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ECOLOGY AND BREEDING BIOLOGY OF THE HAWAII ELEPAIO (*CHASIEMPIS SANDWICHENSIS BRYANI*)[1]

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Abstract. Elepaio (*Chasiempis sandwichensis bryani*) were studied on the island of Hawaii from 1970 through 1981. The species had a protracted breeding season from February through August, with most intensive breeding from April to June. Annual breeding season length varied among years (range 3–7 months). Elepaio retained mates for more than one season and remained in their territory throughout the year. An Elepaio territory encompassed the nest site, all food resources, and had similar boundaries in succeeding years. Nests were statant, open-cupped, with mamane (*Sophora chrysophylla*) trees the preferred nesting substrate. Clutch size of 23 nests was two eggs and did not vary among years. Both parents incubated, brooded, and fed the young. Incubation periods averaged 18 (range 17–19) days; hatching success of eggs incubated to term in 22 nests was 75%. Nestling periods averaged 15.6 days; fledging success was 89.3% and young fledged synchronously. Total reproductive success, based on 19 nests with complete records, was 65.8%. The most important factor that influenced annual Elepaio productivity on Mauna Kea was length of the breeding season, followed by the number of nesting birds and eggs laid that failed to hatch (25%). Inter-island subspecies comparisons revealed many similar behaviors (e.g., courtship chasing, territory type, clutch and egg sizes, nest placement, adult roles in nest building, incubation, brooding and feeding). Differences among subspecies appeared to revolve mainly around the influences of forest-type in which birds bred. In mesic habitats on Oahu and Hawaii, predation of eggs and young by introduced mammals played a major role in decreasing annual productivity, whereas in the dry forest of Mauna Kea predation on *C. s. bryani* nests was much lower.

Key words: Hawaii; Elepaio; Chasiempis sandwichensis bryani; *breeding biology; predation; territory; productivity.*

INTRODUCTION

The Elepaio (*Chasiempis sandwichensis*), an endemic monarchine flycatcher found on three of the Hawaiian Islands, was first described by Latham in 1783 (Wilson and Evans 1890–1899), and has been placed in several genera (*Muscicapa, Cnipolegus, Eopsaltria*), with the most recent being *Chasiempis*. Pratt (1980) recognized three subspecies from the island of Hawaii (*C. s. bryani, C. s. ridgwayi, C. s. sandwichensis*), and one each from Kauai (*C. s. sclateri*) and Oahu (*C. s. gayi*). Olson (1989) showed that for the Oahu form, *C. s. ibidis* Stejneger, 1887, takes precedence over *C. s. gayi* Wilson, 1891. Conant (1977) studied the breeding biology of the Oahu subspecies, and Berger (1981) provided breeding information from Kauai. On Hawaii Island, information on subspecies other than *C. s. bryani* exists on distribution and numbers (Scott et al. 1986), relative abundance and breeding season information from Kohala Mountain (van Riper 1982), breeding aspects from Mauna Loa (H. Sakai and C. J. Ralph, in prep.), and foraging behavior and habitat selection on east Mauna Kea (VanderWerf 1993). The only published information available on *C. s. bryani* is a description of the nest and eggs (Berger 1969). In an effort to provide much needed baseline information on the ecology and breeding aspects of this unique bird, I conducted an 11-year study of the Hawaii Elepaio (*Chasiempis sandwichensis bryani*).

Elepaio are the second most abundant native forest bird in the dry forest on Mauna Kea, Hawaii (van Riper et al. 1978), but changes in annual population sizes remain undocumented. Scott et al. (1986) felt that *C. s. bryani* may have a precarious future because it is isolated from the other subspecies, occupies only a fraction of its potential range, and in 1980 had a population of 2,500 ± 900 (95% CI) birds centered in a dryland forest that is highly susceptible to fire. The purposes of this study were to: (1) examine the ecology of the Mauna Kea Elepaio population; (2) describe the breeding biology; (3) determine what factors most greatly influenced population

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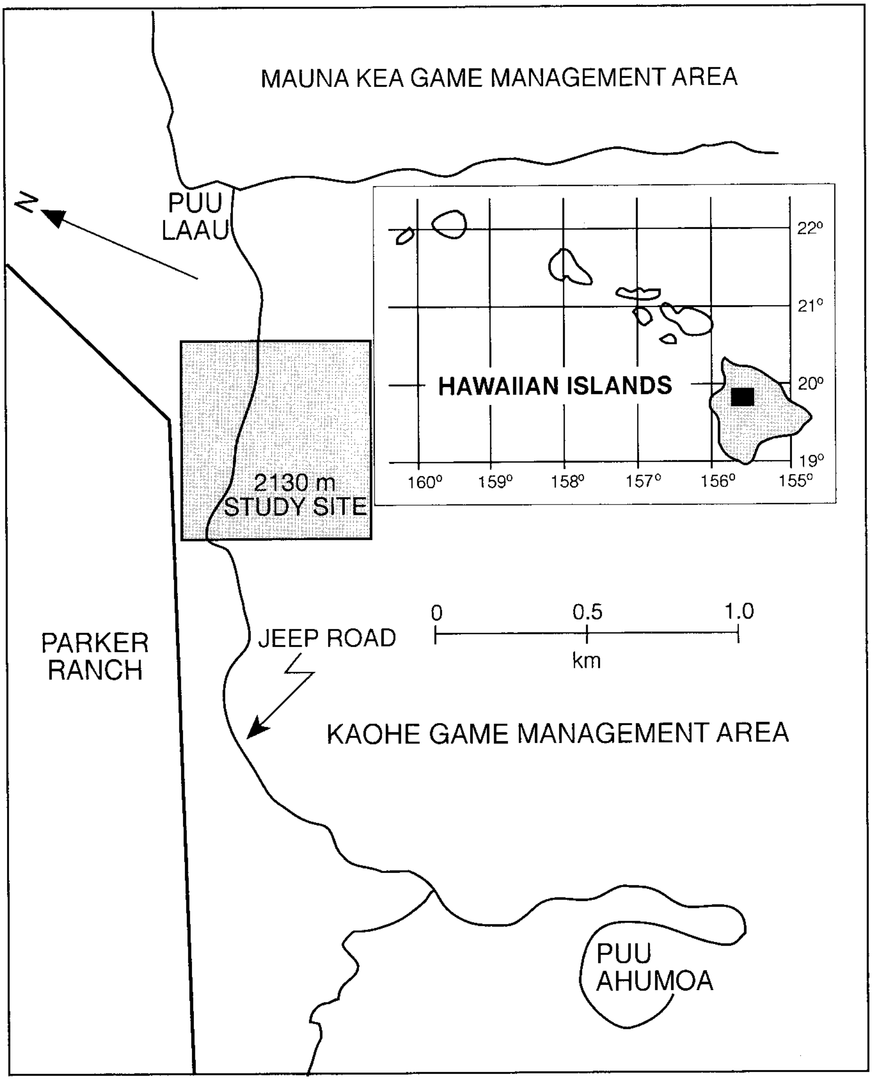


FIGURE 1. Study location of the southwestern slope of Mauna Kea, Hawaii. Stippled area is principal 25 ha Hawaii Elepaio study site.

dynamics; and, (4) compare information on *C. s. bryani* with that of other subspecies in the Hawaiian Islands.

STUDY AREA AND METHODS

From 1970 through 1981 I studied Elepaio behavior and ecology on the island of Hawaii. The period of most intensive field work was from 1973–1975, when I examined the species' breeding biology in a 25 ha study area at 2,130 m elevation on the southwestern slope of Mauna Kea (Fig. 1). During 1970–1972 I concentrated on capture and relocation of birds at three sites (1,980 m, 2,130 m, and 2,290 m elevation), while from 1976–1981 I continued to monitor and color-band birds in the 2,130 m and 2,290 m Mauna Kea study sites to determine the species' feeding ecology (presented in another paper) and longevity.

I captured adults by mist-net and marked each with a U.S. Fish and Wildlife Service metal band and a unique combination of colored plastic bands. Nestlings were banded between eight and 10 days of age. Adult Elepaio were sexed by plumage dimorphism, and it was also possible to differentiate between immature and adult birds

(MacCaughey 1919). I took the following measurements: long-beak and tail length (measured with a flexible celluloid rule, see Amadon 1950: 178), long-tarsus and wing length (measured by calipers), and weight (using a 50 g Pesola scale). Molting patterns were examined for all captured individuals. I also weighed nestlings daily and recorded feather tract and physical development.

Territory size was determined by plotting known boundaries from sightings of color-banded individuals using the home range program of Samuel et al. (1985). Adult aggression was documented by recording, through continuous observation, all chases of banded birds observed on 36 days, spaced throughout the year. Nest measurements included nest height (distance from ground to nest base), nest-tree height and species, circumference at breast height of nest tree (1.4 m from ground), distance from nest to axis of trunk and to end of branch, nest placement within the tree (terminal fork—limbs that formed the most distant group of stems from the trunk in the topmost 20% of canopy; lateral fork—end clusters of limbs in the remaining canopy; branch—any horizonal or vertical limb within the canopy cover); nest dimensions (nest height and width, bowl depth and diameter, rim thickness); and nest mass. The long and short axis of each egg was measured, and color patterns were recorded for each clutch. Vocalizations were recorded with a Uher 4400 report stereo tape recorded at a tape speed of 7.5 ips, and a Uher M514 microphone centrally mounted on a spun aluminum parabolic dish. Audiospectrograms were prepared with a Kay Electric Sound Spectrograph using both narrow and wide band-pass filters. The Elepaio daily song cycle was determined using continuous observation and by counting the total number of primary songs heard from all birds from 08:00–16:00 hr each hour of the day, for five days during the start of peak breeding in April and May 1975.

Annual productivity was calculated by the equation given by van Riper (1987):

$$\text{Index of Productivity} = \frac{(C)(B)(S)}{N}$$

where C = clutch size, B = length of breeding season in days, S = breeding success (the total number of eggs laid that fledged young within a standard area), and N = length of nest cycle in days. Length of the breeding season was considered the number of days per year when active nests were found.

TABLE 1. Measurements from adult *Chasiempis sandwichensis bryani* captured at 2,130 m elevation on the southwestern slope of Mauna Kea, Hawaii.

Measurement	Number measured	Range	$\bar{x}$	SD	P*
Beak length (mm)					
Male	12	11.0–12.0	11.4	0.4	0.64
Female	12	10.4–12.0	11.3	0.5	
Wing length (mm)					
Male	9	72.8–78.8	75.2	1.9	0.18
Female	7	61.6–76.4	72.0	5.4	
Tail length (mm)					
Male	8	63.0–77.0	69.1	5.2	0.75
Female	7	62.0–73.0	68.4	3.9	
Tarsus length (mm)					
Male	10	23.5–31.0	28.1	2.1	0.13
Female	10	23.0–29.0	26.6	2.0	
Mass (g)					
Male	21	13.4–18.0	15.8	1.2	0.17
Female	17	12.8–18.0	15.2	1.3	

* t-test.

RESULTS

SEX RATIOS, MORPHOMETRICS AND MOLT PATTERNS

I captured and color-banded 186 Elepaio during this study. There was no significant difference between capture rates of breeding males (n = 24) and females (n = 22) within the 2,130 m study (t-test; t = 0.51; P = 0.62). Moreover, observations of banded birds within the study plot indicated an even Elepaio sex ratio. Mass and size measurements of males and females did not differ significantly, but males generally had larger values for each variable (Table 1).

The most striking difference of this Elepaio subspecies is its light colored plumage and whitish head (van Riper 1974, Pratt 1980). A dark throat patch that contrasts with the whitish head starts to develop in the young after five months of age. I found molting birds from May to January, but the majority of body molt occurred in June and July, while flight feather replacement took place from June through August.

COURTSHIP BEHAVIOR, PAIR FIDELITY, AND VOCALIZATION

Adult aggression (as measured by sexual chasing) started to increase in the population during Jan-

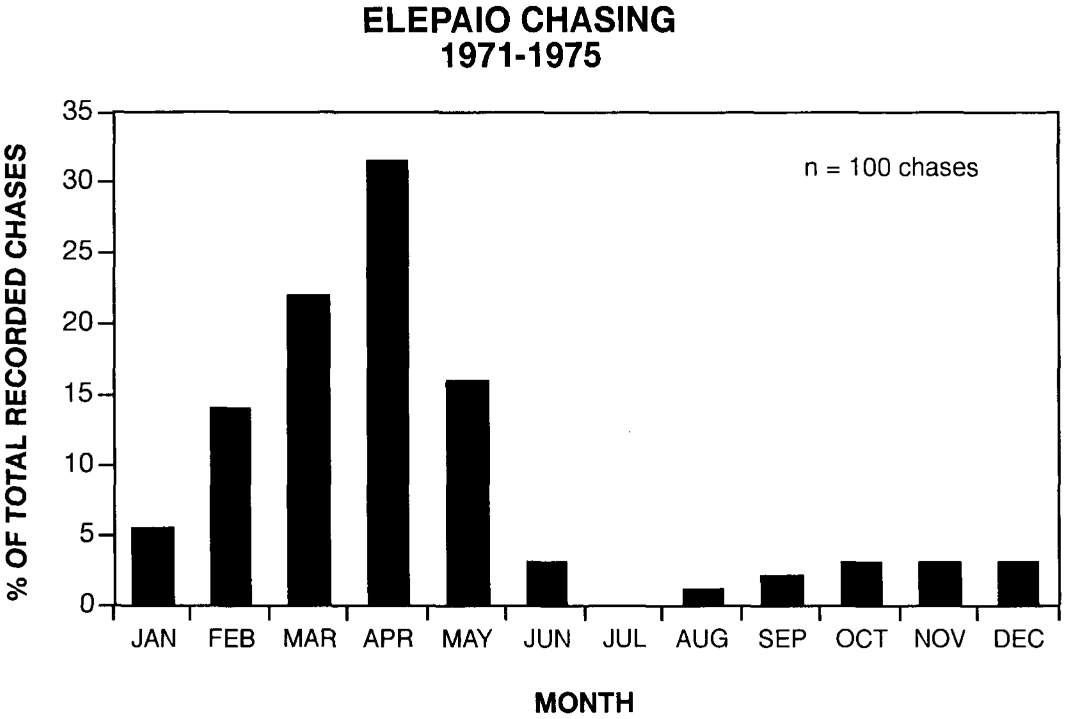


FIGURE 2. Monthly percentages of 100 total Hawaii Elepaio chases recorded during 36 days of field observations on the southwestern slope of Mauna Kea, Hawaii.

uary, just prior to the breeding season, peaked in April, then decreased to minimal levels during the latter part of the breeding season (Fig. 2). Elepaio retained the same mate between years; I did not record any mate switching among four banded pairs between consecutive years of study.

The Elepaio utilized one primary song (Fig. 3). Birds also gave a variety of calls and location notes during foraging, courtship interactions, and distress situations. This subspecies did not use a flying predator call, but vocalized with a series of loud primary songs when either the Short-

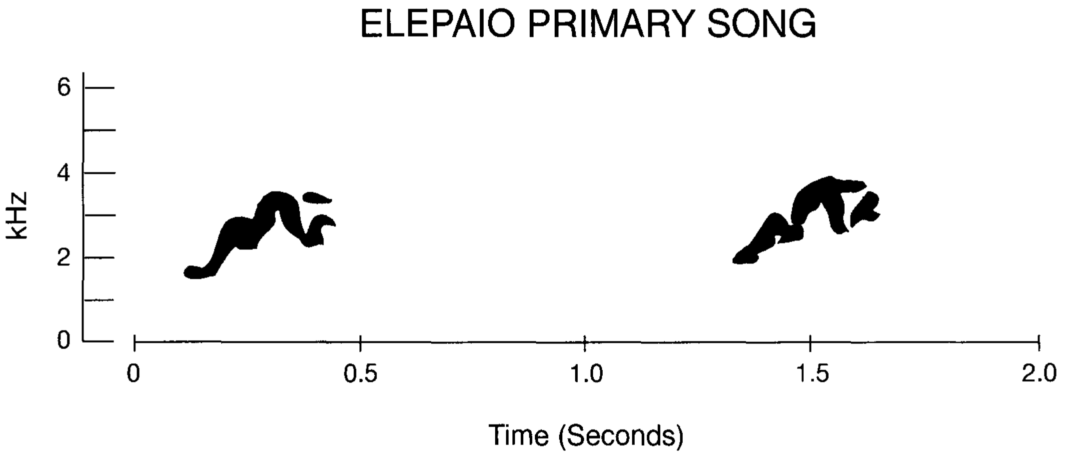


FIGURE 3. An audiospectrogram drawing of two Hawaii Elepaio primary songs. The audiospectrogram was produced on a Kay Electric Sound Spectrograph using a wide band-pass filter.

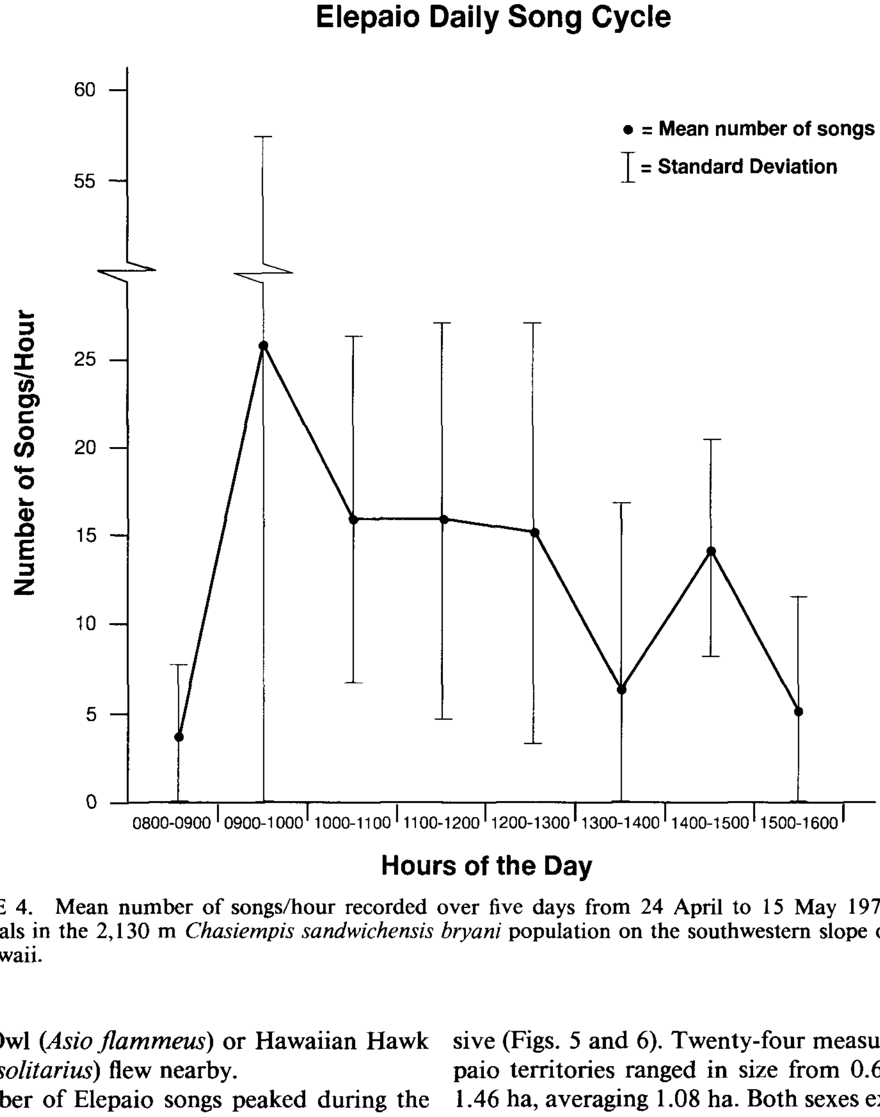


FIGURE 4. Mean number of songs/hour recorded over five days from 24 April to 15 May 1975, for all individuals in the 2,130 m *Chasiempis sandwichensis bryani* population on the southwestern slope of Mauna Kea, Hawaii.

eared Owl (*Asio flammeus*) or Hawaiian Hawk (*Buteo solitarius*) flew nearby.

Number of Elepaio songs peaked during the morning hours, then diminished throughout the remainder of the day, with a slight increase in the late afternoon (Fig. 4). The Elepaio is a very early singer during the breeding season, utilizing a predawn chorus (Table 2); the subspecies on east Mauna Kea also utilizes a predawn song (E. VanderWerf, in litt.). Elepaio began singing later and sang much less frequently during the nonbreeding period.

TERRITORY

Each banded pair ($n = 14$) occupied their territory throughout the annual cycle (Type A—after Nice 1941), and territories were mutually exclusive (Figs. 5 and 6). Twenty-four measured Elepaio territories ranged in size from 0.65 ha to 1.46 ha, averaging 1.08 ha. Both sexes exhibited territorial defense, and this was accomplished through song, perch displacement, chasing, and sometimes physical combat. A territory was held by the same pair ($n = 9$) for two consecutive breeding seasons, but there were boundary alterations between years. Three birds banded in 1974 were found on the same territory until 1979.

THE NEST

I obtained location information from 61 Elepaio nests. Mamane (*Sophora chrysophylla*) was the preferred nesting tree on the southwestern slope of Mauna Kea (72.9% of all nests). However, within the 2,130 m study area only 55.9% of nests

TABLE 2. Representative sequences of early morning avian vocalizations recorded at 2,130 m elevation on the southwestern slope of Mauna Kea, Hawaii.

Time of day	Nonbreeding season		Breeding season
	28 November 1974	28 February 1975	28 May 1975
05:00			05:10 ELEPAIO
			05:17 Wild Turkey
			05:18 Common Amakihi
			05:19 Eurasian Skylark
			05:21 SUNRISE
			05:27 Red-billed Leiothrix
			05:29 House Finch
05:30			05:56 Palila
06:00	06:15 Erckel's Francolin*		
	06:16 California Quail		
	06:17 Pacific Golden Plover		
	06:18 SUNRISE		
	06:19 Eurasian Skylark		
	06:20 Common Amakihi		
		06:22 SUNRISE	
	06:25 Wild Turkey		
06:30		06:30 Ring-necked Pheasant	
	06:31 ELEPAIO	06:32 Northern Cardinal	
		06:33 Common Amakihi	
	06:36 Red-billed Leiothrix	06:35 ELEPAIO	
	06:40 Melodious Laughing-thrush	06:40 Red-billed Leiothrix	
07:00			

* Erckel's Francolin (*Francolinus erckelii*), California Quail (*Callipepla californica*), Pacific Golden Plover (*Pluvialis fulva*), Eurasian Skylark (*Alauda arvensis*), Common Amakihi (*Hemignathus virens*), Wild Turkey (*Meleagris gallapavo*), Elepaio (*Chasiempis sandwichensis*), Red-billed Leiothrix (*Leiothrix lutea*), Melodious Laughing-thrush (*Garrulax canorus*), Ringed-neck Pheasant (*Phasianus colchicus*), Northern Cardinal (*Cardinalis cardinalis*), House Finch (*Carpodacus mexicanus*), Palila (*Loxioides bailleui*).

were located in mamane while 44.1% were in naio (*Myoporum sandwicense*). At this elevation mamane comprised only 26% of the available trees whereas at higher elevations on Mauna Kea it is the dominant tree (van Riper 1980). Within the 2,130 m study area I measured the height of 352 randomly selected naio and 265 mamane trees, and compared them to trees ($n = 34$) that contained nests (Figs. 7 and 8). Nest trees were taller than would be expected if birds selected trees solely on the basis of their availability (Kolmogorov-Smirnov 2-sample Test; $z = 1.3$; $P \leq 0.05$). Furthermore, nest height in both mamane and naio was influenced by tree height in that, as tree height increased, so did nest height ($r^2 = 0.44$; Fig. 9).

Of the 61 Elepaio nests that I found, 82% were located in terminal forks, 13% in lateral forks, and 5% on a branch. There was no significant difference between the distance of the nest from mamane trunks (mean = 259 cm; range = 0–640 cm) and the distance of nests to naio trunks (mean = 157 cm; range = 30–427 cm: $t = 1.7$; $P = 0.11$). There was also no significant difference between the distance of Elepaio nests to the end of mamane branches (mean = 40 cm; range = 8–76 cm) versus the end of naio branches (mean = 36 cm; range = 8–152 cm: $t = 0.35$; $P = 0.73$). Elepaio nest placement favored the southwest quadrant of the tree (Rayleigh Test; $\phi = 192$ degrees; R = 6.385), and nest azimuth by quartiles revealed a significant avoidance of the northeast quadrant of the tree ($\chi^2 = 4.5$; $P = 0.03$).

All nests were statant and cup-shaped. Except for nest height and width, measurements from 16 nests revealed very similar nest-structure parameters within this subspecies (Table 3). Both sexes participated in nest building. Construction averaged 10.6 days ($n = 5$; SD = 7.8 days) and ranged from 0 to 24 days. Construction of the nest lining took one to three days, but considerably more time was spent applying lichen and spider webs to the outside of the nest. The principal materials used in construction of the nest body were fine grasses, rootlets, animal hair and

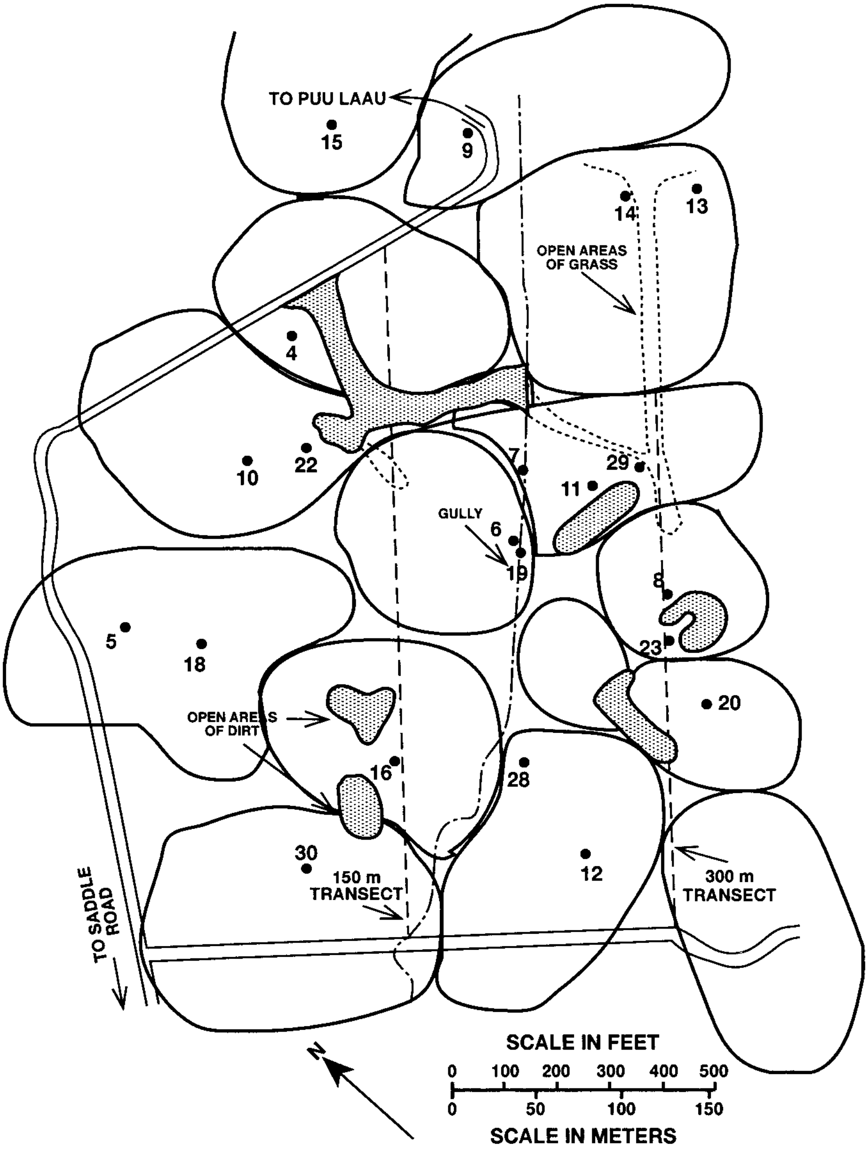


FIGURE 5. Hawaii Elepaio territories during the 1974 breeding season at 2,130 m elevation on the southwestern slope of Mauna Kea, Hawaii. Circles denote territory boundaries and numbers are location of nests within the territory.

sometimes sheep wool (van Riper 1977); lichens (especially *Usnea* sp.) and spider webs were placed on the outside of the nest. Most nest constituents were gathered on the ground within the territory, but on two occasions I did observe interspecific stealing of nest materials.

First nests took longer to build because when renesting, birds used materials taken from a previous nest. In one instance, a pair reused the same nest, following death of the first nestlings. Mean distance between first and second nests within a year was 41.4 m ($n = 20$), with the renesting attempt usually towards the opposite side of the territory. One pair of Elepaio built three nests in one year (Fig. 5), but only the first and third successfully fledged young. Between years, nest locations of the same pair of Elepaio were quite variable; the average distance between

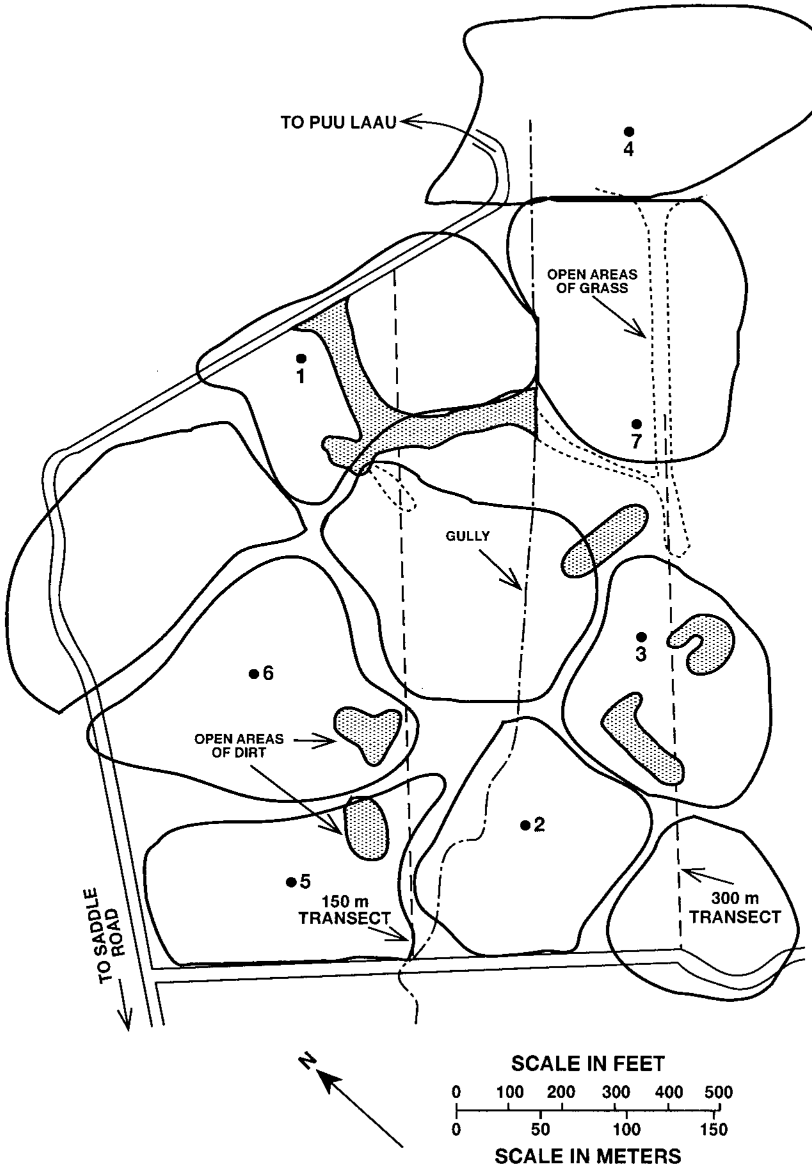


FIGURE 6. Hawaii Elepaio territories during the 1975 breeding season at 2,130 m elevation on the southwestern slope of Mauna Kea, Hawaii. Circles denote territory boundaries and numbers are location of nests within the territory.

six inter-yearly nests was 34.6 m, but ranged from 0.5 m (in the same tree) to 374.9 m.

EGGS AND CLUTCH SIZE

The clutch size in 23 nests was two eggs. Elepaio egg color was whitish with reddish-brown markings concentrated in a cap or ring at the large end. The average weight of three recently laid eggs was 2.23 g (SD = 0.05), whereas the weight of three eggs that were incubated to term but did not hatch averaged 1.88 g (SD = 0.09). Mean length of nine eggs was 21.1 mm (SD = ±0.5; range = 20.5–21.9 mm) and width 15.2 mm (SD = ±0.3; range = 14.7–15.7 mm). Egg shape (after Preston 1953) was oval, while mean egg shape index was 68.1 ± 0.3%.

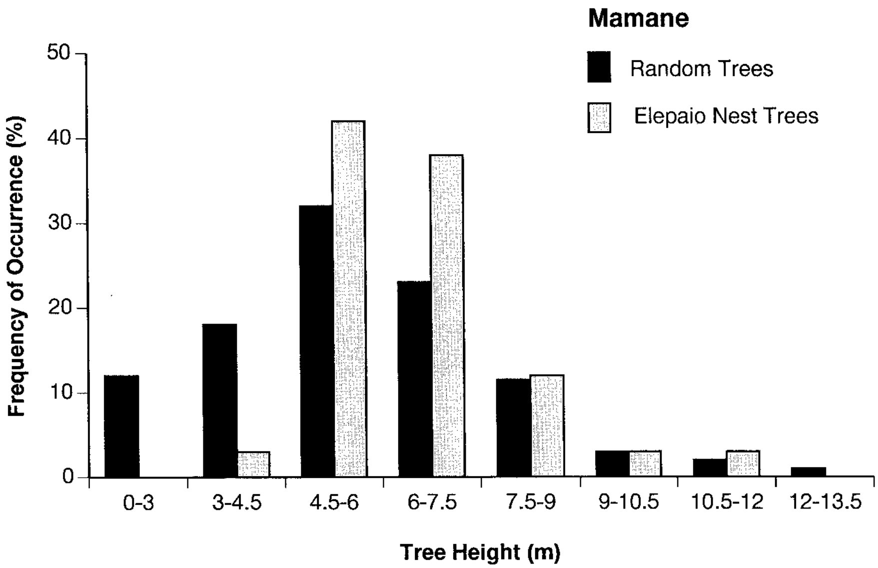


FIGURE 7. Frequency of occurrence in height classes of 34 Elepaio nest trees in relation to heights of a random sample of 265 mamane trees on the southwestern slope of Mauna Kea, Hawaii.

INCUBATION AND NESTLING PERIODS

Mean (and modal) duration of the incubation period at 4 nests was 18 days (range = 17–19 days). Male and female both developed a brood patch and both incubated and brooded, but at 16 nests the female did the majority (83.9%) of the incubation and brooding. Nest attentiveness was very high in that, throughout the incubation period, parents were on the nest most of the day (95.5%). Thermal probes placed in two nests revealed that heat was applied to the eggs throughout the entire night over the incubation period. After hatching, egg shells were carried away, but most of the time shell fragments were simply dropped over the nest rim. Eggs that did not hatch remained in the nest; one pair incubated an infertile clutch for 30 days.

Elepaio nestling periods varied from 14 to 17 days (mean = 15.6 days; *n* = 6). A decline in brooding attentiveness started at day three; by day eight, less than 20% of the daylight hours were spent brooding. During rain showers brooding rates increased slightly; however, females sometimes left the nest while it was still raining. Both the male and female fed the young, with 52.6% of the total observed feedings at seven nests attributed to the male, and 47.4% to females. Both parents regularly removed fecal sacs, and Elepaio nests remained clean throughout the nesting cycle.

NESTLING DEVELOPMENT

Young at hatching had dark-colored skin; eyes were closed and did not open until day five to

TABLE 3. Dimensions and mass of *Chasiempis sandwichensis bryani* nests collected from the southwestern slope of Mauna Kea, Hawaii.

Nest feature	Number measured	Mean	±SD	Range
Nest height	16	7.70 cm	1.21	5.08–11.94 cm
Nest width	16	10.44 cm	1.69	6.98–12.57 cm
Bowl width	16	5.35 cm	0.71	4.45–7.37 cm
Bowl depth	16	3.71 cm	0.43	2.54–4.32 cm
Rim thickness	16	1.18 cm	0.39	1.27–2.80 cm
Nest mass	2	10.1 g	0.71	9.6–10.6 g

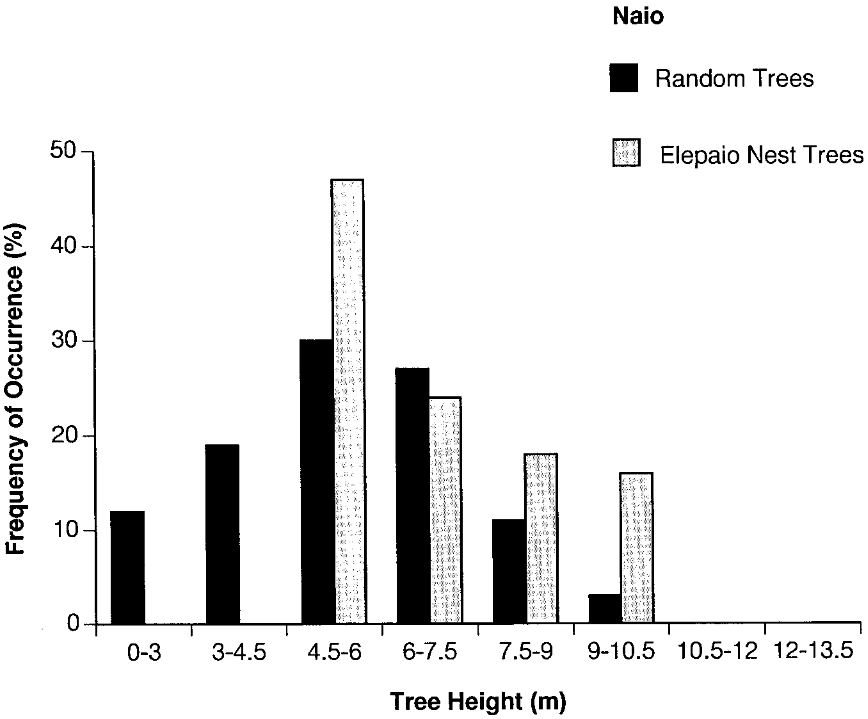


FIGURE 8. Frequency of occurrence in height classes of 34 Elepaio nest trees in relation to heights of a random sample of 352 naio trees on the southwestern slope of Mauna Kea, Hawaii.

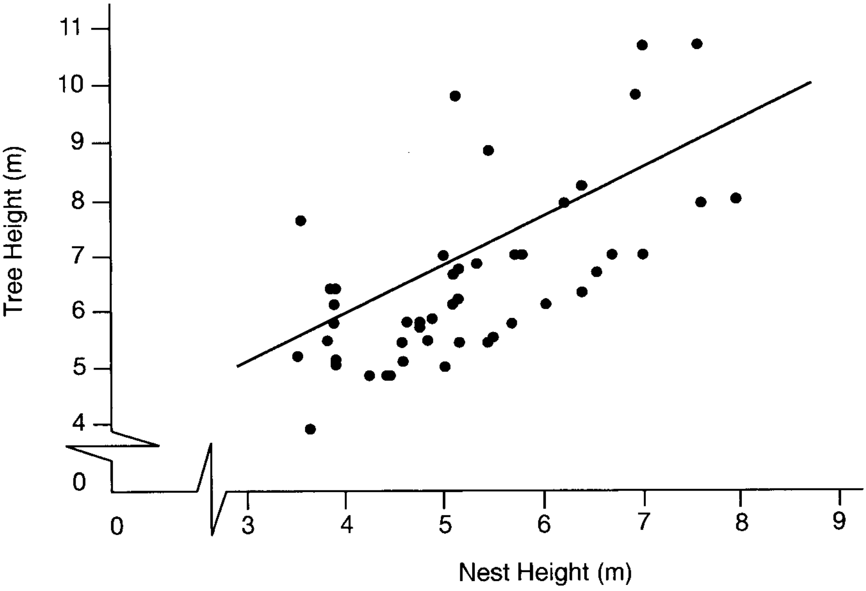


FIGURE 9. Relationship of nest height to tree height for 46 Hawaii Elepaio nests on the southwestern slope of Mauna Kea, Hawaii.

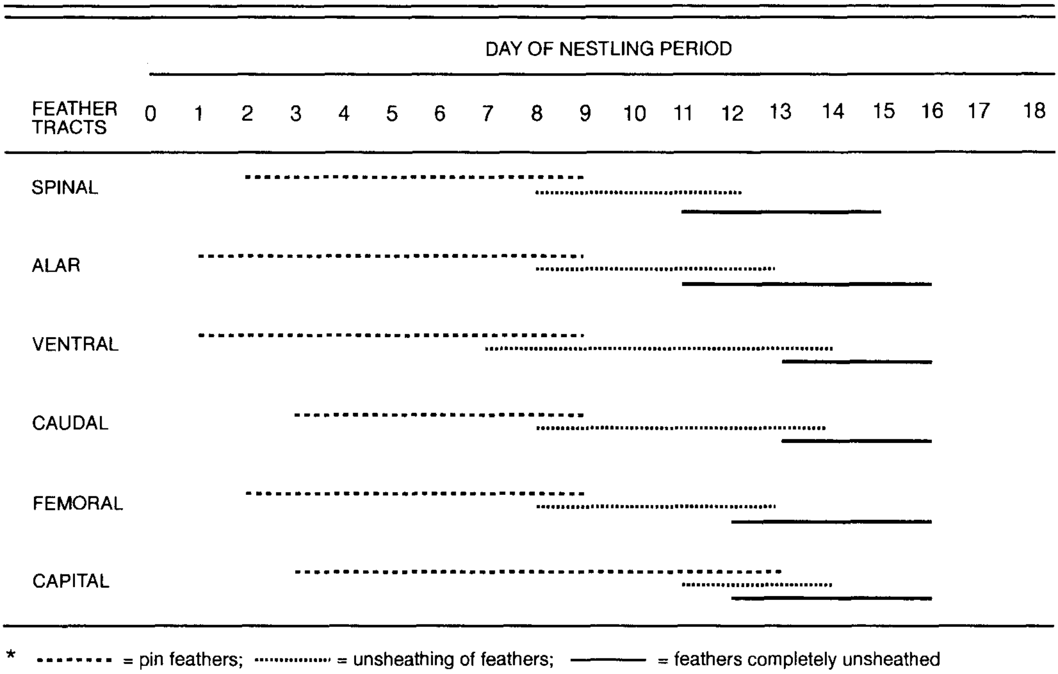


FIGURE 10. Development of feather tracts in 20 *Chasiempis sandwichensis bryani* nestlings at 2,130 m elevation on the southwestern slope of Mauna Kea, Hawaii.

seven. The bill was whitish and the gape pattern revealed a single crimson-red target area. All the pterylae were dark except for the ventral, which ranged from cream to a deep gray. Feather tracts remained the same color until the quills emerged. The feather tracts of 20 nestlings developed at different rates, with the capital last to open (Fig. 10).

Nestling weight increased in a logistic fashion, with a leveling off period after day 11 (Fig. 11). The fear response followed opening of the eyes, but cowering developed gradually; young gaped readily when the nest rim was tapped lightly, usually until day eight. I observed that young from a given nest fledged on the same day (n = 3).

The first week out of the nest was primarily spent preening, resting, and begging for food. Both adults fed the young, but the load shifted to the male if the female readied herself for the next nesting effort. At two nests I observed parents still feeding young from their first nest while in the process of feeding the newly hatched chicks of the second, but this was not usual. Young remained with their parents and on territory throughout the non-breeding period. Young birds were forced from their natal territory just prior to the initiation of the next breeding season.

REPRODUCTIVE SUCCESS

My analysis of Elepaio reproductive success was based on 46 eggs in 23 nests. Of those eggs that were incubated to term (n = 44), 33 hatched, yielding an Elepaio hatching success rate of 75%. Of 28 young that were followed through the nestling period, 25 fledged (fledging success = 89.3%). Overall reproductive success, from 19 Elepaio nests where 38 eggs fledged 25 young, was 65.8%. The greatest reduction in productivity was due to failure of eggs to hatch, which accounted for 25% of all eggs laid. I found a 10.7% nestling death rate, with inclement weather the only recorded mortality factor.

The Index of Productivity for Elepaio in a good reproductive year (e.g., 1974) was 1.21, while in a poor reproductive year (e.g., 1973), it dropped to 0.29. Although similar numbers of Elepaio defended territories among the years of this study, there was a large difference in the number of young produced among those years. For example, 55% more young were produced in 1974 (a good year) than in 1975 (a poor year). Reasons

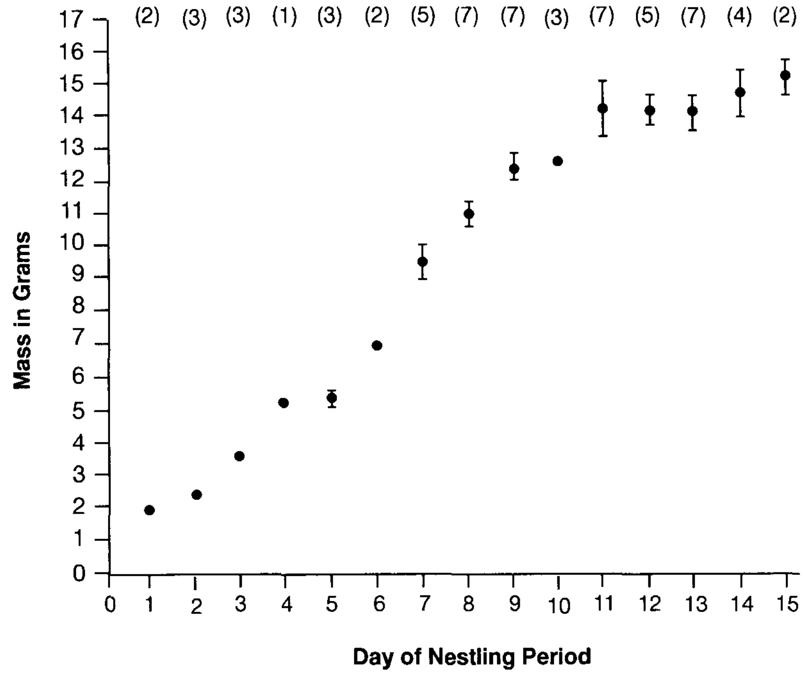


FIGURE 11. Daily weights of Hawaii Elepaio nestlings taken during the 1974 breeding season at 2,130 m elevation on the southwestern slope of Mauna Kea, Hawaii. Circles are means and line ± 95% C.I. Numbers in parentheses at top are the number of Hawaii Elepaio nestlings weighed on that day.

for this disparity were that fewer birds nested, the breeding season was shortened, and renesting did not occur in poor reproductive years.

BREEDING SEASON

I found active Elepaio nests on the southwestern slope of Mauna Kea from February through August (Fig. 12). Initiation of the breeding season was variable among years. For example, the first active Elepaio nests in 1971 and 1972 were in April, 1973 was in March, 1974 February, while in 1975 birds did not start nesting until late April. However, peak of breeding activity was May and June for all study years, with 70.6% of the nests active during this time period (Fig. 12). Young fledged from nests starting in late March, with the highest number of fledgings in June. The majority of Elepaio breeding terminated by July. I found only one nest active into August.

SURVIVAL RATES

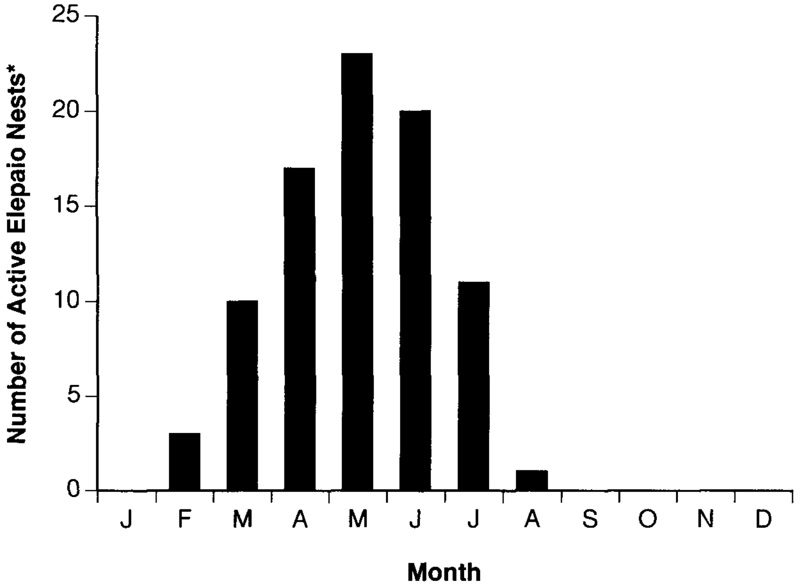
Elepaio are relatively long-lived for a small passerine. Two breeding females captured in March 1974 were still alive in January 1980. Two other females banded in January 1975 as adults (at least >1 year old) were observed through January 1981. Of 11 breeding birds in the 2,130 m study area during 1974, nine were alive two years later; of 17 banded nestlings that fledged during 1974, at least five were alive (and one was breeding) the following year. All breeding birds banded prior to 1973 had, however, been replaced by 1981.

DISCUSSION

In the *C. s. bryani* population on the southwestern slope of Mauna Kea, length of the breeding season, territoriality, and failure of eggs to hatch all influenced productivity. When comparing the ecology and behavior to other Elepaio subspecies, there are numerous similarities (e.g., territoriality, egg and clutch size, nest placement) and several differences (e.g., productivity, breeding season).

FACTORS AFFECTING PRODUCTIVITY

Timing and length of breeding season. It is uncertain what initiates Elepaio breeding, but in Hawaii many native bird species begin nesting



*** An active nest can occupy more than one month.**

FIGURE 12. Elepaio breeding season represented by the number of active nests found during each month, for the years 1970 through 1981, on the southwestern slope of Mauna Kea, Hawaii.

when day length is still decreasing (Berger 1981, van Riper 1987, Ralph and Fancy 1994a). Farner and Lewis (1971) found that photoperiod was never the only mechanism that set the precise time of reproduction, but that in many species additional factors modified the timing. These modifiers appear even more important in nontemperate passerines as Skutch (1950) could find no single stimulus that explained the initiation of breeding in tropical and subtropical species.

A number of factors undoubtedly influence the timing of Elepaio breeding. Whatever the ultimate stimulus that influences the initiation of breeding, during each year of this study the major Elepaio breeding effort coincided with that time of year immediately following peak mamane flowering (van Riper 1980). It may well be, however, that the Elepaio depends both upon exogenous and endogenous timing mechanisms to set an appropriate time for reproduction.

The length of the breeding season as a factor in population regulation becomes important when one considers that a nesting cycle (nest building to fledging of young) takes at least 62 days in the Elepaio. With a breeding season spanning from three to seven months, the Elepaio is able to raise two broods only in a good breeding year. If the breeding season is delayed in starting, or terminates early, the number of young produced is severely affected. This occurred in 1975 when breeding started several months after it did in 1974, and birds did not renest in the shortened 1975 breeding season.

Territoriality. Elepaio defended a classical "Type A territory" (Nice 1941). In the Hawaiian Islands, this territorial behavior is presently known to occur only in Hawaii Common Amakihi (van Riper 1987), the Hawaii Omao (*Myadestes obscurus*; Ralph and Fancy 1994b), the Akiapolaau (*Hemignathus wilsoni*; S. Fancy in litt.), and Oahu Elepaio (Conant 1977). Data from Elepaio breeding on the southwestern slope of Mauna Kea suggest that the relatively large territories limit the total number of breeding birds in the environment because it forces birds to be widely spaced. In that the habitat appears to be saturated with breeding birds (Figs. 5 and 6), territoriality indirectly controls the number of breeding Elepaio that can utilize this open savanna ecosystem.

Clutch size and egg hatchability. In *C. s. bryani* I found that clutch size was not modified by prevailing environmental conditions. During 1974, the relative productivity index of mamane in the 2,130 m study area was 153.9 (see van Riper 1980), and Elepaio clutch size averaged 2.0 eggs for that year. In 1975, mamane productivity dropped to 72.9, but clutch size remained 2.0 eggs.

Of the 44 Elepaio eggs incubated to term, 11 (25%) failed to hatch. This high level of hatching failure might be due to freezing temperatures that occur during the nights at these high elevations on the southwestern slope of Mauna Kea (Kern and van Riper 1984). However, Elepaio covered eggs on the night the first egg was laid; thus, eggs were not subjected to lowered temperatures throughout the night. Poor hatching might also have been influenced by brood patch size (its ability to cover two eggs), but one would expect each egg to have an equal probability of being excluded. There is also the possibility that Elepaio are experiencing a problem with infertility because there was no visible embryo in three eggs that did not hatch, but that were incubated to term. In studies of other passerines (Bull 1946, Mumford 1964, Nice 1937, Seel 1968, Siegfried 1973) the percentage of eggs that failed to hatch after being incubated to term was 6.8% (range 3.7–12). The 25% of eggs that do not hatch in this Elepaio population is unusually high and is one of the principal factors affecting the species' productivity.

Reproductive success. Reproductive success, as measured by the number of eggs laid that fledged young, for the Elepaio (65.8%) was near the upper limits (Range 38–77%; average 49%) given by Nice (1957) for other open-nesting passerine species. However, the total number of Elepaio young produced in the 2,130 m study area varied between years, apparently in response to habitat productivity. For the year 1974 (year of high habitat productivity; van Riper 1980) the Elepaio breeding season lasted five months, and birds were able to successfully raise two broods. While in 1975 (a year of low habitat productivity) the breeding season lasted only three months, fewer birds nested, and second nesting did not occur. However, mamane phenology provides only an indirect indication of food availability for Elepaio, and more study is needed on this facet of the species' breeding productivity.

Ricklefs and Bloom (1977) examined productivity in birds from diverse habitats and found that in a dry montane subtropical area of Ecuador (a habitat similar to that of Mauna Kea), the most important variables of productivity were season length and clutch size. The former became obvious in this study when the productivity rates for the Elepaio population were compared among years. The similarity of variation in Elepaio productivity with that of my previous work on Mauna Kea (van Riper 1987) and with Ricklefs and Bloom's (1977) findings suggests that in savanna ecosystems throughout subtropical regions, annual productivity in small passerine birds is greatly influenced by breeding season length. Thus, in the absence of heavy predation and adverse environmental conditions on the southwestern slope of Mauna Kea, a low egg hatching rate and breeding season length appear to act as principal controlling factors in population regulation of the Elepaio.

COMPARISONS WITH OTHER SUBSPECIES

Similarities. Many facets of *C. s. bryani* breeding biology are similar to those of other subspecies throughout the islands. For example, Conant (1977) also found that sexual chasing was a prominent behavior in *C. s. ibidis.* Elepaio maintain mutually exclusive (Type A) territories, at least on Oahu and Hawaii. Preferred Elepaio nest placement on all three islands is in terminal forks (Berger 1981, Conant 1977, H. Sakai and C. J. Ralph, in prep.), but average height of nest from the ground differs among locations, being directly related to the tree height of the forest in which the bird is nesting (e.g., see Fig. 9). Nest sizes appear very similar among the mesic forest Elepaio subspecies, with the more xeric *C. s. bryani* nest measurements being more variable and slightly smaller (Table 3).

Some of the most consistent parameters among Elepaio subspecies are clutch size and egg measurements. In all studies to date, Elepaio clutch size is most often reported as two eggs with an occasional clutch of three. Elepaio egg sizes only vary from 2.04–2.2 cm in length and 1.5–1.6 cm in width (Newton 1897, Berger 1981, H. Sakai and C. J. Ralph, in prep., this study). Elepaio incubation periods have been reported to be 18 days for *C. s. ridgwayi* (H. Sakai and C. J. Ralph, in prep.), *C. s. sclateri* (Berger 1981), and for *C. s. bryani* in this study. Only Conant (1977) reported a different incubation period (14–16 days) for one nest of *C. s. ibidis* that she observed on Oahu. However, the Oahu Elepaio nestling period was 16 days, the same as that reported on Kauai by Berger (1981) and what I found (15.6 days) on Hawaii.

Differences. Differences among Elepaio subspecies appear to revolve mainly around the influences of the habitat in which the birds breed. For example, *C. s. bryani* territories were smaller (avg 1.1 ha) than Conant (1977) found for *C. s. ibidis* on Oahu (avg 2.0 ha). Vocalizations peaked later in the day for male Elepaio on Oahu (Conant 1977), when compared to male *C. s. bryani* on Mauna Kea. There are also differences in breeding season lengths among xeric and mesic forest Elepaio subpopulations. Breeding seasons ranged from February to August for *C. s. bryani* (this study on Mauna Kea), March to June for *C. s. sclateri* (Berger 1981), January to June for *C. s. ibidis* (Conant 1977), April to September for *C. s. ridgwayi* (H. Sakai and C. J. Ralph, in prep.), and February to August on Kohala Mountain (van Riper 1982). However, the most dramatic differences among Elepaio subspecies were in overall productivity and the particular reasons for nest failures. In mesic habitats on Oahu and Hawaii, predation of eggs and young by introduced mammals played a major role in decreasing annual productivity. On Oahu, Conant (1977) reported a 13% nesting success for *C. s. ibidis,* and on Hawaii, H. Sakai and C. J. Ralph (in prep.) reported that only 24% of their nests fledged young. On the other hand, in the dry forest of Mauna Kea, I found virtually no predation on *C. s. bryani*, and 80% of the nests fledged at least one young. It thus appears that although many behaviors remain similar, differing selective pressures are presently operative on the population dynamics of the Elepaio subspecies in the Hawaiian Islands.

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