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DEMOGRAPHY AND MOVEMENTS OF THE OMAO (*MYADESTES OBSCURUS*)[1]

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Abstract. Density, age-specific survival, timing of breeding and molting, and movements of the Omao or Hawaiian Thrush (*Myadestes obscurus*) were studied at four sites on the island of Hawaii. Mean monthly density (birds/ha) was 3.23 ± 0.57, 1.07 ± 0.33, 3.23 ± 0.16, and 3.74 ± 0.36 at Kau Forest, Hamakua, Keauhou Ranch, and Kilauea Forest study areas, respectively. Annual survival of juvenile Omao (0.40 ± 0.09) was lower than that of adults (0.66 ± 0.08). Emigration and mortality was greatest during November through May. Breeding and molting occurred throughout the year, with peak breeding in May through July. Omao showed strong site fidelity and were highly sedentary. Mean home range size (n = 39) was 2.20 ± 0.26 ha and did not differ between sexes or study sites.

Key words: Omao; Hawaiian Thrush; Myadestes obscurus; *demography; survival; breeding; movements; Hawaii.*

INTRODUCTION

The Omao or Hawaiian Thrush (*Myadestes obscurus*) is one of four extant species of thrushes in the Hawaiian Islands (Pratt 1982). Its nearest relatives, the Olomao (*M. lanaiensis*) of Molokai and the Kamao (*M. myadestina*) and Puaiohi (*M. palmerl*) of Kauai, are all critically endangered with populations numbering fewer than 50 individuals, if they still survive (Scott et al. 1986, Ellis et al. 1993). The Omao is locally abundant in rainforests of the Hamakua, Puna, and Kau districts of the island of Hawaii, where it occurs in native forests of ohia (*Metrosideros polymorpha*) and mixed ohia and koa (*Acacia koa*) above 1500 m elevation (van Riper and Scott 1979, Scott et al. 1986). Omao have disappeared from Kona and the Kohala mountains where they were once common, and. they presently occupy only 30% of their former range (van Riper and Scott 1979). A small population of Omao exists in subalpine scrub and above tree line on Mauna Loa (Dunmire 1961, Berger 1981, pers. observ.).

Very little is known of the life history of any of the Hawaiian thrushes. Omao feed primarily on small fruits but take some insects (Perkins 1903; van Riper and Scott 1979; Ralph, unpubl. data). Pratt (1982) wrote that "Hawaiian thrushes are solitary, highly sedentary birds that live primarily in dense, montane forests." Perkins (1903), in contrast, reported on an incursion of Omao into an area near our Keauhou Ranch site in response to an outbreak of geometrid caterpillars, suggesting instead that the species is fairly mobile. The breeding season is thought to span at least a 9-month period, with peak nesting in May through July (van Riper and Scott 1979, Berger 1981). Omao usually build cup nests in trees, but may nest also in tree cavities and lava tubes (van Riper and Scott 1979, Berger 1981).

STUDY AREAS AND METHODS

We studied demography and movement patterns of Omao at four sites on the island of Hawaii between November 1976 and January 1982: Keauhou Ranch (19°30'N, 155°20'W; 1800 m elevation), Kilauea Forest (19°31'N, 155°19'W; 1,600-1,650 m), Hamakua (19°47'N, 155°20'W; 1,770 m), and Kau Forest (19°13'N, 155°39'W, 1,750 m), as described in Ralph and Fancy (1994a). This work was part of a larger study on population dynamics and foraging ecology of Hawaiian forest birds.

We estimated the density of Omao at each of the four study areas by the variable circular-plot method (Ramsey and Scott 1979, Reynolds et al. 1980) during 8-min counts, as described in

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Ralph (1981) and Ralph and Fancy (unpubl. ms.). Data were analyzed with the program VCP2 (E. Garton, unpubl. data).

We captured Omao in mist nets at the Keauhou Ranch (*n* = 62,006 net hours, November 1976 to January 1982) and Kilauea Forest (*n* = 16,958 net hours, April 1978 to November 1979) study areas, and processed birds as described by Ralph and Fancy (1994). Sex was determined by presence of a brood patch or cloacal protuberance (Ralph et al. 1993). We identified juvenile birds on the basis of plumage characteristics (Fancy et al., in press), skull ossification (Pyle et al. 1987), and behavior. In this paper, we define juveniles as hatch-year and second-year birds retaining juvenal feathers (Fancy et al., in press).

At least monthly, we walked throughout each grid and recorded activities of at least 35 Omao during bouts of 5-60 sec (mean bout length = 20.0 sec) as described in Ralph and Fancy (1994). For each month, we calculated the mean number of seconds of song per minute by dividing the number of seconds of song during each activity bout by the length of the bout. Because rare activities such as singing are more likely to be recorded during longer activity bouts, we weighted each observation by the square root of the length of the bout. During each observation we also noted the presence of any immature bird with the focal bird or, if the focal bird was an immature, any adult bird that appeared to be associated with it. 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 population size and annual survival of Omao at the Keauhou Ranch site from capture-recapture data with Jolly-Seber models (Pollock et al. 1990). The complement of survival probability, that we report here, includes both mortality and permanent emigration. We selected a four-month sampling period each year from November through February, 1976-1981, based on goodness-of-fit tests from preliminary runs. We used only birds captured in nets to calculate population size because use of resighting data would violate the assumption that all birds have the same probability of being captured (Pollock et al. 1990). Birds captured or resighted during the eight-month period from March through October were coded as resightings and used to calculate survival probabilities (Pollock et al. 1990).

We recorded locations of individuals captured in nets or identified during surveys to the nearest 50 m within an expanded 600 x 600-m grid at the Keauhou Ranch and Kilauea Forest sites. 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). After inspecting plots and running correlation analyses of home range size versus sample size, we excluded individuals observed at < 9 locations from further analysis because of biases associated with small sample sizes (Bekoff and Mech 1984, Swihart and Slade 1985). We compared home range size and distance from the center of activity between study sites and sexes by two-way ANOVA. All reported values are means ± 1 SE unless otherwise stated.

RESULTS

SEASONAL VARIATION IN POPULATIONS

Mean monthly density ± SE (birds/ha) of Omao for all months combined was 3.23 ± 0.16 at Keauhou Ranch, 3.74 ± 0.36 at Kilauea Forest, 1.07 ± 0.33 at Hamakua, and 3.23 ± 0.57 at Kau Forest. We found no difference in Omao densities at Keauhou Ranch, Kilauea Forest, and Kau Forest, but density at all three sites was greater than that at Hamakua (Tukey's Studentized range test, df = 95, MSE = 1.96, $P < 0.01$). We found no seasonal pattern in Omao density at any of the four sites (Tables 1 and 2). Numbers of Omao per station followed the same trends as density estimates (Tables 1 and 2).

We obtained an independent estimate of Omao density at Keauhou Ranch using the age-specific Jolly-Seber model JOLLYAGE for Omao captured in nets between November and February, 1976-1982. The mean population estimate was 49.2 ± 19.4 Omao at Keauhou Ranch, or 3.1 birds/ha. The probability of recapturing an individual was 0.60 ± 0.16. Similar estimates could not be obtained for Kilauea Forest, even though monthly capture rates there were greater than those at Keauhou Ranch (paired *t*-test, $t = 2.98$, $P = 0.007$; Fig. 1), because we operated mist nets for less than two years at Kilauea Forest.

TABLE 1. Number of Omao heard or seen during 8-min counts and density of Omao at the Keauhou Ranch and Kilauea Forest study areas, island of Hawaii, 1977-1982.

		Keauhou Ranch					Kilauea Forest				
		Number of	Number		Density		Number of	Number		Density	
Month	Year	stations	Mean	SE	Mean	SE	stations	Mean	SE	Mean	SE
Jul	77	25	2.90	0.50	3.01	1.06					
Aug	77	25	3.07	0.31	2.41	0.83					
Sep	77	25	3.56	0.44	3.63	1.20					
Oct	77	25	3.30	0.04	2.68	0.92					
Nov	77	25	4.33	0.08	3.46	1.09					
Dec	77	25	3.75	0.19	1.94	0.64					
Jan	78	25	4.65	0.47	4.75	1.44					
Feb	78	25	5.01	0.32	3.83	1.09					
Mar	78	50	3.61	0.15	1.81	0.48					
Apr	78	50	3.65	0.12	3.01	0.97	50	3.11	0.14	1.71	0.44
May	78	75	3.16	0.15	2.38	0.63	49	4.11	0.39	1.93	0.43
Jun	78	75	3.60	0.32	2.03	0.41	50	4.98	0.11	8.98	1.81
Jul	78	62	2.91	0.22	2.80	0.75	75	6.21	0.51	3.64	0.54
Aug	78	75	4.15	0.47	2.93	0.56	75	6.51	0.70	4.43	0.64
Sep	78	76	5.19	0.37	3.19	0.57	75	6.12	0.54	3.43	0.49
Oct	78	62	4.58	0.35	2.55	0.53	75	5.43	0.41	4.23	0.63
Nov	78	75	4.00	0.29	3.11	0.62	75	4.86	0.34	3.70	0.64
Dec	78	25	4.75	1.67	3.92	1.15	44	4.82	1.04	3.06	0.73
Jan	79	75	3.77	0.54	2.07	0.44	27	4.88	0.60	3.03	0.85
Feb	79	75	3.58	0.41	2.55	0.51	74	4.96	0.46	4.55	0.89
Mar	79	81	3.31	0.45	3.20	0.71	50	3.22	0.33	2.57	0.71
Apr	79	100	4.61	0.29	7.48	1.11	87	5.16	0.71	6.73	1.16
May	79	75	3.60	0.62	3.35	0.72	75	4.69	0.69	5.59	1.02
Jun	79	101	4.81	0.55	4.41	0.81	75	4.29	0.62	5.57	1.05
Jul	79	75	3.02	0.68	3.28	0.74	75	3.44	0.22	3.62	0.83
Aug	79	72	5.07	0.76	7.45	1.55	75	5.03	0.72	4.94	0.93
Sep	79	79	4.34	0.20	2.84	0.75	75	5.54	0.76	4.42	0.85
Oct	79	76	4.35	0.53	2.75	0.61	75	6.30	0.77	4.60	0.82
Nov	79	87	5.64	0.53	3.50	0.76	75	3.71	0.51	4.80	1.00
Dec	79	87	5.26	0.67	4.18	0.80					
Jan	80	96	3.50	0.25	4.10	0.81					
Feb	80	88	3.72	0.37	4.60	0.92	162	2.03	0.48	2.07	0.56
Mar	80	76	3.54	0.37	3.89	0.84					
Apr	80	87	2.91	0.19	2.19	0.51					
May	80	125	3.15	0.39	3.70	0.73	138	2.07	0.56	2.05	0.57
Jun	80	75	3.09	0.33	3.35	0.72					
Jul	80	73	2.97	0.23	2.96	0.73					
Aug	80	100	3.36	0.42	1.87	0.37	150	2.81	0.79	1.74	0.52
Sep	80	124	4.24	0.38	3.80	0.70					
Oct	80	25	4.65	0.19	3.87	1.29	76	3.21	0.87	1.79	0.37
Nov	80	63	4.08	0.77	3.23	0.68	50	0.00	0.00		
Dec	80	49	3.49	0.36	2.83	0.85					
Jan	81	88	4.13	0.38	3.11	0.59	63	5.42	0.54	3.51	0.66
Feb	81	75	4.52	0.56	4.34	0.83	87	1.01	0.66	0.44	0.18
Mar	81	100	3.32	0.18	2.22	0.44					
Apr	81	50	3.62	0.44	2.90	0.77					
May	81	75	3.83	0.28	3.12	0.61					
Jun	81	75	2.50	0.16	1.84	0.46					
Jul	81	75	4.21	0.43	3.59	0.68					
Aug	81	75	3.43	0.14	4.95	1.13					
Sep	81	75	3.88	0.42	2.55	0.56					
Oct	81	75	3.62	0.45	1.77	0.36					
Nov	81	75	3.21	0.30	2.38	0.63					
Dec	81	75	3.02	0.16	2.07	0.52					
Jan	82	61	2.95	0.20	1.86	0.44					

TABLE 2. Number of Omao heard or seen during 8-min counts and density of Omao at the Hamakua and Kau Forest study areas, island of Hawaii, 1979-1980.

		Hamakua study area					Kau Forest study area				
		Number of	Number		Density		Number of	Number		Density	
Month	Year	stations	Mean	SE	Mean	SE	stations	Mean	SE	Mean	SE
Feb	79	45	1.38	0.32	0.70	0.32					
Mar	79						45	4.22	0.40	5.24	1.54
May	79	30	1.70	0.03	0.78	0.32					
Jun	79						45	3.91	0.60	4.31	1.30
Aug	79	45	2.07	0.08	0.45	0.14					
Sep	79						45	5.12	0.42	2.26	0.81
Dec	79	40	1.22	0.06	0.40	0.16					
Jan	80						45	2.36	0.56	2.99	1.29
Mar	80	15	1.27		0.81	0.53					
Apr	80	15	2.53		0.42	0.23	30	1.85	0.42	1.10	0.47
Jun	80	38	2.54	0.32	0.51	0.17					
Jul	80						40	3.38	0.18	2.00	0.58
Aug	80	45	2.62	0.16	2.62	0.86				1.41	0.60
Oct	80						45	4.01	0.95	5.96	1.56
Dec	80	38	1.98	0.22	2.91	1.11	40	2.25	0.35	3.82	1.42

SURVIVAL PROBABILITY

We calculated survival probability for Omao at Keauhou Ranch from 1255 captures and resightings of 153 adult and 137 juvenile birds. For this analysis, birds were analyzed as juveniles only if they were captured in a net between November and February and retained juvenal feathers. We used Model A2X of program JOLLYAGE (Pollock et al. 1990), which allows time-specific capture and survival probabilities and incorporates data from resightings. Mean survival probability of juveniles (0.40 ± 0.09) was lower ($x^2 = 12.7$, df = 2, $P = 0.002$) than that of adults (0.66 ± 0.11). The probability of resighting an individual in a given year if that individual was alive and in the study area was 0.62 ± 0.08.

Most birds observed for a minimum of two months were last observed during November through May, which is also when capture rates were greatest (Fig. 1). Mortality or emigration were lowest between June and August.

TIMING OF BREEDING AND MOLTING

We captured Omao in breeding condition during every month of the year (Fig. 2). Occurrence of birds with swollen cloacal protuberances peaked in March, and the proportion of birds with brood patches peaked in May. Proportion of juveniles with ≤10% skull ossification was greatest during May through August, indicating that most young fledged during May through July. Peak occurrence of birds molting their primaries, secondaries and tail feathers was in June through August.

Observations of Omao behavior also indicated that breeding occurred throughout the year. We observed copulation in March, July, and December, and Omao were observed carrying nesting material in March and October. Records of adult Omao feeding another adult were made in January, April, October, and November. We recorded Omao calls and songs throughout the year (Fig. 2). Greatest rates of singing occurred between January and May, during the early part of the breeding season.

Observations of Omao during monthly surveys indicated that they were mostly solitary and had a short period of parental care (Fig. 3). Pairing was relatively constant throughout the year, but the low level indicated that the sexes foraged separately. Observations of flocking behavior (i.e., >2 Omao travelling together) were extremely rare.

SITE TENACITY AND MOVEMENTS

Omao showed strong site fidelity and were highly sedentary. Forty-nine of 87 (56%) Omao that were observed in at least two months remained at the study sites for more than one year, and 25 of 87 (29%) remained for more than two years. A female that nested in a koa cavity in June 1978 was observed feeding a juvenile at the same location on 3 April 1979, indicating that at least some Omao nest at the same location in subse-

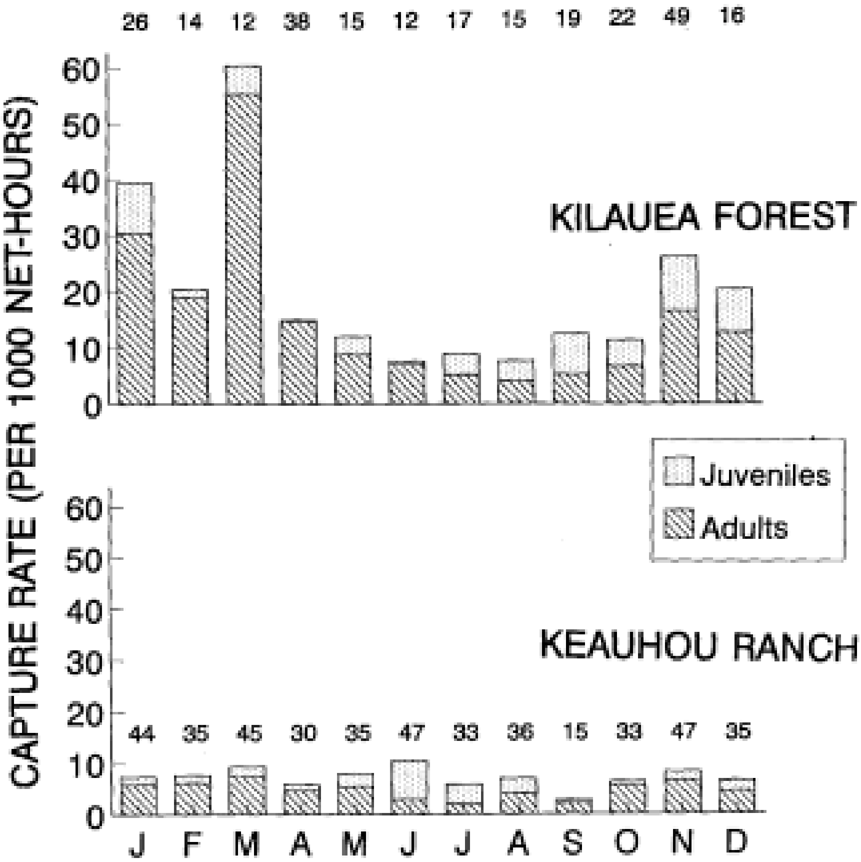

FIGURE 1. Capture rates of adult (striped bars) and juvenile (stippled bars) Omao at Keauhou Ranch and Kilauea Forest, Hawaii, 1976-1982. Total number of birds captured each month is shown above each bar.

quent years. We found no difference between study sites or sex in either home range size (two-way ANOVA, $F = 0.68$, $P = 0.57$) or distance from the center of activity ($F = 0.34$, $P = 0.79$). Mean home range size of 39 Omao for which we obtained >9 locations was 2.20 ± 0.26 ha. Mean distance from the center of activity for the same 39 Omao was 43.6 ± 2.45 m.

DISCUSSION

Our results support Pratt's (1982) statement that the Omao is a solitary, highly sedentary species. Densities at all four sites were relatively constant throughout the study, and the low frequency of sightings of pairs, families and flocks of Omao indicate its solitary habit. Omao densities at Keauhou Ranch, Kilauea Forest, and Kau Forest were significantly higher than at Hamakua, which was characterized by almost a complete lack of understory plants. Olapa (*Cheirodendron trigynum*) and naio (*Myoporum sandwicense*), two of the most important food plants for Omao at the other three sites, were absent from the Hamakua site. Scott et al. (1986) estimated Omao density within the 1,700-1,900-m elevation contour at 1.29 ± 0.07 birds/ha, compared with our estimate of 1.07 birds/ha. The most recent estimate for the Hakalau Forest National Wildlife Refuge was 1.74 Omao/ha (J. Jacobi, unpubl. data). Cattle were removed from the area where bird surveys were conducted during 1991-1993, and the understory is just beginning to regenerate.

The disappearance of Omao from the Kona and Kohala districts during the early part of the 20th century remains an enigma. Scott et al. (1986) speculated that the peculiar present-day distribution of Omao may have resulted from early extinction of susceptible populations in Kona and Kohala due to mosquito-borne diseases, and development of resistance and sub

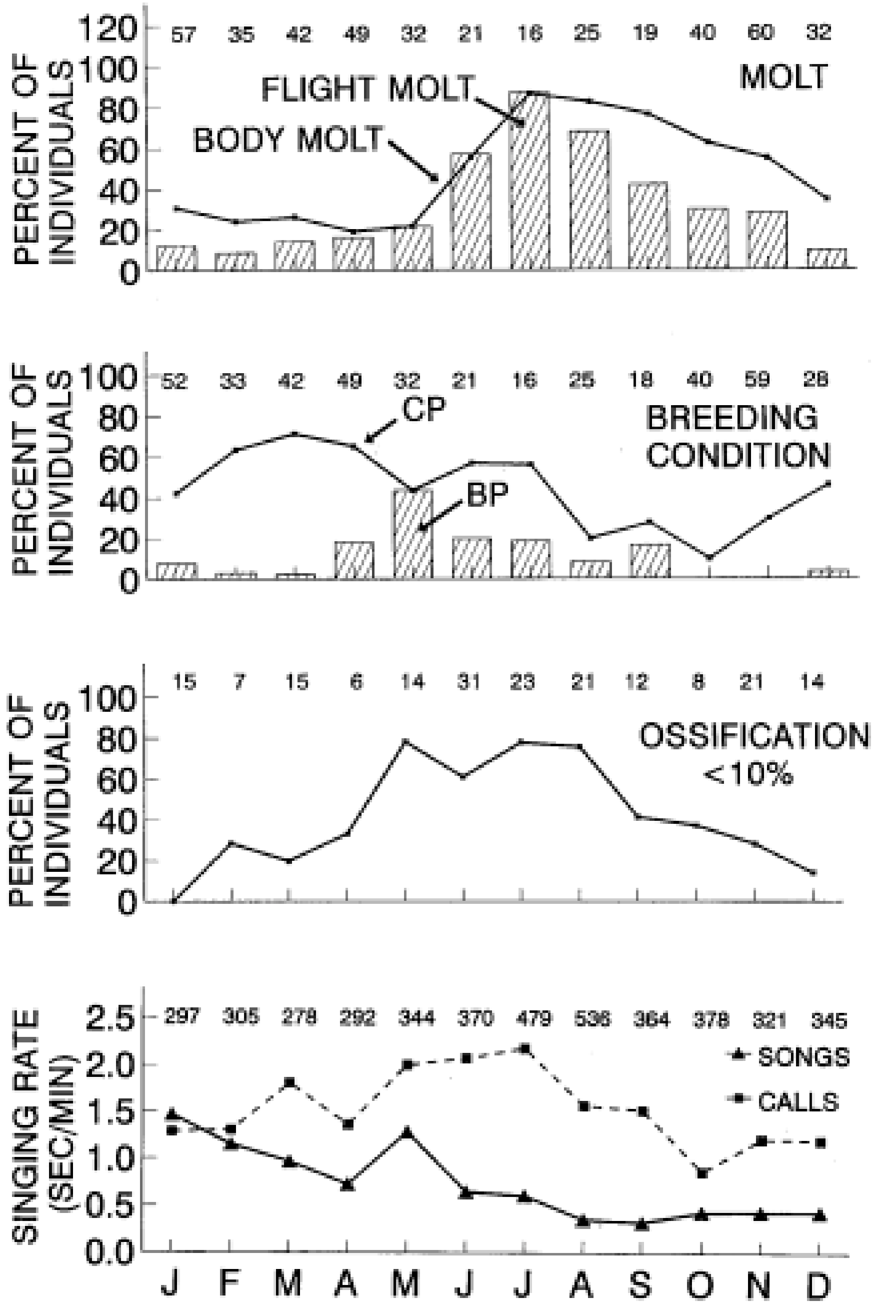

FIGURE 2. Timing of breeding and molting for Omao at Keauhou Ranch and Kilauea Forest, Hawaii. Percentage of birds with swollen cloacal protuberances (CP) and brood patches (BP) each month is shown, as is the proportion of all birds with <100% skull ossification that had <10% ossification. Numbers above each figure are sample sizes.

sequent dispersal of populations in the Hamakua and Puna districts. Mosquitos are the vector for avian malaria and avian pox, which have likely had a dramatic effect on the numbers and distribution of native Hawaiian birds (Warner 1968; van Riper et al. 1986; C. Atkinson, unpubl. data).

Almost all of the Omao's former range in the Kona and Kohala districts is within the zone of

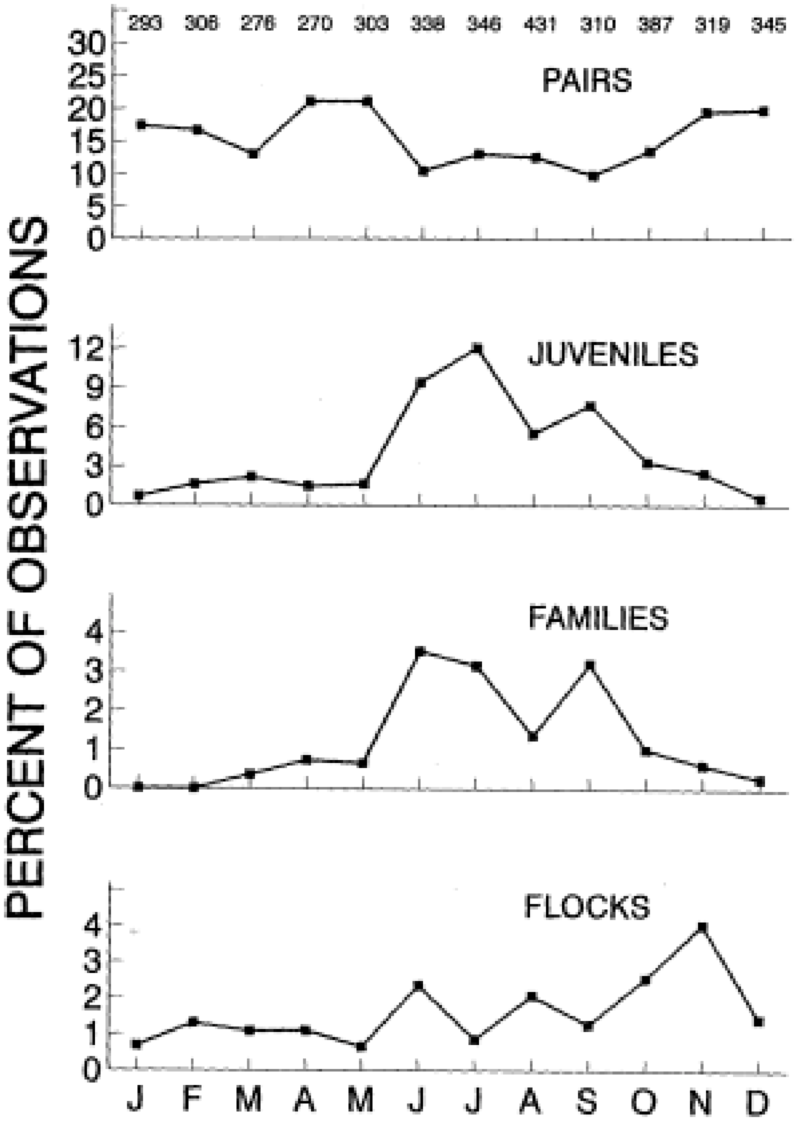

FIGURE 3. Percentage of observations that consisted of observations of two adult Omao (Pairs), solitary birds with juvenal plumage (Juveniles), one adult and one juvenile together (Families), and three or more Omao together (Flocks). Numbers at top of figure are sample sizes.

mosquito occurrence (Scott et al. 1986). In the Puna district, Omao are found at elevations as low as 300 m (Scott et al. 1986) where they coexist with mosquitos, and the prevalence of malarial parasites in Omao captured by van Riper et al. (1986; 1 of 47 Omao infected) and C. Atkinson (pers. comm.; 1 of 15 infected) is low compared with other native species. Thus, if avian diseases caused the extinction of Omao from the Kona and Kohala districts, extinction must have occurred within a relatively short period before Omao could develop resistance to the diseases.

Another explanation for the absence of Omao from the Kona and Kohala districts is the loss of understory food plants because of extensive habitat modification and grazing by introduced ungulates in the early 1900s (Scott et al. 1986). We found significantly lower densities of Omao where the understory had been heavily grazed by cattle. Olapa, a primary food source for Omao, is one of the first plants to be removed when cattle or sheep are introduced into an area (J. Giffin, pers. comm.). Feral pigs also cause extensive damage to understory plants used for food by Omao (e.g., Tomich 1969, Cooray and Mueller-Dombois 1981).

This study was designed primarily to investigate foraging ecology of forest birds, and we were unable to closely monitor the behavior of individual birds long enough to determine their breeding system. However, all of our findings are consistent with the hypothesis that Omao populations are regulated through a system of territorial behavior (i.e., Type-A territories of Nice 1941). For example, density estimates were relatively constant throughout the study, and Omao were highly sedentary. Pratt (1982) found that Omao reacted aggressively to playbacks of songs of other Omao, and we found that Omao sing throughout the year, presumably to advertise territories. We frequently observed Omao chasing other Omao, suggesting territorial defense. The relatively low but constant proportion of birds observed as pairs and families suggests a stable population with a short period of parental care. The lower survival probability for juvenile Omao suggests that juveniles are either displaced by resident adults or have higher mortality because of their inability to establish a territory. Additional research with banded birds is needed to confirm the breeding system for this species.

We found Omao breeding throughout the year, with peak breeding during May through July. Van Riper and Scott (1979) recorded Omao breeding during at least nine months each year. All active nests reported by Berger (1969, 1981) and van Riper and Scott (1979) were found during May through July, although van Riper and Scott (1979) observed recently fledged young on 8 October and 15 October, 1978. Highest rates of singing occurred between January and May, prior to peak breeding. Greatest rates of emigration coincided with increased rates of singing.

Estimates of survival probability for adult Omao are comparable to those for Akepa and Hawaii Creeper (Ralph and Fancy, unpubl. data), and for 35 species of birds in temperate and tropical forests (Karr et al. 1990). Karr et al. (1990) found no difference between survival rates of forest birds in Maryland and Panama, and questioned the generalization that birds in the tropics have higher survival than those in temperate areas (e.g., Ricklefs 1973, Skutch 1985). Our estimates for Akepa, Hawaii Creeper, and Omao, all made with the same methods as Karr et al. (1990), support their conclusion. Since the complement of survival probability includes permanent emigration as well as mortality, the lower survival probability we obtained for juvenile Omao may indicate higher emigration by young birds. However, if, as we argue, Omao have a territorial system that regulates population size, the best breeding areas may already be saturated and emigration may be tantamount to mortality.

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