} = 3.13$, $P = 0.01$), with abundance (mean birds/station) at Keauhou Ranch (0.137 ± 0.016) being higher than at Kilauea Forest (0.074 ± 0.016) and Hamakua (0.092 ± 0.047); Tukey's test, $df = 19$, $P < 0.05$). At Keauhou Ranch, where we did the majority of our mist netting, monthly capture rates of Akiapolaau were highly correlated with the number of Akiapolaau detected per station ($r = 0.35$, $n = 52$, $P = 0.01$) and with the percent of stations at which Akiapolaau were detected ($r = 0.49$, $n = 52$, $P = 0.002$). Mean number of Akiapolaau detected per station at Keauhou Ranch decreased during the study (regression, $n = 55$, $P = 0.0001$).

BODY MEASUREMENTS

Discriminant analyses with exposed culmen, wing, and body mass as variables indicated that the discriminant function that best identified males from females by measurements included only exposed culmen (EXPCUL, mm) and wing length (WING, mm):

$$D = 0.599*EXPCUL + 1.566*WING - 140.0$$

where D is the discriminant score for an individual. Akiapolaau with positive scores should

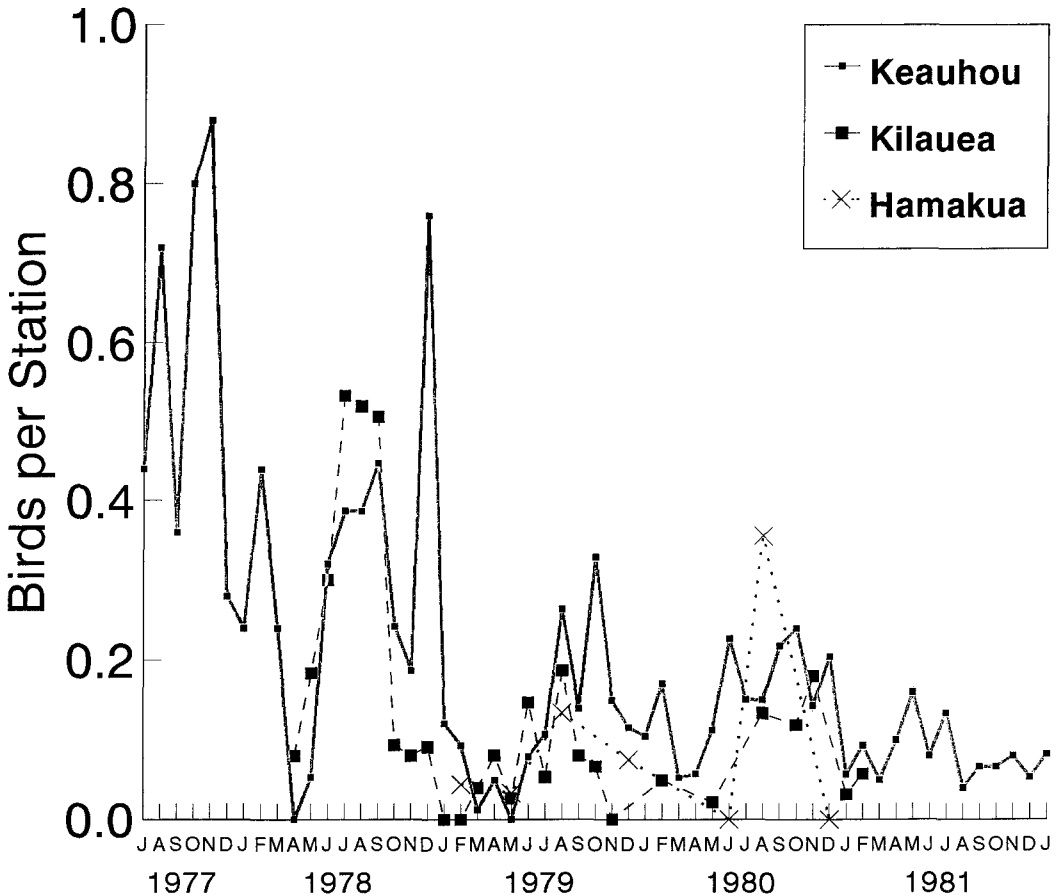


FIGURE 2. Mean monthly density of Akiapolaau at Keauhou Ranch, Kilauea Forest, and Hamakua, Hawaii, 1977–1982.

be classified as males, and those with negative scores should be classified as females. We correctly classified 21 of 22 Akiapolaau of known sex by this method.

In separate *t*-tests, we found that exposed culmen lengths of 12 adult males (29.97 ± 0.49) were longer than those of ten females (25.15 ± 0.88 ; $t = 5.03$, $df = 20$, $P = 0.001$). Males had mean wing lengths of 80.87 ± 0.34 mm, compared with 77.38 ± 0.48 for females ($t = 6.10$, $df = 20$, $P < 0.0001$). Males were also heavier, with body masses of 28.86 ± 0.40 g, as compared with 25.93 ± 0.53 g for females ($t = 4.51$, $df = 20$, $P = 0.0002$).

BREEDING AND NESTING

Akiapolaau demonstrated serial monogamy in our study: of 14 pair-years of observation in which at least one member of the pair was banded we

never observed a pair nesting together for two seasons and we observed four cases where Akiapolaau definitely switched mates between one breeding season and the next. In two cases involving a banded male and an unbanded female, it is possible that the pair remained together for at least two breeding seasons, but we could not confirm this. In three cases where an individual changed mates, the other member of the pair left the study area. However, one female who had mated and produced a young in 1978 left that male for another in early January 1979. She consorted with the new male until mid-February, and then was seen in the company of still another male in April 1979. The first two males remained in the area and were seen infrequently until December 1979 and December 1980, respectively.

Only one young per year was produced by the pairs with at least one banded parent. Twelve

fledged young were produced from the 14 pair-years of observation. During regular surveys to quantify activities and search for banded birds, we observed an Akiapolaau with more than one young on only three of 217 occasions where an adult was seen with one or more young. The duration of the parental dependency period appeared to be very long: four young remained on the study area with their parents for at least four months, and one young was still observed with its parents five months after fledging.

We observed two nests, one for 592 minutes of observation during nest construction and incubation at Keauhou Ranch during 16 July–15 August 1979, and the second, at Kilauea Forest during 21 February–6 March 1980, for 1,910 minutes. Observations began five days before the eggs hatched and ended after the young fledged. The nest at Keauhou Ranch was a cup nest in the small branches near the top of a 20-m high koa tree, and the Kilauea Forest nest was 11.3 m off the ground in a cavity where a limb had broken off of a 20-m high ohia tree.

Only the female incubated and brooded the young. From observations of a single nest, we observed that on days 1–3 of the brooding period the female fed the young and removed fecal sacs, and the male fed the female off the nest in a fashion typical of drepanidines (Perkins 1903, Berger 1981). On days 4–5 the male began coming to the nest, feeding the female there, and possibly also the young. The female continued to feed the young and remove fecal sacs. On days 6–9, the male played an increasing role, feeding the young directly, removing fecal sacs, and continuing to feed the female. The female continued to make more trips to the nest than the male. The single young fledged on day 21.

HOME RANGE

We found no difference in home range size between nine males and eight females after adjusting for the number of locations at which each bird was observed (analysis of covariance, $F_{1,14} = 1.45$, $P = 0.25$). Mean home range size for both sexes combined ($n = 17$) was 10.73 ± 1.01 ha (range 4–17 ha). Home range size for some birds approached the size of the study area and was probably underestimated. We observed considerable overlap among home ranges, but observations of Akiapolaau reacting aggressively to playbacks (M. Moore, unpubl.) and chasing individuals of the same sex suggest that they may

defend part of their large home ranges as territories.

ANNUAL SURVIVAL

We found a high probability (0.80 ± 0.21) of resighting an individual during the September–December sampling period if it was present on the study area. This allowed us to fit a Jolly-Seber model to our data ($\chi^2 = 0.12$, $df = 1$, $P = 0.72$), even though we had data for only 20 adult birds. Annual survival for adults (the complement of which includes permanent emigration) was 0.71 ± 0.03 . We were unable to estimate survival for juvenile Akiapolaau since most of the birds either left the study area or died before they could be banded. However, ten young remained on the grid with one or more of their banded parents for a mean of 105 days (range 38–157) before they disappeared.

FORAGING BEHAVIOR

The use of koa by Akiapolaau for foraging at Keauhou Ranch, Kilauea Forest, and Hamakua was much greater than expected based on the availability of koa (Fig. 3). For example, 63% of foraging observations at Keauhou Ranch were in koa, but koa comprised only 13% of the bark surface area and 12% of foliage volume of trees at that site. Selection for koa was consistent throughout the year (Fig. 4), with 45–65% of foraging observations in koa during each month. At Keauhou Ranch and Kilauea Forest, naio was also used much more than expected, based on its availability (Fig. 3). At the Dry Forest site, 61% of 93 foraging observations were on mamane and 38% were on naio, compared to the relative availability of mamane of 26% and naio of 74%, by both the bark surface area and foliage volume methods. This indicated that Akiapolaau selected mamane over naio for foraging. Kolea (*Myrsine lessertiana*) was rare at all study sites but was used more than expected for foraging (Fig. 3). At the Hamakua study site, 16% of foraging observations were in kolea although the availability of kolea was only 2% based on foliage volume.

Observations of Akiapolaau foraging on koa indicated that they selected for lichen-covered and dead branches, presumably because these substrates harbored more insects. For example, Akiapolaau spent an average of 69% of their time on lichen-covered branches at Keauhou Ranch ($n = 1,954$ observation bouts), 75% of time at

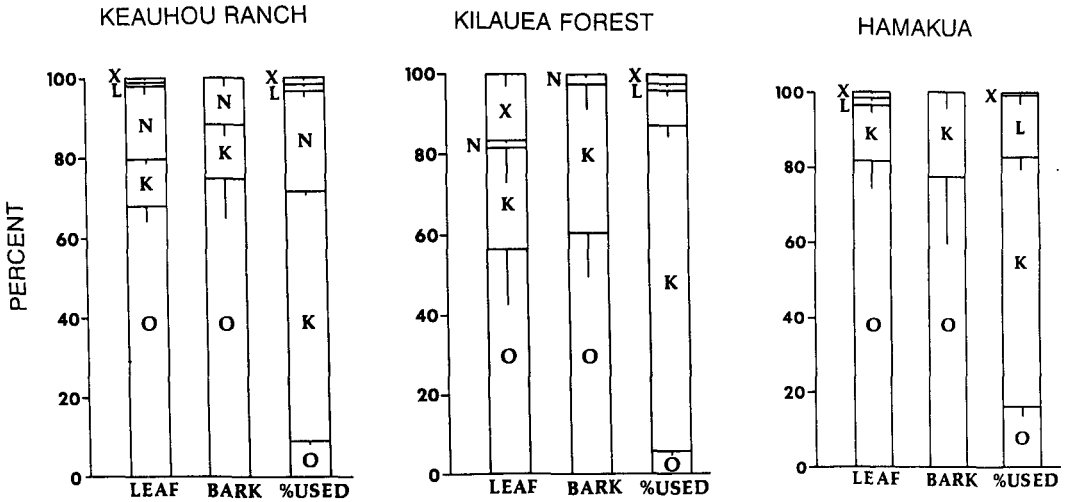


FIGURE 3. Availability of tree species as determined by foliage volume (LEAF) and bark surface area (BARK), and percent of foraging observations of Akiapolaau (% USED) on ohia (O), koa (K), naio (N), kolea (L; *Myrsine* spp.), and all other tree species combined (X), at Keauhou Ranch, Kilauea Forest, and Hamakua, Hawaii.

Kilauea Forest ($n = 661$), and 79% of time at Hamakua ($n = 270$). Similarly, mean time spent on dead branches was 50% at Keauhou Ranch, 70% at Kilauea Forest, and 62% at Hamakua (sample sizes same as above).

Branch sizes selected for foraging by Akiapolaau differed between sexes (Table 1). Males spent more time foraging on the trunk and larger branches of trees, whereas females spent more time on twigs and small branches. After adjusting for tree height, the foraging height for females

was higher than that for males in koa (analysis of covariance, $F_{1,1096} = 58.3, P < 0.0001$) and naio ($F_{1,438} = 12.2, P = 0.0005$), but not in ohia ($F_{1,141} = 3.4, P = 0.067$). Males selected taller koa and ohia trees for foraging than did females (Table 2).

Percent occurrence of arthropods in 38 fecal samples from adult birds are shown in Table 3. Mandibles of lepidoptera larvae were found in 92% of the droppings. Spiders were fairly common (53%), as were cerambicid larvae (42%).

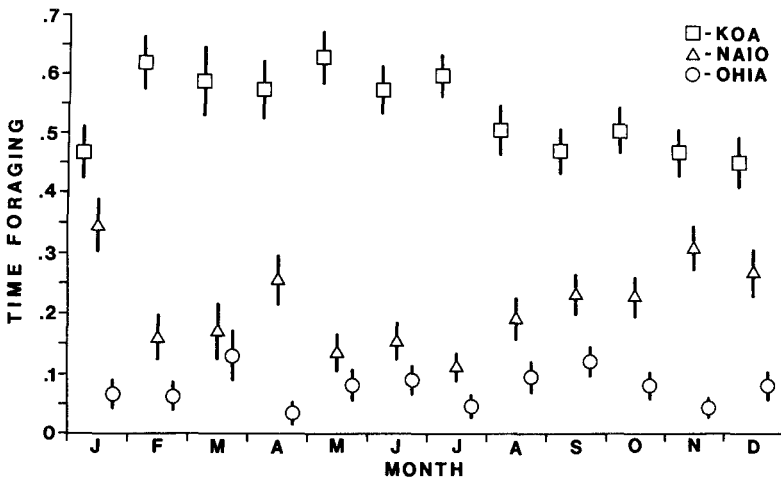


FIGURE 4. Mean monthly time spent foraging on koa, ohia, and naio by Akiapolaau at Keauhou Ranch, Hawaii, 1977-1982.

TABLE 1. Mean percent of time spent foraging by male ($n = 1,044$) and female ($n = 492$) Akiapolau on different sizes of branches of koa, ohia, and naio trees, Keauhou Ranch, Hawaii.

Tree	Branch size	Males		Females		P
		Mean %	SE	Mean %	SE	
Koa	Twigs	1.71	0.35	14.73	1.48	**
	Small branches	17.48	1.10	39.78	2.08	**
	Medium branches	21.94	1.22	14.10	1.49	**
	Large branches	6.50	0.72	2.07	0.59	**
Ohia	Trunks	2.83	0.48	1.22	0.46	
	Twigs	0.68	0.23	1.63	0.55	
	Small branches	3.03	0.51	1.48	0.52	
	Medium branches	3.66	0.56	0.47	0.29	
Naio	Large branches	0.49	0.21	0.41	0.29	
	Trunks	1.45	0.36	0.30	0.22	
	Twigs	3.93	0.56	5.10	0.96	
	Small branches	10.11	0.87	7.99	1.18	
	Medium branches	5.68	0.67	1.09	0.45	**
	Large branches	1.93	0.40	0.20	0.20	
	Trunks	4.48	0.61	0.99	0.41	

** Significant difference found by Tukey's test, $P < 0.05$.

DISCUSSION

Our monthly surveys suggested that the Akiapolau population at Keauhou Ranch and Kilauea Forest increased each fall and then decreased to lowest levels during January through April. However, we found that marked individuals remained on the study area throughout the year and thus the seasonal pattern in abundance indices was not caused by a regular migration of birds into and out of the study area. A combination of larger numbers of young and higher detection rates from increased calling rates, particularly by juvenile birds, could account for the apparent increase in populations each fall. Ralph and Fancy (1994a) found that singing rates of Akiapolau peaked in June but were otherwise fairly constant throughout the year, but calling rates were higher during September–December than in other months, with peak calling in No-

vember (Ralph, unpubl.). Akiapolau breed throughout the year (Ralph and Fancy 1994a), but we recorded the greatest number of sightings of immature birds during the fall and the lowest number in April.

Akiapolau were more abundant at Keauhou Ranch than at Kilauea Forest during the study even though Kilauea Forest had a much higher density of koa (Fig. 3). Keauhou Ranch was regularly grazed, but because the site had no permanent water, it was subjected to less grazing pressure than Hamakua. Also, the fortuitous piling of koa logs from a previous harvest created small areas ranging from 10–500 m² that kept cattle out and allowed some regeneration of native species. Akiapolau density decreased during our study as adjacent areas were being logged for koa, but it is unclear whether there was a cause and effect relationship.

We found that Akiapolau pairs usually pro-

TABLE 2. Heights at which male and female Akiapolau were observed foraging in three species of tree at Keauhou Ranch, Hawaii.

Tree species	Sex	n	Foraging height		Tree height		Proportional height	
			Mean	SE	Mean	SE	Mean	SE
Koa	Male	662	16.46	2.12	22.04	2.11**	0.699	0.006
	Female	435	12.20	0.27	16.26	0.29	0.740	0.007
Ohia	Male	116	10.73	0.43	16.19	0.50**	0.668	0.017
	Female	26	8.00	0.92	10.31	1.07	0.794	0.036
Naio	Male	350	6.53	0.16	10.12	0.18	0.635	0.009
	Female	89	6.94	0.30	9.75	0.31	0.706	0.017

** *t*-test, $P < 0.05$.

duce only one young per year and the relatively long parental investment period, which in most species is correlated with a low reproductive rate (Skutch 1985), apparently causes some pairs to forego breeding in some years. The net productivity of 0.86 young pair⁻¹ year⁻¹ is low compared to most passerines. For example, van Riper (1987) found that Common Amakihi (*Hemignathus virens*) on Mauna Kea produced 2.5 young pair⁻¹ year⁻¹, whereas Palila (van Riper 1980), another endangered honeycreeper, produced 1.8 young pair⁻¹ year⁻¹. In a compilation of several mainland studies, the percent of eggs ($n = 21,951$) that subsequently fledged a young averaged 46% (Nice 1957), and when larger clutch sizes and multiple clutches per season for most species are taken into account (Lack 1954, Skutch 1985), the number of young produced annually by Akiapolaau is low.

Adult survival seems to be average, with an annual survival rate of 0.71. Annual survival of other Hawaiian passerines, estimated with the same methods, was 0.73 for Hawaii Creeper (*Oreomystis mana*) and 0.70 for Akepa (Ralph and Fancy 1994b), 0.72 for Apapane (*Himatione sanguinea*; Ralph and Fancy 1995), 0.66 for Palila (Lindsey et al. 1995) and Omao (*Myadestes obscurus*; Ralph and Fancy 1994c), and 0.55 for Iiwi (Ralph and Fancy 1995). Mean survival for 35 species of temperate and tropical forest birds was 0.56 (Karr et al. 1990).

We found evidence for divergence of male and female Akiapolaau within their narrow foraging niche. Mean measurements between sexes differed by 19% for exposed culmen, 11.3% for body mass, and only 4.5% for wing length, indicating that selection has been highest for dimorphism of the feeding apparatus. Males selected trunks and large and medium branches for foraging, whereas females were most often observed higher in the trees on small branches and twigs. The longer bills of males have probably evolved to exploit the thicker bark on the larger branches of the tree.

Other than the narrow foraging niche, the requirements of the species appear to be broad. Nests have been found in ohia, koa, and mamane trees as either open statant cups or in cavities (Banko and Williams 1993; this study). Breeding and molting can occur throughout the year (Ralph and Fancy 1994a) and the species occurs in both wet and dry forests (Scott et al. 1986).

The primary threats to the survival of Aki-

TABLE 3. Percent occurrence of various insect and arachnid taxa in 38 Akiapolaau droppings.

Taxon	Age of insect	Percent occurrence
Coleoptera	Adult	15.8
	Larvae	5.3
Carabidae	Adult	2.6
	Larvae	42.1
Curculionidae	Adult	2.6
Lepidoptera	Larvae	92.1
Hymenoptera	Adult	7.9
Homoptera		
Cicadellidae	Adult	2.6
Delphacidae	All	5.3
Psyllidae	All	5.2
Heteroptera		
Lygaeidae	Adult	2.6
Diptera	Adult	2.6
Neuroptera	Larvae	23.7
Psocoptera		
Psocidae	All	5.3
Spiders	All	52.6

polaaau seem to be (1) habitat modification, particularly from logging and grazing, (2) predation by introduced rats and cats (*Felis catus*) and native raptors, and (3) avian disease. Koa is a legume, and its young leaves are highly palatable to cattle. Koa wood is also highly prized for woodworking, and many areas of old-growth koa forest have been logged or grazed. Sakai (1988) found that Akiapolaau were absent from almost pure stands of regenerating young koa following mechanical clearing of ohia-koa forest. Several Akiapolaau were detected in the regenerating areas in 1993 and 1994, ca. 14 years after logging and bulldozing, but it is not known whether they had recolonized the areas or were only foraging there. Akiapolaau rely heavily on koa, and to a lesser extent mamane (also a legume) and naio, and they are the only forest passerine that did not use nectar from the extremely abundant ohia flowers (Ralph, unpubl.). We never found any Akiapolaau at our Kau Forest site, where koa was absent. Fancy et al. (1996) found few Akiapolaau outside of koa-dominated forests during surveys in 1990–1995.

The diversity of insects found in fecal samples from Akiapolaau was low; only the Iiwi, which is primarily nectarivorous (Ralph, unpubl.), had a less diverse diet. Akiapolaau were most often observed foraging on lichen-covered surfaces of koa branches. Lichen is characteristic of larger trees, and Akiapolaau are rarely found in signif-

icant numbers outside of old growth forests. The need for a relatively large home range for specialized foraging within a limited distribution of suitable old-growth koa forest undoubtedly contributes to the species' rarity.

Predation by black rats (*Rattus rattus*), feral cats, and the native Hawaiian Hawk (*Buteo solitarius*) and Short-eared Owl or Pueo (*Asio flammeus sandwichensis*), may affect Akiapolaau more than other native birds (Snetsinger et al. 1994). The vocalizations of adult Akiapolaau are loud and frequent, and Akiapolaau forage more often on the trunk and larger branches of trees where they are more accessible to predators. Hawaiian Hawks respond to playbacks of juvenile Akiapolaau calls that are used to lure adults into mist nets. In the dry mamane forest, where trees are of lower stature, we suspect that predation is the primary factor that will soon lead to the local extinction of Akiapolaau (Fancy et al. 1996). Only one juvenile Akiapolaau has been observed in the dry forest population since 1990, despite close monitoring of several banded pairs (T. Pratt, unpubl.), and the remaining population consists only of a few males.

Avian malaria and pox have had a profound effect on native Hawaiian forest birds (Warner 1968, van Riper et al. 1986), and many areas of apparently suitable old growth koa-ohia forest where Akiapolaau are absent can be found on Hawaii below approximately 1,500 m (Scott et al. 1986; Jacobi 1990; Fancy et al. 1996). There are no data to determine whether Akiapolaau are more susceptible to avian diseases than are other Hawaiian honeycreepers, but the fact that Akiapolaau are currently found only where mosquitoes are absent or rare suggests that avian disease is a major cause of their range contraction. The protection and enlargement of existing habitat among Hawaii's remaining old-growth ohia and koa forests above the zone of mosquito occurrence is thus critical for the continued survival of Akiapolaau. If adequate habitat is available, the species appears capable of maintaining viable populations.

ACKNOWLEDGMENTS

We thank Dawn Breese, Marc Collins, Tim Ohashi, Peter Paton, Howard Sakai, and Claire Wolfe for their assistance with field work. Kamehameha Schools/Bishop Estate kindly provided access to their lands for this study. Sheila Conant, Lenny Freed, Jeff Hatfield, Thane Pratt, and Charles van Riper III provided many helpful comments on an earlier draft of the manuscript.

LITERATURE CITED

- AMADON, D. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). *Bull. Am. Mus. Nat. Hist.* 95:157-262.
- ANDERSON, B. W., R. D. OHMART, AND J. RICE. 1983. Avian and vegetation community structure and their seasonal relationships in the lower Colorado River valley. *Condor* 85:392-405.
- BANKO, P. C., AND J. WILLIAMS. 1993. Eggs, nests, and nesting behavior of Akiapolaau (Drepanidinae). *Wilson Bull.* 105:427-435.
- BERGER, A. J. 1981. Hawaiian birdlife. 2nd ed. Univ. Hawaii Press, Honolulu.
- FANCY, S. G., S. A. SANDIN, M. H. REYNOLDS, AND J. D. JACOBI. 1996. Distribution and population status of the endangered Akiapolaau. *Pac. Sci.* 50: in press.
- FREED, L. A., S. CONANT, AND R. C. FLEISCHER. 1987. Evolutionary ecology and radiation of Hawaiian passerine birds. *Trends Ecol. Evol.* 2:196-203.
- JACOBI, J. D. 1990. Distribution maps, ecological relationships, and status of native plant communities on the Island of Hawaii. Ph.D. diss., Univ. of Hawaii, Honolulu.
- JOHNSON, N. K., J. A. MARTIN, AND C. J. RALPH. 1989. Genetic evidence for the origin and relationships of Hawaiian honeycreepers (Aves: Fringillidae). *Condor* 91:379-396.
- KARR, J. R., J. D. NICHOLS, M. K. KLIMKIEWICZ, AND J. D. BRAUN. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? *Am. Nat.* 136:277-291.
- LAAKE, J. L., S. T. BUCKLAND, D. R. ANDERSON, AND K. P. BURNHAM. 1994. DISTANCE User's guide, 2.1. Colorado Coop. Fish & Wildlife Res. Unit, Colorado State Univ., Fort Collins, CO.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- LINDSEY, G. D., S. G. FANCY, M. H. REYNOLDS, T. K. PRATT, K. A. WILSON, P. C. BANKO, AND J. D. JACOBI. 1995. Population structure and survival of Palila. *Condor* 97:528-535.
- MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology* 42:594-598.
- MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.
- NICE, M. M. 1957. Nesting success in altricial birds. *Auk* 74:305-321.
- PERKINS, R.C.L. 1903. Vertebrata (Aves), p. 368-465. In D. Sharp [ed.], *Fauna Hawaiiensis*. Vol. 1, University Press, Cambridge.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildl. Monogr.* 107:1-97.
- PRATT, T. K., S. G. FANCY, C. K. HARADA, G. D. LINDSEY, AND J. D. JACOBI. 1994. Identifying sex and age of Akiapolaau. *Wilson Bull.* 106:421-430.
- PYLE, P., S.N.G. HOWELL, R. P. YUNICK, AND D. F. DeSANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.
- RALPH, C. J., AND S. G. FANCY. 1994a. Timing of

- breeding and molting in six species of Hawaiian honeycreepers. *Condor* 96:151-161.
- RALPH, C. J., AND S. G. FANCY. 1994b. Demography and movements of the endangered Hawaii Creeper and Hawaii Akepa. *Wilson Bull.* 106:615-628.
- RALPH, C. J., AND S. G. FANCY. 1994c. Demography and movements of the Omao (*Myadestes obscurus*). *Condor* 96:503-511.
- RALPH, C. J., AND S. G. FANCY. 1995. Demography and movements of Apapane and Iiwi in Hawaii. *Condor* 97:729-742.
- RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Manual of field methods for monitoring landbirds. U.S. Forest Service, Gen. Tech. Rep. PSW-GTR-114. Albany, CA.
- RALPH, C. P., S. E. NAGATA, AND C. J. RALPH. 1985. Analysis of droppings to describe diets of small birds. *J. Field Ornithol.* 56:165-174.
- SAKAI, H. F. 1988. Avian response to mechanical clearing of a native rainforest in Hawaii. *Condor* 90:339-348.
- SCOTT, J. M., C. B. KEPLER, C. VAN RIPER III, AND S. I. FEFER. 1988. Conservation of Hawaii's vanishing avifauna. *BioScience* 38:238-253.
- SCOTT, J. M., S. MOUNTAINSPRING, F. L. RAMSEY, AND C. B. KEPLER. 1986. Forest bird communities of the Hawaiian islands: their dynamics, ecology and conservation. *Stud. Avian Biol.* 9:1-431.
- SKUTCH, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. *Ornithol. Monogr.* 36:575-594.
- SNETSINGER, T. J., S. G. FANCY, J. C. SIMON, AND J. D. JACOBI. 1994. Diets of owls and feral cats in Hawaii. *Elepaio* 54:47-51.
- VAN RIPER, C., III. 1980. Observations on the breeding of the Palila *Psittirostra bairdii* of Hawaii. *Ibis* 122:462-475.
- VAN RIPER, C., III. 1987. Breeding ecology of the Hawaii Common Amakihi. *Condor* 89:85-102.
- VAN RIPER, C., III., S. G. VAN RIPER, M. L. GOFF, AND M. LAIRD. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56:327-344.
- WARNER, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* 70:101-120.