BREEDING PRODUCTIVITY AND SURVIVAL OF THE ENDANGERED HAWAI'I CREEPER IN A WET FOREST REFUGE ON MAUNA KEA, HAWAI'I

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Abstract. We studied the demography of the endangered Hawai'i Creeper (*Oreomystis mana*) from 1994–1999 at three sites in Hakalau Forest National Wildlife Refuge (NWR). Hawai'i Creepers bred from January to June, with peak breeding in February through May (about 120–180 days), and molted from May to August. A small proportion (4.9%) of individuals overlapped breeding and molting activities. We located and monitored the fates of 60 nests. Mean clutch size was 2.1 eggs, nest building required 19 days, incubation was 16 to 17 days, and nestling period lasted 18 days. Of all nest attempts, 25% were abandoned before egg laying, 6.7% were removed for captive propagation, 13.3% had undetermined fates, 38.3% failed during incubation or nestling periods, and 16.7% were successful. Thus, of 33 nests that were active through egg laying and outcome was confirmed, only 30% were successful. The daily survival rate of active nests was 0.960 ± 0.009 SE. An average of 1.7 chicks fledged from successful nests. Thirty-two percent of hatch-year birds were alive and in the study area at least one year later. Annual adult survival was high (0.88 ± 0.03). The primary factors limiting productivity of Hawai'i Creeper in Hakalau Forest NWR appear to be low reproductive potential in combination with high rates of nesting failure. Further research into the causes of nest failure, the length of the breeding season, and renesting behavior of females is needed, and protection of the forest from the degrading impacts of introduced mammals is paramount.

Key Words: endangered species; Hawai'i Creeper; nesting success; *Oreomystis mana*; productivity; survival.

The high elevation, wet forests on the island of Hawai'i are important habitat for many native Hawaiian honeycreepers, several of which are endangered (Scott et al. 1986). These high-elevation forests act as refugia for Hawaiian honeycreepers from the devastating effects of habitat loss and disease, which have led to the extirpation of most lower-elevation populations (Warner 1968, van Riper et al. 1986). However, most of these wet forest habitats are not pristine; forest composition and associated ecological processes have been degraded by the activities of feral ungulates. The forest is also home to high densities of introduced mammals and birds. Introduced mammals may act as nest predators (Atkinson 1977) and damage or destroy native plants and create areas of disturbance, and introduced birds may compete for food or nest sites with native species (Banko and Banko 1976, Mountainspring and Scott 1985). These factors may threaten the persistence of native bird species by affecting their nesting success, recruitment, and survival.

The Hakalau Forest National Wildlife Refuge (Hakalau), located at 1,600 m elevation on the windward slope of Hawai'i, contains some of the best remaining habitat for native forest birds on the island. The forest harbors important populations of several endangered forest birds, including the 'Akiapōlā'au (*Hemignathus munroi*), 'Akepa (*Loxops coccineus coccineus*), and

Hawai'i Creeper (*Oreomystis mana*). In this paper, we report on the demography and ecology of the Hawai'i Creeper, a small, 15-g insectivorous bird that forages by creeping along the trunks and major branches of large trees, gleaning insects from the bark (Scott et al. 1979, Mueller-Dombois et al. 1981b). Hawai'i Creepers defend a small (10–20 m radius) area immediately surrounding the nest, and forage over a 4–7 ha home range during the breeding season (Ralph and Fancy 1994a, VanderWerf 1998b). Females do all or most of the nest building and incubate, brood, and feed the chicks; males assist by feeding the female both on and off the nest and by feeding the young (Sakai and Johanos 1983, VanderWerf 1998b; J. Nelson, unpubl. data). During the nonbreeding season, pairs range over a wider area (about 11 ha) and join other forest birds in mixed-species flocks (VanderWerf 1998b). At Kīlauea Forest and Keauhou Ranch study sites on Hawai'i, creepers breed from about January to June (Sakai and Johanos 1983, Ralph and Fancy 1994b) and have relatively high adult survival (Ralph and Fancy 1994a). However, only 17 nests of this species have been documented (Sakai and Ralph 1980a, Scott et al. 1980, Sakai and Johanos 1983, VanderWerf 1998b), and little is known about their nest success, ability to renest, or seasonal fecundity.

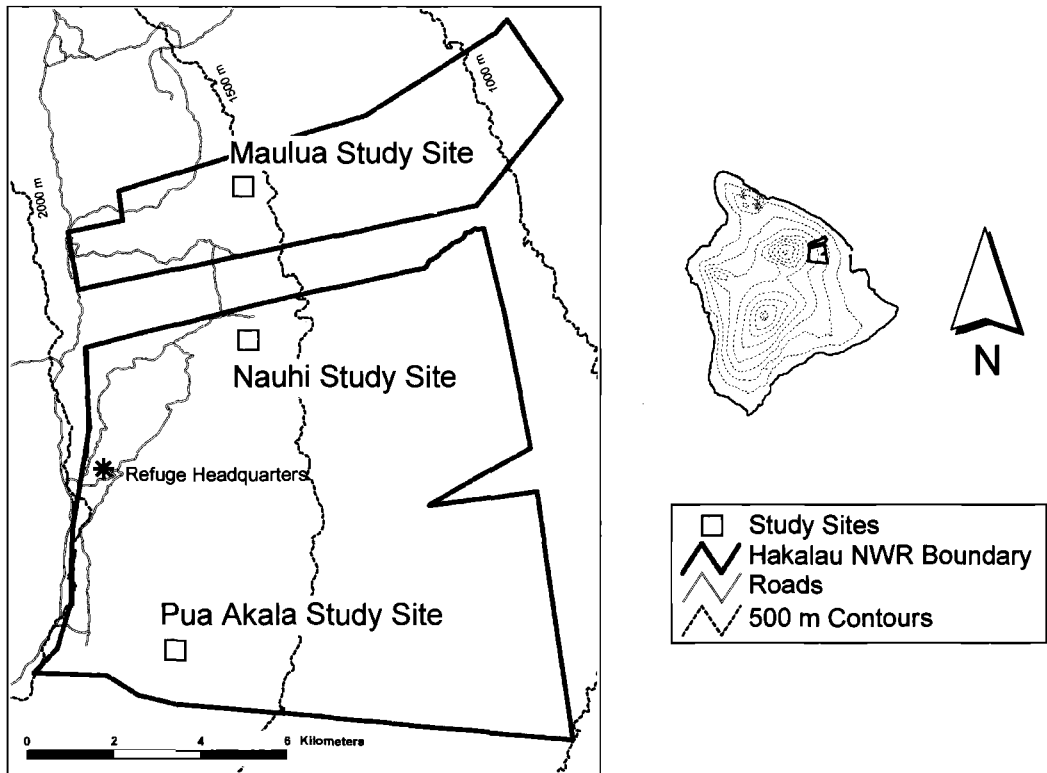The Hawai'i Creeper was once widely distrib-

FIGURE 1.   Map of Hakalau Forest National Wildlife Refuge on the windward slope of Mauna Kea, Hawai'i, showing the location of the three study areas: Maulua, Nauhi, and Pua 'Ākala.

uted in dry and wet habitats on the island of Hawai'i as low as 600 m in elevation (Scott et al. 1986). As of 1979, the creeper was confined to four disjunct populations in wet and mesic forests, primarily above 1,500 m (Scott et al. 1986). Two populations near Kona totaled only about 300 birds, and a third, near Ka'ū, consisted of about 2,100 birds. Hakalau, where 10,000 ± 1,200 birds reside, is the location of the largest remaining population of Hawai'i creepers (Scott et al. 1986). Our ability to assess and monitor the health and persistence of this core population depends on reliable estimates of the birds' recruitment and survival. Here we present data on population density, nesting success, productivity, juvenile and adult survival, and natal dispersal in order to understand further the population dynamics and conservation status of the creeper in Hakalau, and to assess potential management and restoration actions.

METHODS

STUDY AREA

We studied the wet forest bird community in Hakalau (19°51′N, 155°18′W), a tropical montane rain for-

est at 1,600 m elevation on the windward slope of Mauna Kea, Hawai'i (Fig. 1). Data were collected during 1994–1999 as part of an ongoing study of the wet forest bird community at three study sites within the refuge (Pua 'Ākala, Nāuhi, and Maulua), ranging in elevation from 1,500–1,640 m (Fig. 1). The forest canopies of all three study areas are dominated by 'ōhi'a (*Metrosideros polymorpha*) and koa (*Acacia koa*), but sites differ in their disturbance history and the composition of the understory. Common shrubs and subcanopy trees are 'ōlapa (*Cheirodendron trigynum*), ōhelo (*Vaccinium dentatum*), pūkiawe (*Styphelia tameiameiae*), and hāpu'u tree ferns (*Cibotium* sp.). Permanent markers were placed at 50 m or 75 m intervals in a 56–110 ha grid on each study area, where resighting, nest searching, and censusing were conducted, and at 25 m intervals on a smaller "intensive" grid within the larger grid at two of the study areas (350 × 450 m at Nauhi, 500 × 500 m at Pua 'Ākala), where banding was also done.

MIST NETTING AND BANDING

We captured birds in nylon mist nets (12 m × 2.6 m, 36 mm mesh) placed at a height of 6 m on two-tiered poles or suspended at 10–15 m height from branches in the canopy. Nets were operated from approximately 0700 to 1600 hours, except during inclem-

ent weather. From February 1994 to April 1996, we operated about 20 nets for 3–12 days at least quarterly at each of the three study areas. From January 1997 to June 1998, we netted only at the Nauhi study area, and operated from 18 to 48 nets approximately 14 days/mo. We moved each net approximately once each month to ensure complete coverage of the intensive grid each year. Banding effort through 1998 totaled 74,097 mist-net hours (13,214 net-hours at Pua 'Ākala, 56,953 net-hours at Nāuhi, and 3,930 net-hours at Maulua). From 1994–1998, we captured and banded 84 adult and 49 hatch-year Hawai'i Creepers.

POPULATION DENSITY

Densities of Hawai'i Creeper on the study areas were estimated using the variable circular-plot method (Reynolds et al. 1980) and the analysis techniques described in Fancy (1997). Counts were located 150 m apart at 36–48 stations on each study area and were conducted quarterly from February 1994 (Pua 'Ākala, Nāuhi) or August 1994 (Maulua) to August 1997. Observers were field biologists with extensive experience with the birds in Hakalau and were trained or recalibrated in distance estimation before each count. Observers counted all birds heard or seen during 8-minute counts, and estimated the horizontal distance to each bird. All counts were conducted between dawn and 1100 hours, and were discontinued in periods of heavy wind or rain.

We combined data for 37 surveys, which included a total of 685 detections of Hawai'i Creeper. We examined the effects of wind, rain, cloud cover, and time of day on detection distance using multiple linear regression following methods described in Ramsey et al. (1987); the effect of each of these variables was nonsignificant ($P > 0.50$). Variation between observers in hearing acuity and distance estimation skills can lead to differences in their effective detection distances (Ralph and Scott 1981 and papers therein, Scott et al. 1986). Buckland et al. (1993) recommended 60–80 detections for each observer as a practical minimum for estimating a detection function. Because of the rarity of the Hawai'i Creeper, the sample size of detections for most observers was inadequate for inclusion in the regression model, and so we were unable to correct for the effect of observers on detection distance.

We used the program DISTANCE (Laake et al. 1994) to calculate effective area from detection distances for Hawai'i Creeper. We truncated the distribution of detection distances by 4% to remove the elongated tail of the distribution (96 percentile distance = 96 m). Based on between-model goodness-of-fit tests, we grouped data into seven intervals of 13.5 m width, which resulted in an estimated effective detection distance (m) of 37.03 ± 1.06 SE (uniform key, $\chi^2 = 4.6$, df = 3, P = 0.21). Density was estimated at each station by dividing the number of creepers detected at that station by the effective area surveyed.

BREEDING SEASON AND MOLT

We banded birds with a U.S. Fish and Wildlife Service (USFWS) aluminum band and a unique combination of three colored leg bands. Birds were weighed using an electronic platform scale or 100-g Pesola spring scale, and measured for exposed culmen length and bent wing chord. Male and female Hawai'i Creepers cannot be reliably sexed using plumage characteristics, so sex was determined when possible by the presence of an active brood patch or swollen cloacal protuberance (Pyle et al. 1987). Brood patches were recorded as smooth (breast feathers molted but breast not yet vascularized), vascularized (fully developed, fluid-filled), or receding (wrinkled and/or pin feathers coming in around edges). Cloacal protuberances were classified as absent, small, medium, or large. Because birds with a smooth brood patch or small cloacal protuberance might be confused with nonbreeding birds in the field, we excluded such birds from analysis of breeding season and molt-breeding overlap. Juvenile (hatch-year) birds were identified by their plumage, primarily by the presence of a yellowish-white superciliary stripe and paler undersides (Scott et al. 1979). Birds were also examined for presence of flight or body molt, fat, and active pox lesions or missing digits (which may be indicative of past pox infection).

NESTING BIOLOGY AND SUCCESS

We systematically searched the study areas for color-marked birds for an average of 34 hr/mo (total = 1,235 hr) from 1994 through 1997, resulting in 236 observations of color-banded birds. Overall, about 40% of the Hawai'i Creepers on our study area were banded, as indicated by both our mist-netting and resighting data. We recorded data on social interactions, foraging behavior, and breeding activity of all color-marked creepers encountered. We located nests by following nest building or incubating birds to the nest. In general, we monitored nests every 2–8 days. Most nests were inaccessible and were monitored from concealed locations from a distance of about 25 m. We determined nesting stage by behavioral clues of the parents (incubation, egg turning, brooding, nest sanitation, or feeding). Monitoring visits typically lasted 30–60 minutes, and longer nest watches were conducted at some nests. We returned to nests at 5–7 day intervals three or more times after the nest became inactive and searched an approximately 100 m radius area for signs of renesting attempts.

We calculated daily nest survival rate and its associated variance using the Mayfield method (Mayfield 1975, Johnson 1979). We estimated transition dates between nest stages by forward dating or back dating from known events in the nesting cycle, assuming (1) a nest-building period of 16 days, (2) incubation period of 16 days, and (3) nestling period of 18 days (Sakai and Johanos 1983, VanderWerf 1998b; this paper). Where no other data were available, we assumed the event to have occurred on the date midway between intervals of checking the nest (Mayfield 1975). Abandonment was inferred if the nest was inactive for at least one hour on at least three consecutive visits. Hawai'i Creeper nest-building activity slows considerably in the few days before egg laying (U.S. Geological Survey, unpubl. data). Based on this, if a nest was abandoned <5 days after active building ceased, we assumed that eggs were never laid, although we recognize that we may have missed cases of egg predation very early in the nesting cycle. Nests that received eggs but fledged no young were classified as failed. Finally, a nest was successful if it fledged at least one

chick; in all cases success was confirmed by observation of the fledglings on the nest rim or out of the nest. In calculating the Mayfield estimate, we included exposure days for six nests with partial histories (four nests where eggs were removed for captive propagation, and two nests where fieldwork ceased before nest outcome was known).

Beginning in 1996, alien mammals were experimentally removed from one-half (48 ha) of the Nāuhi grid in conjunction with a concurrent study of the influence of introduced predators on nesting success and productivity of forest birds. Although this manipulation of predator numbers may have influenced nest success rates in this study, due to small sample size, statistical power to detect a difference in Hawai'i Creeper nest success between predator control and reference grids was low. There was no statistically significant effect of the treatment on creeper nest success rates (B. Woodworth, unpubl. data), and so we present the data for predator control and reference grids combined. Details of the predator control and its implications for other wet forest birds will be presented elsewhere.

Nest and nest-site characteristics were recorded for 52 nests in 1997–1999. Nests were classified as one of three types: (1) open cup; (2) pseudo-cavity, nest situated behind a bark slab or limb scar with more than two routes of ingress and <90% hidden; and (3) cavity, nest situated behind a bark slab or limb scar with one route of ingress and >90% hidden. Nest height was measured from the base of the nest tree using a clinometer and tape measure.

ADULT AND JUVENILE SURVIVAL RATES AND DISPERSAL

We estimated survival from 58 captures of 43 color-marked adult birds captured or resighted on the Nāuhi study area between 1994–1997. We used the program JOLLY (Pollock et al. 1990) to produce estimates of survival rate under five different capture-recapture models that vary in their assumptions about capture and survival probabilities. The reliability of Jolly-Seber estimates requires that data meet several assumptions (treated in detail in Pollock et al. 1990). First, all birds present in the population at the time of a given sample must have the same probability of being captured in that sample (homogeneity of capture probabilities). We excluded data from the Pua 'Ākala and Maulua study areas because mist netting ended there in April 1996. Second, all birds present in the population immediately after a given sampling period must have the same probability of surviving until the next sampling period (homogeneity of survival probabilities). Because juvenile survival rate is likely to be less than that of adults, we handled juveniles separately (see below). Although survival rates may vary between male and female honeycreepers (e.g., Lepson and Freed 1995), sample size was too low to account for differences in survival rates between sexes in this study. The third assumption is that bands are not lost or overlooked. Fourth, the sampling period must be short relative to the survival period. To approximate this assumption, we limited analysis to data collected from February to April each year (the months with the most complete data). JOLLY provides goodness-of-fit tests to assess the fit of a model to a given data set. Where several models fit the data, likelihood ratio tests

were used to test between models. The simplest adequate model was preferred because fewer parameters were estimated, and it therefore resulted in a more precise estimate. Survival rates are presented as mean ± SE. For comparison of survival rates, we used the program CONTRAST (Hines and Sauer 1989), which uses the chi-square statistic proposed by Sauer and Williams (1989).

Juvenile survival was estimated by enumeration, because sample size was insufficient to use model-based estimators. Juvenile survival rate was calculated as the proportion of birds originally banded as hatch-year birds that were recaptured or resighted in a subsequent year. Only hatch-year birds banded at the Nāuhi study area were included because other study areas had inconsistent coverage in later years. Mortality of juvenile birds is highest during the first few weeks after fledging (reviewed in Ricklefs 1973, Anders et al. 1997), but because recent fledglings are less mobile than older hatch-year birds, they are less likely to be captured in our mist nets. This will tend to increase our estimate of juvenile survival.

Natal dispersal is usually measured as the distance between the natal nest and the first breeding nest (Greenwood and Harvey 1982); because these data were not known in this study, we approximated natal dispersal by measuring the distance between a bird's first capture as a juvenile and its first capture as an adult. We recognize that birds dispersing long distances are less likely to be detected, and so the observed dispersal distance will be an underestimate of true dispersal distance, a limitation in all studies of dispersal that cover finite areas.

RESULTS

POPULATION SIZE AND DENSITY

Our quarterly variable circular-plot counts indicate that Hawai'i Creepers are more common at the Pua 'Ākala study area (2.18 ± 0.50 birds/ha) than at Nauhi (1.09 ± 0.29 birds/ha) or Maulua (0.57 ± 0.23 birds/ha), indicating a decreasing south-north gradient in density (GLM, df = 2, $P < 0.001$; Fig. 2a). Estimated density of creepers declined each November, probably reflecting a seasonal decrease in singing frequency (and therefore detectability) in the fall (Ralph and Fancy 1994b). In contrast, capture rates of Hawai'i Creepers, summed over all years, are similar among the three sites (Fig 2b; 0.348 birds/100 net-hours in Pua 'Ākala, 0.360 birds/100 net-hours at Nāuhi, and 0.229 birds/100 net-hours at Maulua; Kruskal-Wallis $\chi^2 = 1.3$, df = 2, $P = 0.53$), perhaps because Hawai'i Creepers forage fairly high in the canopy above the reach of most of our nets. Overall capture rate for the three study areas was 0.351/100 net-hours. For comparison, overall capture rates of the more common species at our study sites were 3.76/100 net-hours for 'I'iwi (*Vestiaria coccinea*) and 2.28/100 net-hours for Hawai'i 'Amakihi (*Hemignathus virens*).
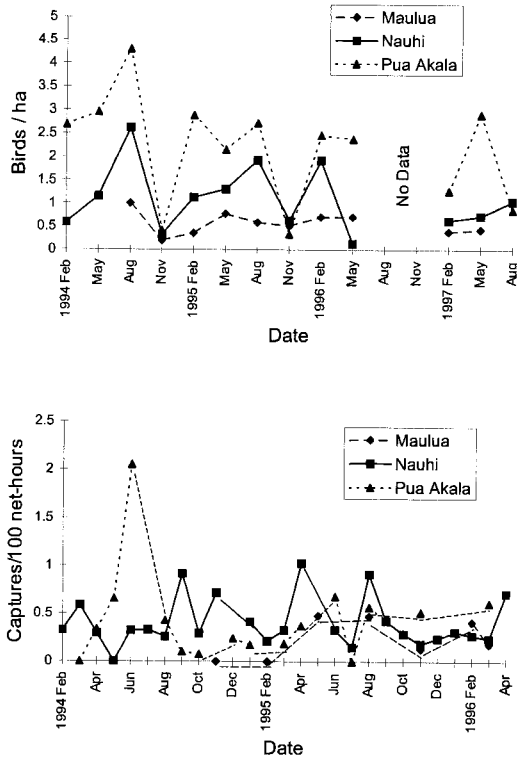
FIGURE 2. (a) Seasonal population density (birds/ha) of Hawai'i Creepers in Hakalau Forest National Wildlife Refuge on Pua 'Ākala, Nāuhi, and Maulua study areas, 1994–1997. (b) Capture rates of Hawai'i Creeper by month in Hakalau Forest National Wildlife Refuge on Pua 'Ākala, Nāuhi, and Maulua study areas, 1994–1996.

BREEDING SEASON AND MOLT

We used four different indicators of breeding season in Hawai'i Creepers. First, mist-netting data from 131 recaptures of 61 adult Hawai'i Creepers over four years (1994–1997) showed that females were in breeding condition from February to June, with a peak in May and June. In contrast, males with enlarged cloacal protuberances were captured over a protracted period from February to November (Fig. 3a). Second, hatch-year birds began to appear in the population in large numbers in June and peaked in September and October, based on mist-netting data (Fig. 3b). Similarly, hatch-year birds in our resight sample also increased in June, but then decreased, possibly because it was more difficult to identify late season hatch-year birds in the field than in the hand. Third, nest initiations peaked from February through May (Fig. 3c). Finally, one banded female began building her first (known) nest on about 12 February, and her last known nest failed on 11 May 1997. Thus,
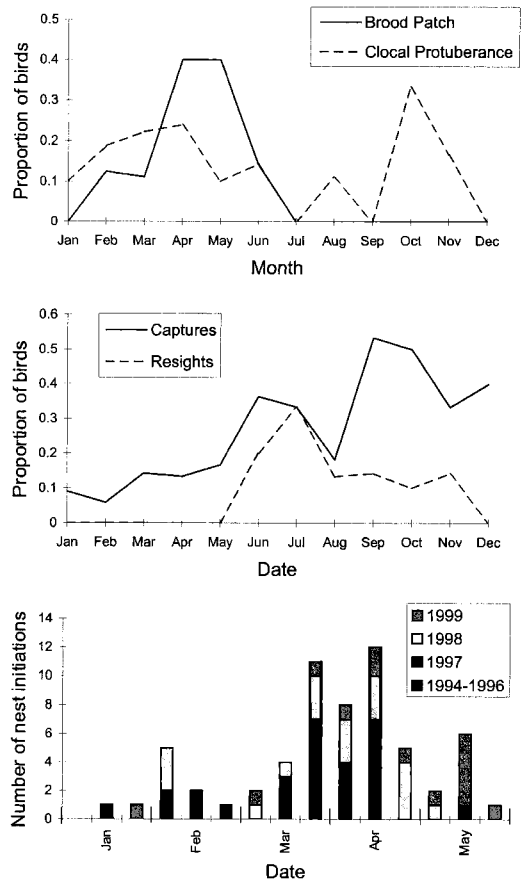

FIGURE 3. Breeding season of Hawai'i Creeper in Hakalau Forest National Wildlife Refuge. (a) Frequency of birds caught with an active brood patch or enlarged cloacal protuberance by month, 1994–1997. (b) Frequency of mist net captures and sightings of hatch-year birds by month, 1994–1997. (c) Dates of nest initiation (beginning of nest building) by 10-day intervals, 1994–1999.

the breeding season of this female lasted at least 3 months (none of her three nests were successful).

In 1998, when an El Niño event caused a severe drought from December to March, many Hawai'i Creepers delayed breeding in our study area until late March and April. Despite this late start to the breeding season, no new nests were initiated after the end of May.

Breeding was followed closely by feather molt (Fig. 4). Molting of flight feathers and body feathers peaked during June–August and overlapped breeding by about 2 months. However, only 3 of 61 adult birds (4.9%) were in breeding condition (i.e., had an active brood patch or an enlarged cloacal protuberance) while simultaneously molting body or flight feathers. This is
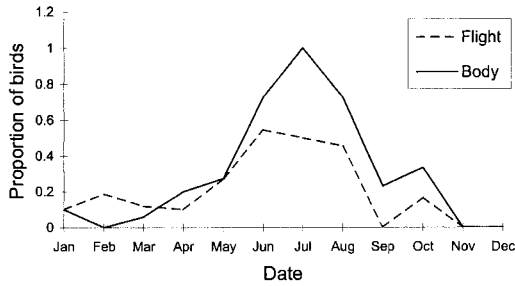
FIGURE 4. Timing of flight (wing and tail) and body molt of Hawai'i Creeper in Hakalau Forest National Wildlife Refuge, 1994–1997.

TABLE 1. FATE OF 60 HAWAI'I CREEPER NESTS, HAKALAU FOREST NATIONAL WILDLIFE REFUGE, HAWAI'I, 1994–1998

Fate of Nests	Number of nests[a] (percent)
Abandoned prelaying	15 (25.0)
Eggs pulled during incubation for captive propagation	4 (6.7)
Failed	23 (38.3)
Successful	10 (16.7)
Fate undetermined	8 (13.3)

[a] Data are from all study areas and years combined.

consistent with the frequency of molt-breeding overlap found in other studies of tropical birds (e.g., 3.1–8.5% of individuals; Payne 1969, Foster 1975, Ralph and Fancy 1994b).

NESTING BIOLOGY AND SUCCESS

We found a total of 60 nests, the majority (>90%) during nest-building activity and incubation. At least one member of the pair was color-banded at 29 of these nests. Nests were built in a variety of locations, from major forks in branches to clusters of small twigs and cavities, with a mean nest height (m) of 13.9 ± 5.0 SD (range 2.8–24.1, N = 52). Most (50/58) were open-cup nests, three were built in cavities, and five in pseudo-cavities (no data for other three nests). Nests were most often built in 'ōhi'a trees (88.5%, N = 60), and the remainder in large koa. This is not different from the percentage of 'ōhi'a trees available on the study area ('ōhi'a trees comprise 88.6% of the trees >30 cm dbh on the study area; B. Woodworth, unpubl. data). An analysis of creeper nest-site selection in relation to habitat availability will be presented elsewhere.

It is unknown whether Hawai'i Creepers routinely breed in their first year, but one banded female in this study was confirmed nesting in her first year. Nest building occupied 19 days at one nest, and mean clutch size in eleven nests was 2.1 eggs. Based on 4 eggs that were artificially incubated, incubation lasted 16–17 days, and captive-reared chicks fledged at 18 days of age (C. Keuhler, pers. comm; compare incubation period of 13–14 days and nestling period of 18–21 days in Sakai and Johanos 1983, VanderWerf 1998b). Pairs renested after failure, as indicated by ten renesting attempts by eight different pairs (two pairs nested three times within a season). The interval between failure of one nest (removed from the wild for captive propagation) and initiation of the replacement clutch was 22 days. Young remained dependent

on the parents for at least 23 days at one nest. Two pairs attempted to raise a second brood after a successful nesting attempt.

An estimated 25% of all nests that we found were abandoned before egg laying was begun (N = 60, Table 1). Fate of eight nests was undetermined because we left the study area or because we were unable to determine nest outcome. Eggs from four nests were collected and taken to a captive propagation facility to develop methods for rearing Hawaiian honeycreepers. Of the remaining nests (N = 33), nest failure occurred during egg laying, incubation, or nestling stages in 70% of nests (Table 1). Four of these failures coincided with severe wind or rainstorms (in one case the nest tree was toppled, destroying the nest). Seven successful nests fledged an average of 1.7 chicks each (range 1–2; number of chicks in three other successful nests could not be determined). We observed kleptoparasitism of nest material at six nests by I'iwi, 'Apapane (*Himatione sanguinea*), and Hawai'i 'Amakihi.

The daily survival rate of active nests was 0.960 (95% C.I. 0.942–0.977, N = 34 nests, 470.5 exposure-days). Based on this estimate, overall survival for the 34-day nesting cycle (from egg laying to fledging) would be about 25%.

ADULT AND JUVENILE SURVIVAL RATES AND DISPERSAL

Jolly-Seber Model D, which assumes constant survival and capture probability, was selected as the simplest adequate model to explain the data. Based on this model, annual adult survival rate from 1994–1997 on the Nāuhi study area was 0.88 ± 0.03, and capture probability over the four years was 0.37 ± 0.02.

Nine of 28 (32%) hatch-year birds captured in our mist nets were caught or resighted as adults. These hatch-year birds dispersed between 36–700 m from their first capture site to their first relocation as adults (median dispersal dis-

tance = 240 m; median time to relocation = 1.25 yr).

DISCUSSION

PRODUCTIVITY

Nesting success

Hawai'i Creepers built a large number of nests that never received eggs (25%). VanderWerf (1998b) also documented a high rate of abandonment (33%, N = 6 nests with known outcomes). Although human disturbance may cause abandonment (reviewed in Götmark 1992), most nests in this study were inaccessible and were observed from a distance, so nest disturbance was minimal. Disturbance from predators, an approaching end to the breeding season, disagreement between mates regarding a nest site, interference from other nesting birds, death of a mate, or the habit of building "dummy" nests for courtship or roosting may all result in building of inactive nests (Nolan 1978). In Hakalau, kleptoparasitism of nest material by other birds appears to be a frequent occurrence, having been noted at six nests in this study and in two nests by VanderWerf (1998b). Other passerines have been reported to build a high proportion of nests that did not receive eggs, e.g., four species of Hawaiian honeycreepers, 16–32% (Eddinger 1970); Prairie Warbler (Dendroica discolor), 23% (Nolan 1978); Laysan Finch (Telespiza cantans), 20% (Morin 1992b); and Puerto Rican Vireos (Vireo latimeri), 28% (Woodworth 1997).

In this study, 70% of active nests failed during incubation or nestling stages. Because nest contents could not be monitored in most nests, we could not confirm the cause of nest failure; disease, predation, starvation, exposure, and addling (failure to hatch) are all potential causes. Avian pox (Poxvirus avium sp.) and malaria (Plasmodium relictum) may infect and kill nestling birds (C. Atkinson, pers. comm.) and may decrease breeding activity of adults (E. VanderWerf, pers. comm.). However, the primary mosquito vector, Culex quinquefasciatus, is rare above 1,200 m elevation. Only about 3% of all birds of any species showed signs of pox infection during our study, and of 137 captures and 116 recaptures of Hawai'i Creeper over five years, we observed only one Creeper with an active pox lesion and one with a missing digit. The bird with pox lesions survived the infection and was recaptured and resighted several times over the following 15 months. Malaria antibodies were detected in only 6.6% of all birds captured and sampled at Nāuhi in 1998 (N = 242), and none of nine Hawai'i Creepers sampled showed evidence of past or active infection (J.

Lease, pers. comm.). Furthermore, mosquitoes are not known to breed in Hakalau; three surveys of mosquito breeding sites (Nov 1994, Feb 1995, Oct 1997) that sampled a total of 1,024 water sources at the three study areas (1,500–1,700 m elevation) failed to discover any larvae. The presence of disease at higher elevations may be the result of irregular or seasonal "disease events," whereby mosquitoes are carried by winds from lower elevations, or when mobile birds such as 'I'iwi or 'Apanane return from lower elevations with infection. Although we have no data on other potential diseases (e.g., Mycoplasma), we have no reason to suspect disease as a frequent cause of nest failures in Hakalau. Wind storms and heavy rains may cause nest failure; four of the nest failures during this study coincided with severe wind or rain, including one nest which was destroyed when the nest tree was toppled by heavy winds.

Nest predation is the most frequent cause of nest failures in small landbirds (Nice 1957, Martin 1992a), and predation is likely to be an important cause of nest failures in Hawaiian wet forests. Hakalau is home to six species of introduced mammals, most of which are potential predators on bird nests: feral cats (Felis catus), mongoose (Herpestes auropunctatus), roof rats (Rattus rattus), Polynesian rats (R. exulans), Norway rats (R. norvegicus), and house mice (Mus musculus). Of these, the roof rat is the most common and arboreal, and is potentially a major cause of nesting mortality in Hakalau (Lindsey et al. 1999; B. Woodworth, unpubl. data). Two avian predators are also found on the study area: the 'Io (Buteo solitarius) is common and has been observed preying upon nestling 'Amakihis on our study area, and the Barn Owl (Tyto alba) is present in low numbers.

Combining abandonments before egg laying and failure of active nests, about 79% of all Hawai'i Creeper nest starts failed to produce young (excluding 8 nests where outcome was unknown and 4 nests pulled for captive propagation). Similarly, in Kīlauea Forest and Keauhou Ranch, 89% (N = 9) of nests found were unsuccessful (reviewed in Sakai and Johanos 1983); and at a site upslope from our Pua 'Ākala study area, 50% of six known-outcome nests failed (VanderWerf 1998b). In contrast, nest mortality rate averaged 51% in 24 studies reviewed by Nice (1957) and 56% in 36 studies reviewed by Martin (1992a). The high rate of nest failure observed in this study is alarming, and further study is needed to elucidate the causes of these failures. If introduced mammals are responsible for a large proportion of failures, then controlling exotic predators in these habitats should have a large positive effect on forest bird pro-

ductivity, and may be an important management tool in Hawaiian native forests.

Breeding season and renesting

Additional important components of annual productivity are the probability that a female will renest after nest failure and successful nesting, and the length of time available for birds to breed. Data from marked pairs suggest that Hawai'i Creepers readily renest after failure, but we have no data on how often they raise a second brood. The closely related 'Alauahio (*Paroreomyza montana*) is not known to renest after fledging young (Baker and Baker in press). Parent Hawai'i Creepers feed fledglings for at least three weeks post-fledging, but within one month of leaving the nest young are foraging independently for food (although still following parents; VanderWerf 1998b; U.S. Geological Survey, unpubl. data). If a complete nesting cycle requires about 50 days plus postfledging care, and breeding seasons typically last at least 120 days, then there appears to be ample time for pairs to start a second brood. However, a daily nest failure rate of 5% might effectively prevent this from occurring very often. For example, one female that nested three times over the 1997 breeding season suffered two failures and one abandonment, and to our knowledge did not succeed in fledging young that season. Using a model of seasonal fecundity (Pease and Grzybowski 1995), based on the nesting data presented herein, we estimated that the average female probably fledges only about 1.85 young (0.93 females) per season.

Although nests of the Hawai'i Creeper have been located from January to August (Sakai and Ralph 1980a, Scott et al. 1980, Sakai and Johanos 1983, VanderWerf 1998b; this study), and despite our presence on the study area year-round 1994–1997, only four of our nests were found outside of the period February to May. Consistent with this, our data indicated a breeding season of about four months from February to May, based on breeding condition of females, the appearance of juvenile birds in the population, the timing of nest initiations, and the timing of molt. Ralph and Fancy (1994b) found a similar pattern based on mist netting and resight data at Keauhou Ranch and Kīlauea Forest. The 'Alauahio also breeds from late March to late July, peaking in April and May (Baker and Baker 2000a).

The breeding season of Hawai'i Creepers is long compared to that of many neotropical migrants (50–90 days; Ricklefs 1969, Nolan 1978), and compared to the nectivorous 'I'iwi and 'Apapane in the same habitat (Ralph and Fancy 1994b). However, it is more restricted than those of birds in wet lowland tropical areas, which may extend for up to 10 months (Ricklefs 1973). The ultimate factors controlling the length of the breeding season are unknown. At high-elevation montane sites, breeding seasons might be constrained by weather or food availability. Food (or food quality) may be too limited later in the season for parents to successfully feed nestlings; birds may need to accomplish postbreeding molt before the "lean season"; or if survival rates of late-fledging chicks are poor, selection may act to limit late-season reproduction. In Hawai'i 'Amakihi, the major breeding effort coincides with the time of year of maximum resource availability (when māmane, *Sophora chrysophylla*, bear the maximum number of flowers; van Riper 1987). Similarly, 'Apapane and 'I'iwi breed during the peak in 'ōhi'a flowering (Ralph and Fancy 1994b). Reproduction in tropical House Wrens (*Troglodytes aedon*) is generally timed so that postbreeding activities such as molt and dispersal of young coincides with the peak in arthropod abundance (Young 1994). However, Ralph and Fancy (1994b) found no predictable seasonal pattern in the biomass of insects available on 'ōhi'a foliage or 'ōhi'a terminal buds at a nearby site of similar elevation. As they point out, it is possible that insects found on bark substrates where creepers forage show a more marked pattern of seasonal abundance than do foliage insects.

What, then, are the factors controlling the onset and end of breeding in Hawai'i Creepers at Hakalau? This problem has important significance for conservation of the creeper and other Hawaiian wet forest birds: through the combined effects of disease and habitat loss, the species may now be confined to high elevation breeding habitats where their breeding season is too short to allow annual productivity to balance survival. The problem is exacerbated by the presence of mammalian predators which were historically absent from Hawai'i.

SURVIVAL AND DISPERSAL

Survival rate of adult birds in our sample (0.88 ± 0.03) was similar to that documented by Ralph and Fancy (1994a) of 0.73 ± 0.12 (χ^2 = 1.54, df = 1, P = 0.21). Baker and Baker (2000a) report a similarly high adult survival rate for the 'Alauahio (87% by enumeration methods). Both estimates are remarkably high, especially considering the small size and insectivorous habit of these species. Karr et al. (1990) found that the annual survival rates of 35 tropical and temperate species averaged 56%; Martin (1995) found an average survival of 53% for 34 temperate species; and Johnston et al. (1997) found an average survival of 65.3% for 17 Trin-

idadian species. Other Hawaiian passerines have similarly high survival rates, for example the Hawai'i 'Ākepa, 0.70 ± 0.12 SE (Ralph and Fancy 1994a) and 0.82 ± 0.04 SE (Lepson and Freed 1995); and 'Apapane, 0.72 ± 0.12 SE (Ralph and Fancy 1995).

The high survival rate of Hawai'i Creepers in Hakalau in part may reflect the rarity of disease in this high-elevation refugia, above the level of mosquito populations. However, a preliminary population model indicated that the population growth rate of Hawai'i Creepers is strongly influenced by adult survival (B. Woodworth, unpubl. data). Thus, the invasion of disease into these areas could have severe consequences for the population. Controlling the spread of mosquitoes into upper elevations (including control of feral pigs, which create mosquito breeding sites through their foraging activities) should be a high priority for management.

In general, reproductive potential of the creeper appears to be low due to its small clutch size, relatively long developmental period, and limited breeding season. This low reproductive potential is exacerbated by the high rate of nesting failures documented in this study, possibly due to the introduction of mammalian nest predators to Hawai'i. High adult and juvenile sur-vival rates may compensate to some extent for low annual productivity, but if disease were to reach the upper elevation rain forests it could have devastating effects. More detailed demographic data are needed to assess the implications for population persistence of Hawai'i Creeper in this high-elevation refuge. Finally, maintenance of the native wet forest bird communities on Hawai'i will require preserving the integrity of the habitat and its essential quality for the breeding birds—in particular, mosquito control, feral ungulate control, and rodent control will be important tools for management.

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