SHORT COMMUNICATIONS

The Condor 100:541–545

BREEDING BIOLOGY AND TERRITORIALITY OF THE HAWAII CREEPER[1]

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Abstract. The Hawaii Creeper (*Oreomystis mana*) is an endangered honeycreeper restricted to high-elevation forests on the island of Hawaii. I found eight Hawaii Creeper nests at Hakalau Forest National Wildlife Refuge from 1991–1997. Three nests fledged one or two chicks each, one failed because of bad weather, and two were abandoned after kleptoparasitism of nest material by other bird species. Females did most nest construction and all incubation and brooding. Both sexes fed the nestlings by regurgitation, with the male making 57% of feedings. The male fed the female during incubation and brooding. At two nests construction took 11–15 days and the incubation period was 13 days. At one nest the clutch size was two and the nestling period was 18 days. Mean nest tree height and diameter were 21.7 ± 2.9 m and 54.9 ± 23.6 cm, respectively, and mean nest height was 12.0 ± 4.3 m. Four nests were in cavities and four were open. One pair built an open and a cavity nest in the same season. During the breeding season males defended a small "type-B" territory with a radius around the nest of 15–20 m. Home ranges were larger in the nonbreeding season (11.9 ± 7.7 ha) than in the breeding season (4.5 ± 0.2 ha) and overlapped extensively.

Key words: breeding biology, Hawaii, Hawaii Creeper, kleptoparasitism, nest site variability, Oreomystis mana, *territoriality.*

The Hawaii Creeper (*Oreomystis mana*) is an endangered Hawaiian honeycreeper (Drepanidinae) endemic to the island of Hawaii. Hawaii Creepers are insectivorous and forage primarily on trunks and large branches of koa (*Acacia koa*) and ohia (*Metrosideros polymorpha*) trees (Mueller-Dombois et al. 1981). Their total population is estimated to be 12,500 in four disjunct areas of wet or mesic forest above about 1,400 m elevation (Scott et al. 1986). Decline of the Hawaii Creeper may be linked to habitat loss and alteration, introduced diseases such as avian malaria (*Plasmodium relictum*) and avian pox virus (*Avipox* sp.), nest predation by introduced rodents, and nest site limitation (Scott et al. 1986, Ralph and Fancy 1994a).

Hawaii Creepers are relatively long-lived; annual adult survival is estimated to be 0.73 (Ralph and Fancy 1994a), but little is known about their breeding system or degree of territoriality (Berger 1981). Nesting was first described quite recently (Sakai and Ralph 1980, Scott et al. 1980), and only a single successful Hawaii Creeper nest has previously been monitored (Sakai and Johanos 1983). I monitored eight Hawaii Creeper nests and followed movements of color-banded individuals in 1991 and 1994–1997.

METHODS

All observations were at 1,850–1,900 m elevation in the Pua Akala tract of Hakalau Forest National Wildlife Refuge, on the east slope of Mauna Kea on the island of Hawaii. Over 100 years of cattle ranching and logging have transformed the montane rain forest on the refuge into a mosaic of dense, closed-canopy forest and highly disturbed open woodland. The forest canopy is dominated by ohia and koa trees. Understory in the closed-canopy forest is fairly dense, but in the open forest there is little understory vegetation and the groundcover consists primarily of introduced grasses. For a more detailed description of these two habitats, see VanderWerf (1993).

While I was conducting research on other birds, I opportunistically located nests and resighted color-banded Hawaii Creepers within a grid system having numbered poles 50 m apart. I measured height and diameter at breast height of nest trees with a clinometer and tape measure, respectively. Nests were observed from the ground, 20 to 35 m away, using binoculars and a telescope. Most observation periods were 1 hr long, and total time spent observing each nest ranged from 1.0 to 15.2 hr. Sexes could be distinguished because some birds were color-banded and because sexes differ in behavior and in some cases in plumage (Scott et al. 1979, Pratt 1992). The female at one nest was a second-year bird that had much paler plumage than the male.

For birds resighted ≥ 7 times, home ranges were determined by the minimum convex polygon method using WILDTRAK (Todd 1992). Ranges of birds with < 7 points were smaller, suggesting that those ranges may have been biased (Swihart and Slade 1985). After birds with < 7 points were excluded, regression of home range size on sample size was not significant ($n = 10$, $R^2 = 0.071$, $F_{1,8} = 0.61$, $P = 0.46$). Mean ± SD number of points per bird was 11.5 ± 1.3 (range

[1] Received 16 September 1997. Accepted 11 March 1998.

7–19) during the nonbreeding season. Home ranges were determined separately during the breeding season for two pairs by following birds from the nest and using the most distant points in each direction. Values given below are means ± SD.

RESULTS

NESTING SEASON, SUCCESS, AND LOCATION

I found eight nests that were active from February through May. One was initiated in February, three in March, and four in April. Three nests fledged at least one chick, all in May, three failed, and the fate of two was unknown. The successful nests were the latest in the season. In 1994, two of five nests were successful, and three of four pairs fledged at least one chick. One successful nest was in dense forest and two were in disturbed woodland. One pair had two unsuccessful nests in dense forest, but the banded male was later seen with a very recent fledgling, and their third nest must have been nearby.

All nests were in tall ohia trees that reached the upper canopy. Mean nest tree height and diameter were 21.7 ± 2.9 m (range 18.0–26.0 m) and 54.9 ± 23.6 cm (range 17.3–83.7 cm), respectively. Mean nest height was 12.0 ± 4.3 m (range 5.0–16.5 m). Location of nests within the tree varied considerably. Four nests were in cavities: the hollow tip of a 15-cm thick branch broken off 2 m from the trunk; a deep nook in the trunk above a 20-cm thick branch; a cavity with a circular entrance in the trunk; and a cavity with a narrow vertical opening. Four nests were open and ranged from 0–7 m from the trunk: a crotch of the trunk and a large branch; a fork of two branches 10 and 5 cm thick; the terminal foliage at the end of a branch; and between the trunk and a strip of peeling bark. One pair that built two nests in one season switched from an open to a cavity nest.

NEST CONSTRUCTION

Construction took 11 days at one nest, whereas a second required 11 days to finish when 30% complete, or approximately 15 days total. Two nests were abandoned following kleptoparasitism of nest material by other bird species (see below). The female brought nest material 12.0 ± 1.5 times hr^{-1} (n = 4 nests). At three nests I did not observe the male help in nest construction, but at a fourth the male brought material 2.0 ± 0.8 times hr^{-1}, and in each of four observation periods. When females brought material, males at three of four nests often followed them to within a few meters of the nest and sang. Males usually waited for females to finish modifying the nest and followed them when they left. Females never sang, which proved useful in separating the sexes. Early in construction, ohia bark was the most common item brought to the nest, and it formed the bulk of each nest. The female returned to the same location to collect material up to eight times in a row, and brought up to five strips of bark at once. Collection of bark for nest material by creepers resulted in pale, bare patches on trunks of several ohia trees near each nest. Later in construction, grass and lichen were brought more frequently, presumably to be used in the nest lining and to camouflage the outside of the nest.

KLEPTOPARASITISM OF NEST MATERIAL

At two nests I observed repeated kleptoparasitism of nest material by ‘Apapane (*Himatione sanguinea*) and ‘I’iwi (*Vestiaria coccinea*), which stole material up to 5 and 11 times hr^{-1}, respectively. These nests actually decreased in size after I found them, were never completed, and apparently were abandoned due to kleptoparasitism of nest material. No birds that stole material were banded, so it was not possible to determine if more than one individual of each species was involved. ‘I’iwi sometimes removed many pieces of bark at once that were equivalent to several trips by a creeper. I never saw a creeper attempt to defend its nest against either an ‘I’iwi or an ‘Apapane, even though the creepers were sometimes near their nests. A Japanese White-eye (*Zosterops japonicus*) once attempted to steal nest material, but was chased away by the female.

COURTSHIP AND COPULATION

I observed six courtship feedings in 10 hr of observation during construction at three nests. Females solicited courtship feedings by crouching, quivering their wings, and giving high-pitched begging calls. Males occasionally gave soft "whisper" songs that consisted of fragments of typical descending trills mixed with a variety of soft calls and mimicry of other species, including ‘Elepaio (*Chasiempis sandwichensis*) and ‘I’iwi. Whisper songs were given as part of a pre-copulatory display in which the male rapidly hopped or flew back and forth in front of the female. One copulation was observed immediately following a courtship feeding and whisper song, two days before incubation began. Mounting of the female lasted about 5 sec, after which the male sang and the female preened.

INCUBATION AND CLUTCH SIZE

The incubation period at two nests was 13 days. Only the female incubated at both nests. I looked inside one nest using a mirror pole while the female was away foraging, and it contained two eggs. The female spent 5 min at the nest without adjusting material the day before incubation began, possibly to keep the first egg warm until the second egg was laid. Faint begging calls were heard at the nest on day 13, and when returning the female paused on the rim of the nest for 10 sec with her head lowered as if feeding nestlings, although none were visible.

Nest attendance (proportion of time female on nest) was high during incubation (Fig. 1). Females left the nest to forage 2.0 and 2.4 times hr^{-1}, with absences of 4.6 ± 4.1 and 3.0 ± 1.2 min, respectively. During incubation males fed females 1.4 and 1.6 times hr^{-1}. At one nest, 40% of feedings were at the nest, whereas at a second nest all feedings were away from the nest an average of 8.3 ± 2.9 m. Males usually gave a softer version of the typical "squeet" call when approaching the nest, prompting females to fly off the nest to be fed. During feedings the female behaved as in courtship feedings. Occasionally males would accompany females back to the nest after a feeding. I watched a nest until dark one evening, and the male appeared to roost for the night in dense foliage of an adjacent tree 5 m from the nest. He began singing from the same tree before dawn the next morning.

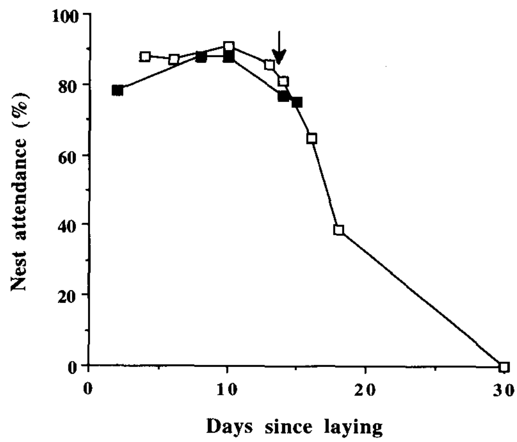

FIGURE 1. Attendance (% of time incubating or brooding) by female Hawaii Creepers at two nests. An arrow indicates hatching on day 13. One nest (solid squares) failed during early brooding, the second (open squares) fledged two chicks on day 31. Attendance probably dropped to zero before day 30, but no observations were made between days 18 and 30.

CARE OF NESTLINGS AND NESTLING PERIOD

Only the female brooded the chicks at two nests. Duration of foraging trips by the female increased as brooding progressed, resulting in decreased nest attendance (Fig. 1). Both parents fed the nestlings, with the male bringing food more often than the female (2.1 vs. 1.6 times hr^{-1}). Feedings by the male also tended to last longer (42 ± 22 vs. 27 ± 18 sec, Mann-Whitney *U*-test, $P = 0.07$), and may have provided more food. On three visits the male fed the chicks directly, twice he fed only the female, and she passed at least some food to the nestlings, and three times he fed both the female and the nestlings. Adults appeared to feed the nestlings by regurgitation. Upon returning to the nest, adults made exaggerated gulping motions by lowering the head and slowly raising it with the bill partially open, as if bringing food up from the crop, then passing it to the gaping chicks. Feeding bouts consisted of one to several regurgitations, with longer feedings having more regurgitations.

The nestling period was 18 days at one nest, which fledged two chicks. The head of one chick was first visible two days after hatching. One nest failed four or five days after hatching during several days of heavy rain and wind. One day before fledging the chicks sometimes stood on the nest rim, stretched, and flapped their wings. When nestlings were small both parents removed fecal sacs from the nest, but when they were older nestlings deposited fecal sacs over the side of the nest or on the rim.

POST-FLEDGING CARE

Fledglings gave high-pitched "ti-ti-ti" begging calls that made them conspicuous, and were fed by parents for at least 3 weeks. After a month, fledglings foraged independently, but still followed their parents from tree to tree. Beginning in late June parents and fledglings joined large, mixed-species flocks with other Hawaii Creepers, Hawaii 'Akepa (*Loxops c. coccineus*), Hawaii 'Amakihi (*Hemignathus v. virens*), 'I'iwi, Japanese White-eyes, and sometimes 'Elepaio and 'Akiapola'au (*Hemignathus munroi*).

TERRITORIALITY AND HOME RANGE

I observed territorial behavior between nesting male creepers on several occasions. The male at a nest under construction called loudly and appeared agitated when a neighboring male sang nearby. When the neighboring pair approached to within 20 m, the nesting male chased the intruding male away. The nesting female followed the male in the chase, but was not aggressive toward the intruding pair. Later that day the nesting pair tolerated the intruders until they were only 15 m away. Another male immediately chased a creeper that landed 10 m from the nest. The female did not react when a neighboring female collected nest material 10 m from this nest.

Nearest neighbor distances between nests of different pairs were fairly uniform (117 ± 17 m, range = 102 to 132, Fig. 2). Distances among three nests made by the same pair in one year were 84 and 119 m.

Home ranges of two pairs during the breeding season were 4.3 and 4.6 ha, and overlapped by 5.0% and 4.7% of their total sizes (Fig. 2). Breeding ranges of two additional pairs overlapped the mapped ranges more extensively, but were not measured. Home ranges were much larger in the nonbreeding season, averaging 11.9 ± 7.7 ha (range 4.3–27.1, $n = 10$). Nonbreeding ranges of the same two pairs that were mapped in the breeding season were 14.9 and 8.3 ha, increases of 346% and 180%, respectively (Fig. 2). Nonbreeding range overlap of any 2 of the 10 creepers averaged 31.6 ± 29.8%, with a maximum of 99%.

DISCUSSION

Breeding biology of the Hawaii Creeper is similar in most respects to those of many species of honeycreepers (Berger 1981, Pratt 1992), especially the closely-related Hawaii 'Amakihi (van Riper 1987). The creeper species on Kauai and Maui at least share characteristics of nest building (Eddinger 1972, van Riper 1972). These results generally agree with those of Sakai and Johanos (1983) from a Hawaii Creeper nest in the Kilauea Forest Reserve. In both studies, nestlings were fed slightly more often by the male than by the female, males fed females during incubation most often away from the nest, and males fed both females and nestlings during brooding. The nestling period was shorter at Hakalau than at Kilauea (18 vs. 20–21 days). Females left the nest to forage more often at Hakalau than at Kilauea (2.4 and 2.0 vs. 1.7 hr^{-1}), but the average absence was shorter at Hakalau (3.0 and 4.6 vs. 5.0 min), resulting in similar total time away per hr (7.2 and 9.0 vs. 8.5 min). Number of trips to the nest with food by both parents combined was higher at Hakalau than at Kilauea (3.7 vs. 1.8 hr^{-1}), and feedings were longer at Hakalau (36 vs. 23 sec).

I found similar numbers of creeper nests in open- and closed-canopy forests, but Sakai and Johanos (1983) found more nests per unit effort in closed-canopy forest, although sample sizes in both studies are small. Ralph and Fancy (1994a) found population den-

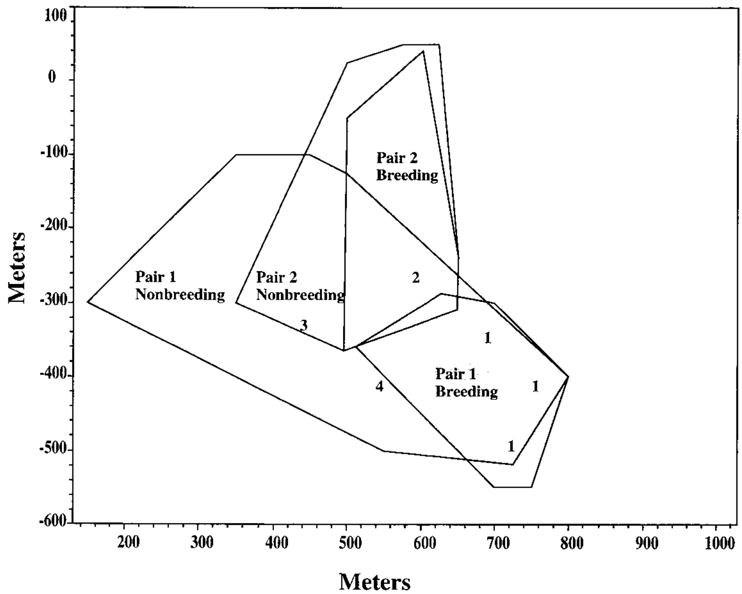

FIGURE 2. Home ranges of two Hawaii Creeper pairs in the breeding (shaded) and nonbreeding (open) seasons. Locations of six nests in 1994, three by pair 1, are marked with the pair number. Pairs 3 and 4 were not banded so their ranges could not be mapped, but they overlapped the mapped ranges extensively.

sity to be as high at two disturbed sites as at two less disturbed sites. Habitat loss has undoubtedly decreased the original range of Hawaii Creepers, but they are able to nest in some types of disturbed forest, suggesting that habitat alteration is not the primary factor limiting their current distribution.

Of nine Hawaii Creeper nests recorded in other areas, two were in cavities and seven were open; nest trees were ohia or koa 15 to 23 m tall, and two nest trees had diameters of 106 and 28 cm (Sakai and Ralph 1980, Scott et al. 1980, Sakai and Johanos 1983). At Hakalau, all creeper nests were in medium to large canopy-height ohia trees, but placement of nests within a tree varied. The four cavity nests were in the largest nest trees. One pair even switched from an open to a cavity nest in the same season, which also has been observed by J. Lepson (pers. comm.), suggesting that choice of nest placement is not genetically based and varies within individuals (Freed et al. 1987). Differences in life histories often seen in cavity-nesting birds, such as larger clutch size and longer incubation and nestling periods (von Haartman 1957, Lack 1968, Nilsson 1986), may not occur in Hawaii Creepers. Comparison of these attributes in open and cavity nests might help demonstrate whether they are an adaptation to or a consequence of cavity-nesting, and whether cavity nests are less vulnerable to predation by introduced mammals. Hawaii Creepers may prefer to nest in cavities of large trees if they are available, but they can use a wide range of tree sizes and nest positions. It is unlikely that distribution of Hawaii Creepers is limited by availability of nest sites.

Creeper nests were active at Hakalau from February–May. In other areas nests have been found from January–August, with a peak in birds in breeding condition in May (Ralph and Fancy 1994b). The three earliest nests in the season were unsuccessful, two of which were abandoned after kleptoparasitism of nest material by ‘I’iwi and ‘Apapane. The breeding season of Hawaii Creepers may be partly shaped by the breeding season and kleptoparasitic behavior of ‘I’iwi and ‘Apapane, which at Hakalau build nests primarily from January–March (unpubl. data; J. Lepson, pers. comm.). No kleptoparasitism was observed after early April. Creepers did not defend nests against ‘I’iwi or ‘Apapane, indicating both species are behaviorally dominant over Hawaii Creepers. ‘I’iwi and ‘Apapane are dominant over Hawaii ‘Amakihi (Carothers 1986), which are similar in size to Hawaii Creepers. Creepers that nest after the majority of ‘I’iwi and ‘Apapane have finished nest building may be less subject to kleptoparasitism and have a greater chance of success.

In the breeding season male Hawaii Creepers defended a small “type-B” territory (Nice 1941) with a radius around the nest of 15–20 m. Males chased potential rivals from the nest territory, but females did not. Males also respond aggressively to playbacks of recorded songs (L. Freed and J. Lepson, pers. comm.), but only in the breeding season (E. VanderWerf, unpubl. data). Nests were evenly spaced, but the area defended was smaller than the distance between nests. Creepers often foraged outside the nest territory, and home ranges were not exclusive among pairs.

Home ranges were larger (11.9 vs. 4.5 ha) and overlapped more extensively in the nonbreeding season than during breeding. Ralph and Fancy (1994a) found an average home range of 7.48 ha, and that ranges overlapped, but presented no evidence that creepers defend a nest territory, and did not specify whether their estimates included observations from breeding or nonbreeding seasons. Hawaii Creepers may occasionally move even longer distances in the nonbreeding season, and the home range sizes found in this study and by Ralph and Fancy (1994a) may be underestimates. In the fall of 1994 I observed two creepers over 1 km from where they were banded, but there were too few resightings of these individuals to construct home ranges. Another creeper banded in January at Pua Akala was observed 4 km away in March (J. Lepson and T. Pratt, pers. comm.), and Snetsinger (1995) observed a creeper at Kanakaleonui in January, at least 7 km from the nearest known population at Hakalau Forest N.W.R.

However, even these distances are relatively small compared to the large expanses of unforested land separating populations of creepers island-wide (Scott et al. 1986). Dispersal of creepers between populations and their ability to recolonize former habitat may be limited by high philopatry (B. Woodworth et al., unpubl. data). Creeper populations on Hawaii Island are probably isolated, and it is unlikely that they function as a metapopulation. Additional studies are needed to examine current levels of differentiation among populations and methods for increasing or facilitating dispersal.

I thank Joby Rohrer and Jason Bennett for assisting with nest observations, Pat Hart for helping to resight banded birds, and Dick Wass and Jack Jeffrey for permission to work at Hakalau Forest N.W.R. Walt Koenig, Jaan Lepson, Tim Male, Bonnie Nielsen, and two anonymous reviewers made valuable comments on the manuscript. This research was supported by a grant from the MacArthur Foundation to L. Freed, R. Cann, and S. Conant, and by grants to E. VanderWerf from the Hawaii Audubon Society, Sigma Xi, the ARCS foundation, the Ecology, Evolution, and Conservation Biology program of the University of Hawaii, and the University of Florida.

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