Wilson Bull., 106(4), 1994, pp. 615–628

DEMOGRAPHY AND MOVEMENTS OF THE ENDANGERED AKEPA AND HAWAII CREEPER

C. JOHN RALPH[1] AND STEVEN G. FANCY[2]

ABSTRACT.—We studied populations of the endangered Akepa (*Loxops coccineus coccineus*) and Hawaii Creeper (*Oreomystis mana*) at four sites on the island of Hawaii. Mean monthly density (±SE) of Akepa was 5.74 ± 0.87, 1.35 ± 0.41, 0.96 ± 0.13, and 0.76 ± 0.12 Akepa/ha at Kau Forest, Hamakua, Keauhou Ranch, and Kilauea Forest study areas, respectively. Hawaii Creepers were found at densities of 1.68 ± 0.53, 1.79 ± 0.42, 0.48 ± 0.06, and 0.54 ± 0.08 birds/ha, respectively, at the four study areas. Highest capture rates and numbers of birds counted from stations occurred from August through November and February through March. Hatching-year birds were captured from May through December for Akepa and April through December for Hawaii Creeper. Annual survival for adults at Keauhou Ranch was 0.70 ± 0.27 SE for 61 Akepa and 0.73 ± 0.12 SE for 49 Hawaii Creepers. Lowest rates of mortality and emigration occurred between May and August. Both species appeared to defend Type-B territories typical of cardueline finches, retained mates for more than one year, and showed strong philopatry. Home ranges for Hawaii Creepers ($\bar{x}$ = 7.48 ha) were larger than those for Akepa ($\bar{x}$ = 3.94 ha). No difference was found between home range sizes of males and females for either species. *Received 21 Dec. 1993, accepted 20 April 1994.*

The Hawaii subspecies of the Akepa (*Loxops coccineus coccineus*) and the Hawaii Creeper (*Oreomystis mana*) are endangered Hawaiian honeycreepers (Fringillidae: Drepanidinae) found only in wet and mesic forests above 1000 m elevation on the island of Hawaii. The two species are similar in that they are insectivorous and occur at highest densities in native forests of ohia (*Metrosideros polymorpha*) and koa (*Acacia koa*) where they are mostly syntopic (Scott et al. 1986). Both species have extended breeding and molting periods that reflect the low degree of seasonality in their food supply and environment (Ralph and Fancy 1994a). Because they live in dense, remote rainforests, usually in low density, little is known about the life history of either species.

The Akepa on Hawaii occurs in four disjunct populations totaling 14,000 birds, with highest densities in subalpine ohia woodland in the Kau Forest Reserve (Scott et al. 1986, Pratt et al. 1989). Akepa were once abundant and widely distributed on Hawaii (Perkins 1903). Pratt (1991) considered the Akekee on Kauai to be a separate species (*L. caeruleirostris*) and suggested that the very rare Maui and Oahu forms of Akepa may warrant recognition as full species. Akepa have unusual bills with crossed mandibles which they use to extract spiders and other invertebrate prey from ohia

[1] U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Dr., Arcata, California 95521.
[2] National Biological Survey, Hawaii Field Station, P.O. Box 44, Hawaii National Park, Hawaii 96718.

terminal buds; they also glean insects from foliage (Perkins 1903, Mueller-Dombois et al. 1981b, Ralph and Noon 1986, Ralph 1990). The Akepa on Hawaii appears to be an obligate cavity nester (Freed et al. 1987).

Scott et al. (1986) found four widely separated populations of Hawaii Creepers on Hawaii and estimated the total population at 12,500 birds. Highest densities occurred between 1500 and 1900 m elevation in relatively undisturbed forests in the Kau Forest Reserve and on the eastern slope of Mauna Kea and the northeastern slope of Mauna Loa (Scott et al. 1986). Perkins (1903) reported that *O. mana* was "a very abundant bird and generally distributed over the large island," although he noted distributional anomalies in forests of the middle Kona and Puna districts. Hawaii Creepers feed primarily by bark gleaning on larger stems and branches of trees, whereas Akepa are predominately foliage gleaners that use the perimeters of tree crowns (Mueller-Dombois et al. 1981b).

In this paper, we present findings from a field study of Hawaii Creepers and Akepa which was part of a research program on foraging ecology and population dynamics of Hawaiian forest birds conducted by the U.S. Forest Service 1976–1982.

STUDY AREAS AND METHODS

We studied Hawaii Creepers and Akepa at four sites on the island of Hawaii between November 1976 and January 1982. The Keauhou Ranch study area (19°30′N, 155°20′W; 1800 m elevation) had a discontinuous canopy dominated by ohia and naio (*Myoporum sandwicense*) and had a long history of grazing by cattle and logging for koa and ohia. A 16-ha grid marked at 50-m intervals was established at this wet (ca 2000 mm annual rainfall) forest site. The 16-ha Kilauea Forest study area (19°31′N, 155°19′W; 1600–1650 m) was in a relatively pristine, closed-canopy, wet forest dominated by 20–30 m tall koa and 15–25 m tall ohia trees, and was approximately 1.8 km NW of the Keauhou Ranch study area. This site was described in detail by Mueller-Dombois et al. (1981a:216–220). The 50-ha Hamakua study area near Pua Akala (19°47′N, 155°20′W; 1770 m) was similar to the Keauhou Ranch site but had a more continuous canopy and an almost complete lack of native understory plants because of intensive grazing by cattle. The 50-ha Kau Forest study area (19°13′N, 155°39′W; 1750 m) had a closed canopy of ohia and a largely ungrazed understory of kolea (*Myrsine lessertiana*), olapa (*Cheirodendron trigynum*), kawau (*Ilex anomala*), and native ferns.

We estimated densities of Hawaii Creepers and Akepa at each of the four study areas by the variable circular-plot method (Reynolds et al. 1980, Ramsey and Scott 1979) during eight-min count periods as described in Ralph (1981). All observers were trained extensively to identify birds by songs and calls and to estimate distances to birds (Kepler and Scott 1981). At the Keauhou Ranch and Kilauea Forest sites, we established 25 count stations at 100-m intervals on a square, 16-ha grid, and attempted to count birds at each site three times each month (Table 1). At the Hamakua and Kau Forest sites, we counted birds at approximately four-month intervals during 1979–1980 from 15 stations spaced at 100-m intervals along U-shaped transects. Data were analyzed with the program VCP2 (E. Garton, unpubl. data), which calculates bird densities from data collected by the variable circular-plot method. Paired *t*-tests were used to compare densities between Akepa and Hawaii Creepers within each of the four study areas.

TABLE 1
NUMBER OF EIGHT-MIN COUNT PERIODS CENSUSED

Year	Study area	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1977	Keauhou Ranch							25	25	25	25	25	25
1978	Keauhou Ranch	25	25	50	50	75	75	62	75	76	62	75	51
	Kilauea Forest				50	49	50	75	75	85	85	75	44
1979	Keauhou Ranch	75	75	81	100	75	101	75	72	78	76	87	87
	Kilauea Forest	40	74	50	87	75	75	75	75	75	75	75	
	Hamakua		45			30			45				40
	Kau Forest						45			45			
1980	Keauhou Ranch	96	88	76	87	125	75	73	75	99	26	63	49
	Kilauea Forest		162			142			150		75	50	
	Hamakua			15	15		36		45				38
	Kau Forest	45			45			40			45		40
1981	Keauhou Ranch	84	75	100	50	75	75	74	75	75	75	75	75
	Kilauea Forest	63	87										
1982	Keauhou Ranch	62											

We captured birds in mist nets at two of our study areas, Keauhou Ranch (N = 62,006 net-h) and Kilauea Forest (N = 16,958 net-h) and conducted monthly surveys to search for color-banded birds. We regularly operated nets at 16 permanent sites and placed 10 additional nets at other locations throughout the grids as personnel were available. We operated a net within 75 m of every point in each study site at least once every three months. Captured birds were banded with USFWS bands and a unique combination of three colored plastic bands. Each bird was inspected to determine molt status and presence or absence of a brood patch or enlarged cloacal protuberance (Pyle et al. 1987, Ralph et al. 1993). Sex was determined by plumage characteristics or presence of a brood patch or cloacal protuberance, or for a few individuals, by observations of breeding behavior during subsequent monthly surveys. We identified HY birds on the basis of plumage characteristics, skull ossification, and behavior.

At least monthly, we conducted surveys at Keauhou Ranch and Kilauea Forest to identify and record activities of color-banded birds (Ralph and Fancy 1994a). We noted the presence, and where possible, identified any birds associated with the focal bird. The date and location of individuals identified during these surveys were used in conjunction with banding records to calculate survival rates and home range size.

We estimated annual survival of Akepa and Hawaii Creepers from capture-recapture (including resightings) data with the Jolly-Seber model (Pollock et al. 1990). The Jolly-Seber method is superior to those equating survival with recapture rates because the model explicitly allows for the possibility that an individual is alive and in the study area but is not observed (Nichols and Pollock 1983). Annual survival (the complement of which includes both mortality and permanent emigration from the study area) was calculated with Model AX of program JOLLY (Pollock et al. 1990) which incorporates data from resightings and allows for time-specific capture and survival probabilities. We selected a series of four-month sampling periods from January through April of each year during 1977–1981 based on goodness of fit tests from preliminary runs. All birds captured or resighted during the eight-month period from May through December were coded as resightings (Pollock et al. 1990:85).

We recorded locations of individuals captured in nets or identified during surveys to the nearest 50 m within an expanded 600 × 600 m grid at the Keauhou Ranch and Kilauea Forest sites. Bird locations and associated attribute data (e.g., date, sex, and age of individual) were analyzed with a geographic information system to determine the extent of overlap among individuals. Differences between species and age classes in the length of time that individuals were observed at Keauhou Ranch were tested by two-way ANOVA. Home ranges were calculated by the minimum convex polygon method (Mohr 1947, Hayne 1949). For each individual, we also calculated the median distance from the bird's center of activity to each location where it was observed (Hayne 1949, Fancy et al. 1993). We compared home range size and distance from the center of activity between sexes and species by two-way ANOVA. After inspecting plots of home range size versus sample size, we excluded individuals observed at <10 locations from further analysis because of biases associated with small sample sizes (Bekoff and Mech 1984, Swihart and Slade 1985).

RESULTS

Density and capture rates.—Mean monthly density (birds/ha) of Akepa for all months combined was 0.96 ± 0.13 SE at Keauhou Ranch, 0.76 ± 0.12 at Kilauea Forest, 1.35 ± 0.41 at Hamakua, and 5.74 ± 0.87 at Kau Forest, respectively. Hawaii Creepers were found at mean densities of 1.68 ± 0.53, 1.79 ± 0.42, 0.48 ± 0.06, and 0.54 ± 0.08 birds/ha, respectively, at the four study areas. Densities of Akepa at Kau Forest were higher than those for the other three sites (Tukey's test, df = 97, $P < 0.05$) which did not differ from each other. Densities of Hawaii Creeper did not differ between Kau Forest and Hamakua nor between Keauhou Ranch and Kilauea Forest, but densities at Kau Forest and Hamakua were both greater than those at the other two sites (Tukey's test, df = 97, $P < 0.05$).

At all sites except Kau Forest, we observed a post-breeding increase in the Akepa population during late summer or fall each year (Figs. 1–4). Seasonal changes in densities of Hawaii Creepers were less pronounced than those for Akepa, and the timing of post-breeding peaks was inconsistent among study areas (Figs. 1–4). Densities of Akepa were higher than those of Hawaii Creepers at Keauhou Ranch (. = 4.51, df = 54, P = 0.0001) and Kau Forest (t = 8.68, df = 7, P = 0.0001) but not at Kilauea Forest (t = 1.51, df = 28, P = 0.14) or Hamakua (t = 0.81, df = 8, P = 0.44).

Monthly capture rates (Fig. 5) were correlated with mean monthly densities (all years combined) for both Akepa (r = 0.64, P = 0.02) and Hawaii Creepers (r = 0.62, P = 0.03). Highest capture rates occurred during August through November and in February and March for Akepa, and during October through March for Hawaii Creeper. We captured HY Akepa from May through December, with a peak in August through October, and HY Hawaii Creepers from April through December, with a peak in August through November (Fig. 5).

Annual survival.—We calculated survival probability for Akepa and Hawaii Creepers at only the Keauhou Ranch site because we mist netted at

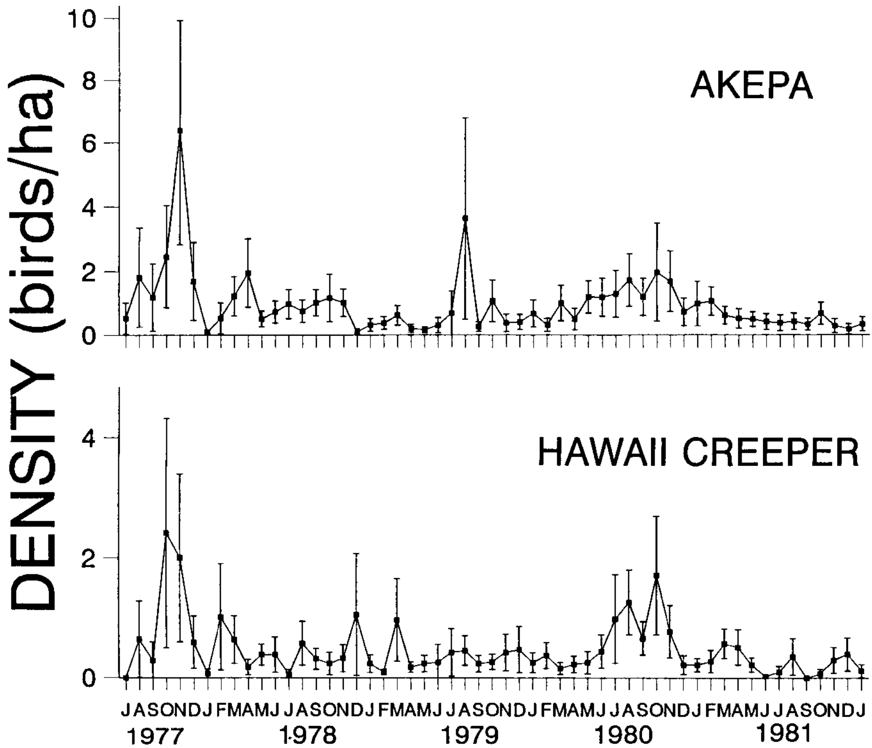

FIG. 1. Mean density (birds/ha, ± 1 SE) of Akepa and Hawaii Creeper at Keauhou Ranch.

Kilauea Forest for only two years. Capture and resighting data for birds first captured as HY birds was inadequate to fit an age-specific model, but we were able to calculate survival of adults (after hatching year, AHY). Fifteen of the 30 HY Akepa we captured at Keauhou Ranch were never seen again, and six of the remaining HY Akepa were last seen within six months of their initial capture. Only seven of the 30 (23%) HY Akepa were alive and still in the study area after one year. Twenty Hawaii Creeper were first captured as HY birds at Keauhou Ranch; 10 of these were never seen again, two were last seen within six months of their initial capture, and eight (40%) were still in the study area one year later.

Mean annual survival for AHY Akepa, based on 442 records of 61 birds at Keauhou Ranch, was 0.70 ± 0.27. The probability of resighting an individual in a given year if that individual was alive and in the study area was 0.60 ± 0.22. Similar calculations for 493 captures and resightings of

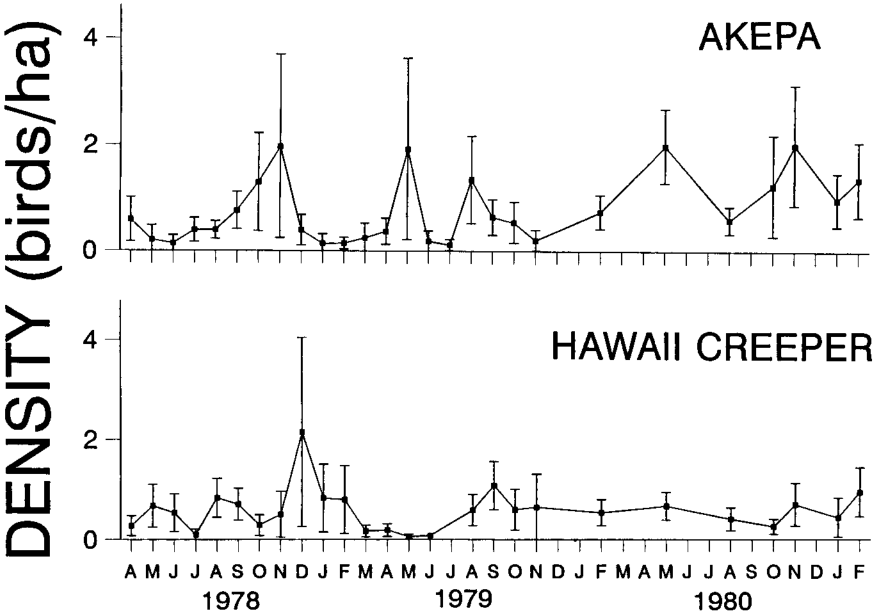

FIG. 2. Mean density (birds/ha, ± 1 SE) of Akepa and Hawaii Creeper at Kilauea Forest.

49 Hawaii Creepers yielded an estimated survival probability of 0.73 ± 0.12, with a resighting probability of 0.73 ± 0.26. Most birds observed for a minimum of two months were last observed during the winter, between September and March, in both species. Lowest rates of mortality or emigration occurred between May and August.

Philopatry and movements.—We observed Akepa and Hawaii Creepers with the same mates in more than one year, and many individuals showed strong philopatry. For example, one male Akepa remained at the Keauhou Ranch site from March 1977 until the end of the study in January 1982. He was frequently observed with a female that was captured in February 1978 and last seen in January 1981. Another Akepa pair, both captured in July 1977, remained together at Keauhou Ranch until February 1979 when the female disappeared. A pair of Hawaii Creepers that were captured together on 16 March 1977 and fledged a chick at the Keauhou Ranch site in April remained together at the study site through July 1978, after which the male disappeared. We never noted any case of mate switching in either species.

We found differences in philopatry between species and age classes (Table 2). The mean number of months that Hawaii Creepers (N = 10 HY,

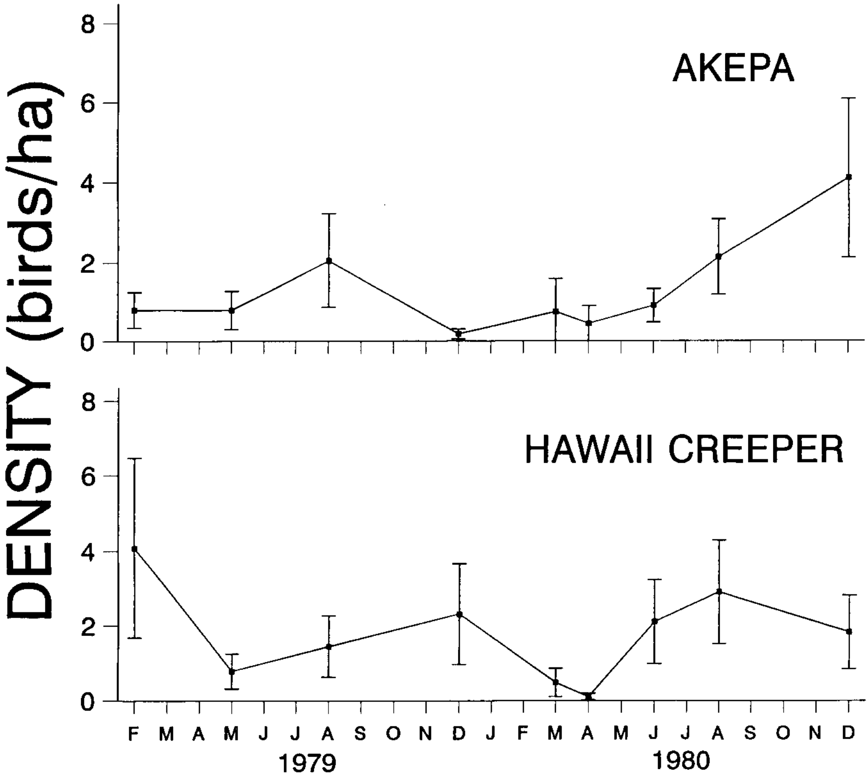

FIG. 3. Mean density (birds/ha, ± 1 SE) of Akepa and Hawaii Creeper at Hamakua.

29 AHY) remained at the Keauhou Ranch site was greater than that for Akepa (N = 15 HY, 33 AHY; $F = 7.86$, $P = 0.006$), and birds first captured as AHY birds remained longer than did HY birds ($F = 4.95$, $P = 0.028$). Considering only AHY birds, 19 of 52 (36.5%) Akepa were seen only once on the study area, compared to nine of 38 (23.6%) Hawaii Creepers.

Home ranges of Akepa and Hawaii Creeper overlapped extensively with other individuals of the same species, and neither species appeared to defend Type-A territories (Nice 1941). Plots of locations where breeding pairs of Akepa and Hawaii Creepers were observed during the peak breeding season of March through June (Ralph and Fancy 1994a) showed overlap among pairs and occurrence of one or more unpaired males within each pair's home range. Home range size of individuals with ≥10 locations was highly correlated with distance from the center of activity for both species

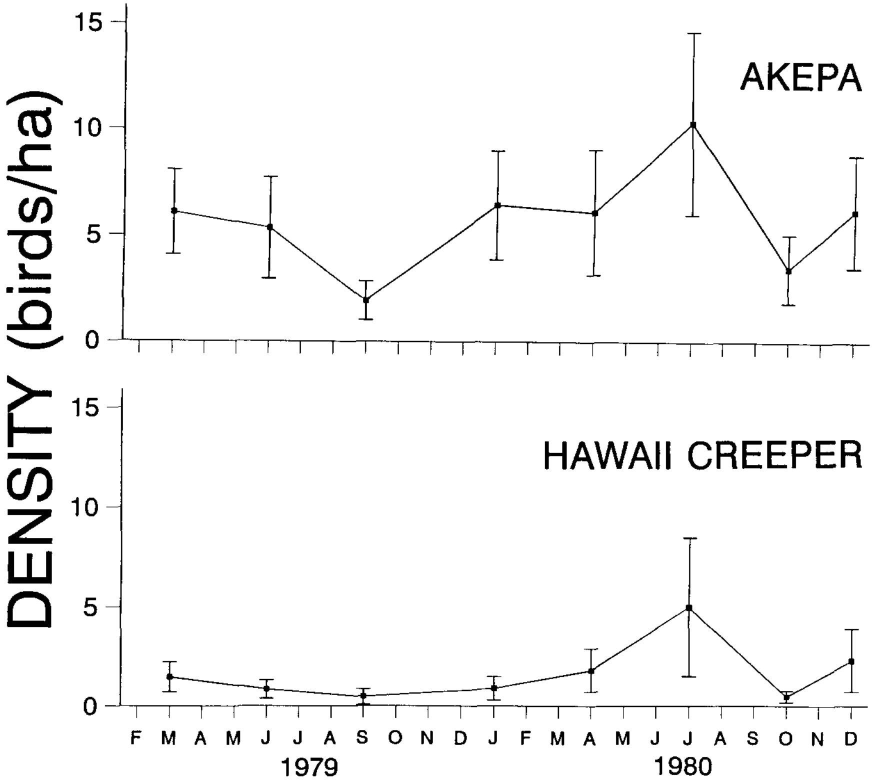

FIG. 4. Mean density (birds/ha, ± 1 SE) of Akepa and Hawaii Creeper at Kau Forest.

(r = 0.76, N = 18, P = 0.0002 for Akepa; r = 0.67, N = 20, P = 0.0012 for Hawaii Creepers), and statistical tests were always in agreement for the two measures. We found no difference in home range size (F = 0.37, P = 0.55) or median distance (F = 0.33, P = 0.57) between males and females of either species (Table 3). Home range size for Hawaii Creepers ($\bar{x}$ = 7.48 ha, N = 20, data for both sexes combined) was significantly greater than that for Akepa ($\bar{x}$ = 3.94 ha, N = 18, F = 9.42, P = 0.0045).

DISCUSSION

We found highest densities of Akepa and Hawaii Creepers at the Kau Forest and Hamakua study areas, as did Scott et al. (1986) during the Hawaiian Forest Bird Surveys. Mean Akepa density in the Kau Forest was 5–6 times higher than those estimated for the Keauhou Ranch and Kilauea Forest sites. Hawaii Creepers were most common at the Hamakua and Kau

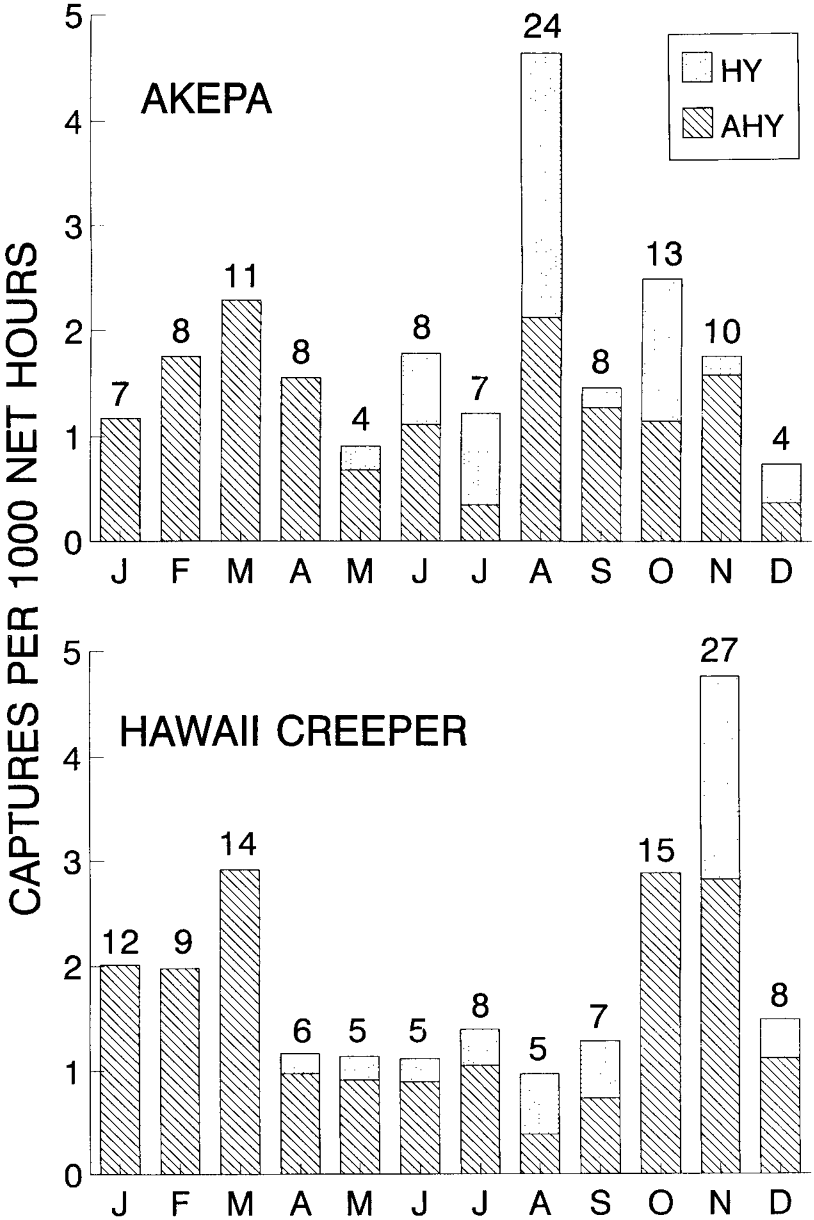

FIG. 5. Capture rates at Keauhou Ranch. Total number of birds captured each month is shown above each bar.

TABLE 2
NUMBER OF MONTHS INDIVIDUALS WERE OBSERVED

Species	Age at first capture[a]	N	Mean	SE	Range
Akepa	HY	30	6.8	1.82	1–40
	AHY	52	10.5	1.73	1–58
Hawaii Creeper	HY	20	10.9	3.43	1–53
	AHY	38	18.4	2.72	1–57

[a] HY = hatching year; AHY = after hatching year.

Forest study areas, where densities were at least three times as high as those at Keauhou Ranch and Kilauea Forest. Our density estimates for Akepa and Hawaii Creepers were higher than those obtained by Scott et al. (1986), partly because Scott et al. (1986) surveyed much larger areas and included transects where each species was absent or occurred in low numbers. Our study areas were intentionally located where these species were relatively common. Mueller-Dombois et al. (1981b) reported density estimates of 0.43 birds/ha for Akepa and 0.50 birds/ha for Hawaii Creepers at a site near our Kilauea Forest study area, but they used variable distance strip transects to estimate densities, and their results may not be directly comparable to ours.

Scott et al. (1986) found the highest density of Akepa (3.0 birds/ha) in subalpine ohia woodland in Kau during surveys in May and June 1976. We obtained a density estimate of 5.74 Akepa/ha in a nearby ohia forest at Kau during 1979–1980. Within the 1700–1900 m elevation band of their Hamakua study area, Scott et al. (1986) reported densities for Akepa and

TABLE 3
MOVEMENTS OF AKEPA AND HAWAII CREEPER

Sex	N	Home range size (km²)		Median distance (m)[a]	
		Mean	SE	Mean	SE
Akepa					
Males	11	4.49	0.86	82.04	5.63
Females	7	3.07	0.47	75.18	4.78
Hawaii Creeper					
Males	10	7.93	1.38	104.63	6.24
Females	6	7.94	2.36	104.30	12.41

[a] Median distance from the center of activity to all locations.

Hawaii Creepers of 0.83 and 0.61 birds/ha, compared to our estimates of 1.35 and 1.79 birds/ha, respectively. Our study area is now part of the Hakalau Forest National Wildlife Refuge which was established primarily to protect some of the best remaining habitat for Akepa, Hawaii Creepers, and the Akiapolaau (*Hemignathus munroi*).

Sakai and Johanos (1983) suggested that Hawaii Creepers prefer relatively undisturbed koa-ohia forests, based on their finding of 1.62 nests/person·year of effort in our Kilauea Forest study area versus only 0.07 nests/person·year at the more disturbed Keauhou Ranch site. However, we found comparable densities of Hawaii Creepers at the two study areas, and capture rates of Hawaii Creepers at Keauhou Ranch were higher than those at Kilauea Forest (paired *t*-test, $t = 3.14$, $P = 0.009$). Furthermore, the density of Hawaii Creepers was similar at Hamakua and Kau Forest study areas, and yet Kau Forest has a largely intact native understory, whereas the Hamakua study area lacked a native understory because of intensive grazing.

Scott et al. (1986) reported a strong relationship between the presence of Hawaii Creepers and koa trees, and found that Hawaii Creepers in their Hamakua study area were nearly five times more common in koa-ohia than in ohia. Our Kilauea Forest site had more koa than the other three sites, and yet densities of Hawaii Creepers at Kilauea Forest were much lower than at Kau Forest or Hamakua. Thus, differences in density among sites cannot be explained only by the extent of disturbance to the understory or the availability of koa, and additional research is needed to understand why densities of Hawaii Creepers differ greatly among study areas.

Our estimates of annual survival (0.70 for Akepa and 0.73 for Hawaii Creepers) are similar to those reported by Freed (1988) for Akepa, Ralph and Fancy (1994b) for adult Omao (*Myadestes obscurus*), and Ralph and Fancy (unpubl. data) for Apapane (*Himatione sanguinea*). Freed (1988) calculated an adult survival rate of 0.77 for Akepa in the Kau Forest based on recaptures of three of five Akepa banded two years earlier. Annual survival rates of Akepa and Hawaii Creepers are near the upper end of the range of survival estimates reported by Karr et al. (1990), using the same methods of analysis, for 35 species of birds in temperate and tropical forests.

Our data on movements and activity of Akepa and Hawaii Creepers are consistent with the hypothesis that these species defend Type-B territories (Nice 1941) that are typical of cardueline finches (Newton 1972) and several species of Hawaiian honeycreepers. On Kauai, Eddinger (1970) found that Common Amakihi (*Hemignathus virens*), Anianiau (*H. parvus*), Apapane, and Iiwi (*Vestiaria coccinea*) all defended small areas around the nest during the breeding season but did not defend feeding territories. Male

Laysan Finches (*Telespiza cantans*; Morin 1992) and Palila (*Loxioides bailleui*; T. Pratt, unpubl. data) similarly defend mates and nest sites, but not food resources. Among Hawaiian honeycreepers, Type-A territories have been documented only for Common Amakihi (Baldwin 1953, van Riper 1987) and Akiapolaau (T. Pratt, unpubl. data).

Habitat loss and modification, introduction of avian diseases, predation by introduced mammals, and competition from alien species have all been cited as causes of the rapid decline of Hawaiian forest bird populations (Warner 1968, Atkinson 1977, Berger 1981, Mountainspring and Scott 1985, Ralph and van Riper 1985, Scott et al. 1986). In the recovery plan for the Akepa and Hawaii Creepers (USFWS 1982), the elimination and alteration of native forest ecosystems by feral ungulates and man were considered to be the most serious threats to these species. Studies of the effects of avian malaria and avian pox on native Hawaiian forest birds (Warner 1968; van Riper et al. 1986; C. Atkinson, unpubl. data) have confirmed that Hawaiian honeycreepers are highly susceptible to these diseases.

The remaining strongholds for Akepa and Hawaii Creepers appear to be higher-elevation native forests where mosquitos, the primary vector for avian malaria and pox, are absent (Scott et al. 1986; van Riper et al. 1986; C. Atkinson, unpubl. data; J. Lepson and L. Freed, unpubl. data). In suitable habitat, Akepa and Hawaii Creepers appear to be able to sustain relatively high densities with high adult survival. Although many aspects of the life history and demography of these two endangered species are poorly understood, the most obvious conservation strategy appears to be the protection of Hawaii's remaining native forests above the zone of mosquito occurrence.

ACKNOWLEDGMENTS

We thank the many field crew members who assisted with this study and, in particular, we thank Dawn Breese, Marc Collins, Peter Paton, Tim Ohashi, Howard Sakai, and Claire Wolfe for their efforts. We thank Tonnie Casey, Lenny Freed, Jeff Hatfield, Jaan Lepson, Thane Pratt, Mike Scott and Charles van Riper III for helpful comments on an earlier draft of the manuscript.

LITERATURE CITED

ATKINSON, I. A. E. 1977. A reassessment of factors, particularly *Rattus rattus* L., that influences the decline of endemic forest birds in the Hawaiian Islands. Pac. Sci. 31:109–133.

BALDWIN, P. H. 1953. Annual cycle, environment and evolution in the Hawaiian honeycreepers (Aves: Drepaniidae). Univ. Calif. Publ. Zool. 52:285–398.

BEKOFF, M. AND L. D. MECH. 1984. Simulation analyses of space use: home range estimates, variability, and sample sizes. Behav. Res. Meth., Instr. Comput. 16:32–37.

BERGER, A. J. 1981. Hawaiian birdlife. (2nd ed.) Univ. Press Hawaii, Honolulu, Hawaii.

EDDINGER, C. R. 1970. A study of the breeding biology of four species of Hawaiian honeycreepers (Drepanididae). Ph.D. diss., Univ. of Hawaii, Honolulu.

FANCY, S. G., R. T. SUGIHARA, J. J. JEFFREY, AND J. D. JACOBI. 1993. Site tenacity of the endangered Palila. Wilson Bull. 105:587–596.

FREED, L. A. 1988. Demographic and behavioral observations of the Hawai'i 'Akepa on Mauna Loa. 'Elepaio 48:37–39.

———, T. M. TELECKY, W. A. TYLER, III, AND M. A. KJARGAARD. 1987. Nest-site variability in the 'Akepa and other cavity-nesting forest birds on the island of Hawaii. 'Elepaio 47: 79–81

HAYNE, D. W. 1949. Calculation of size of home range. J. Mamm. 30:1–18.

KARR, J. R., J. D. NICHOLS, M. K. KLIMKIEWICZ, AND J. D. BRAWN. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? Amer. Nat. 136:277–291.

KEPLER, C. B. AND J. M. SCOTT. 1981. Reducing bird count variability by training observers. Stud. Avian Biol. 6:366–371.

MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. Amer. Midl. Nat. 37:223–249.

MORIN, M. P. 1992. The breeding biology of an endangered Hawaiian honeycreeper, the Laysan finch. Condor 94:646–667.

MOUNTAINSPRING, S. AND J. M. SCOTT. 1985. Interspecific competition among Hawaiian forest birds. Ecol. Monogr. 55:219–239.

MUELLLER-DOMBOIS, D., K. W. BRIDGES, AND H. L. CARSON. (EDS.). 1981a. Island ecosystems: biological organization in selected Hawaiian communities. Hutchinson Ross, Stroudsburg, Pennsylvania.

———, R. G. COORAY, J. E. MAKA, G. SPATZ, W. C. GAGNE. F. G. HOWARTH, J. L. GRESSITT, G. A. SAMUELSON, S. CONANT, AND P. Q. TOMICH. 1981b. Structural variation of organism groups studied in the Kilauea Forest. Pp. 231–317 *in* Island ecosystems: biological organization in selected Hawaiian communities (D. Mueller-Dombois, K. W. Bridges, and H. L. Carson, eds.). Hutchinson Ross, Stroudsburg, Pennsylvania.

NEWTON, I. 1972. Finches. William Collins Sons, London, England.

NICE, M. M. 1941. The role of territory in bird life. Amer. Midl. Nat. 26:441–487.

NICHOLS, J. D. AND K. H. POLLOCK. 1983. Estimation methodology in contemporary small mammal capture-recapture studies. J. Mammal. 64:253–260.

PERKINS, R. C. L. 1903. Vertebrata (Aves). Pp. 368–465 *in* Fauna Hawaiiensis (D. Sharp, ed.), Vol. 1, part 4. University Press, Cambridge, England.

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, H. D. 1991. Species limits in Akepas (Drepanidinae: *Loxops*). Condor 91:933–940.

PRATT, T. K., J. G. GIFFIN, AND F. P. DUVALL, III. 1989. Recent observations of 'Akepa and other endangered forest birds in Central Kona, Hawai'i Island. 'Elepaio 49:62–64.

PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.

RALPH, C. J. 1981. An investigation of the effect of seasonal activity levels on avian censusing. Stud. Avian Biol. 6:265–270.

———. 1990. The island forests of Hawaii: few species, many specialists. Pp. 275–283 *in* Biogeography and ecology of forest bird communities (A. Keast, ed.). SPB Academic Publishing, The Hague, The Netherlands.

——— AND S. G. FANCY. 1994a. Timing of breeding and molting in six species of Hawaiian honeycreepers. Condor 96:151–161.

——— AND ———. 1994b. Demography and movements of the Omao (*Myadestes obscurus*). Condor 96:503–511.

———, G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook of field methods for monitoring landbirds. U.S. Forest Service, Gen. Tech. Rep. PSW-GTR-144. Albany, California.

——— AND B. R. NOON. 1986. Foraging interactions of small Hawaiian forest birds. Pp. 1992–2006 *in* Acta XIX Congressus Internationalis Ornithologici, Vol. II. Univ. Ottawa Press, Ottawa, Canada.

——— AND C. VAN RIPER, III. 1985. Historical and current factors affecting Hawaiian native birds. Bird Conserv. 2:7–42.

RAMSEY, F. L. AND J. M. SCOTT. 1979. Estimating population densities from variable circular plot surveys. Pp. 155–181 *in* Sampling biological populations (R. Cormack, G. Patil and D. Robson, eds.). Intern. Co-operative Publishing House, Fairland, Maryland.

REYNOLDS, R. T., J. M. SCOTT, AND R. A. NUSSBAUM. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309–313.

SAKAI, H. F. AND T. C. JOHANOS. 1983. The nest, egg, young, and aspects of the life history of the endangered Hawaii Creeper. Western Birds 14:73–84.

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.

SWIHART, R. K. AND N. A. SLADE. 1985. Influence of sampling interval on estimates of home range size. J. Wildl. Manage. 49:1019–1025.

USFWS. 1982. Hawaii forest bird recovery plan. U.S. Fish and Wildlife Service, Honolulu, Hawaii.

VAN RIPER, C., III. 1987. Breeding ecology of the Hawaii Common Amakihi. Condor 89:85–102.

———, 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.