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BREEDING BIOLOGY OF THE WHITE-RUMPED SHAMA ON OAHU, HAWAII

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ABSTRACT.—We studied the breeding biology of the White-rumped Shama (*Copsychus malabaricus*) on Oahu, Hawaii, during 1986–1987. This species is sexually dichromatic and sexually dimorphic, with males being larger. It forms monogamous pair bonds that may last two breeding seasons. The breeding season was from March through August, and territories of nesting pairs that were provided nest boxes averaged 0.09 ha in size. Only three- and four-egg clutches were observed, with four eggs being the modal clutch size. The incubation period averaged 13.6 days and the nestling period averaged 12.4 days. Both adults fed young but only the female incubated and brooded. Shamas can raise two broods in one breeding season, and reproductive success for double-brooded pairs was higher (91%) than that for single-brooded pairs (62%). *Received 4 Jan. 1993, accepted 15 Sept. 1993.*

More species of birds have been introduced to Hawaii than to any other place (Long 1981). Caum (1933) reported that 96 bird species had been introduced in Hawaii, and Bryan (1958) reported 94 introduced species. The number of accidental or intentional introductions is now estimated at 178 (Berger 1981). Little is known about the biology of most of these species, and many were introduced without prior knowledge of their ecology or their potential for impact on Hawaiian ecosystems.

The White-rumped Shama (Muscicapidae: Turdinae: *Copsychus malabaricus*), introduced to Kauai in 1931 by Alexander Isenberger, is native to South Asia, where there are four known subspecies: *Copsychus m. malabaricus* in west India, *C. m. indicus* in east India and Nepal east to northwest Burma, *C. m. leggie* in Sri Lanka, and *C. m. albiventris* in the Andaman islands south of Burma (Ali and Ripley 1973). Ali and Ripley (1973) identified the particular subspecies on Kauai and Oahu as *C. m. indicus.* In 1940, the Hui Manu Society moved White-rumped Shamas from Kauai to Oahu (Harpham 1953; Berger 1974, 1975). The exact numbers of birds involved in these introductions is not known. During the 48 years since its introduction to Oahu, the shama has spread throughout most of the island (Berger 1981).

We sought to answer several questions during the study. Does the introduced population of shamas on Oahu differ morphologically from the species in its native range? What are the basic reproductive characteristics of the shama in Hawaii (e.g., nature of the pair bond, territory size, clutch size, number of broods raised per year)? Are there any aspects of breeding

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biology that may maximize reproductive success? For example, are larger clutches or territory sizes associated with greater success, or do double-brooded pairs raise more young than single-brooded pairs?

METHODS

We studied White-rumped Shamas from January 1986 to November 1987 in Makiki Valley on Oahu; additionally two nesting pairs in Waimanalo (13 km from Makiki), Oahu, were observed in 1986. Makiki Valley lies between the ridges of Roundtop and Tantalus in Makiki State Park. The study area was about 0.4 km^2 and 121.9–304.8 m above mean sea level. Kanealole and Moleka streams dissect the area. Rainfall in the Makiki area usually does not exceed 318 cm a year, and most rainfall is recorded during November, January, and February (Taliaferro 1959). The soil is composed of volcanic ash and alluvial material, and outcrops of basalt may be found within the valley (Foote et al. 1972).

The forest is composed mainly of introduced trees, although the native koa (*Acacia koa*) may be found scattered throughout the valley. *Eucalyptus* spp., *Aleurites moluccana* (kukui), *Casuarina equisetifolia* (ironwood), *Psidium guajava* and *P. cattleianum* (guava and strawberry guava), *Citharexylum caudatum* (juniper berry or fiddlewood), *Pimenta dioica* (allspice), and *Syzygium cuminii* (java plum) are the most common species of trees. Dense thickets of hau (*Hibiscus tiliaceaus*) are found along the banks of Kanealole Stream, and impenetrable stands of *Caesalpinia dicapetala* (wait-a-bit) are found in parts of the lower valley area. Stands of ironwood trees are found mainly along a smaller ridge within the valley, and most other species of trees are scattered throughout the valley area.

We observed birds with binoculars and a spotting scope and timed their activities with a stopwatch. Prior to each breeding season, we placed nest boxes in the study area where males were known or thought to be defending territories. The boxes, made from 0.6 cm exterior plywood, were 20.3 cm high, 24.8 cm wide, and 20.3 cm deep, with a 10.2 cm diameter circular hole for an entrance. The exterior sides of the nest box were painted dark brown.

For banding and measurement, birds were captured in 36 mm mesh mist nets. Bands were placed on each tarsus, including three color bands and one U.S. Fish and Wildlife Service numbered aluminum band. To distinguish them from their siblings, newly hatched nestlings were marked on the tarsus with different colors of nail polish or permanent marker until they were banded. We made measurements with vernier calipers, a metal ruler, and Pesola scales.

Territory sizes were determined by spot mapping banded birds, usually singing males. We had divided the study area into marked 50 × 50 m grids which were transposed onto a map to allow determination of exact locations of birds. We considered twenty observation points sufficient to determine the size of each territory. To characterize patterns of male singing behavior, ten eight-minute counts were conducted monthly. The ten stations were 150 m apart, and the number, distance, and means of detection of each shama were recorded during each count (i.e., visual, call note, song).

We checked nest boxes once or twice monthly during the non-breeding season and once every other week during the breeding season to detect nesting activity. Once nest building had commenced, nests were monitored daily to determine the dates of egg laying, hatching, and hatching sequence.

We observed birds for one to three hours during days 1 (the day after the clutch was completed), 3, 6, 8, 11, 12, and 13 of incubation. Once brooding had commenced, we monitored nests for one hour every other day from day 1 to day 12 of the nestling period. To avoid excess disturbance in the nesting territories, measurements of chicks were taken

TABLE 1

MORPHOLOGICAL MEASUREMENTS OF WHITE-RUMPED SHAMAS

	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total culmen (mm)	Nare to bill tip (mm)	Sternum (mm)	Mass (g)
Males							
Mean	90.20	134.97	28.98	16.84	11.75	22.33	31.70
SE	0.58	1.96	0.21	0.25	0.20	1.33	0.50
N	20	20	20	20	20	13	20
Females							
Mean	84.10	111.90	24.89	14.75	10.85	20.30	26.89
SE	0.88	2.12	0.33	0.27	0.14	0.58	0.35
N	17	17	17	17	17	12	16
t-test	6.0	7.99	2.85	5.74	3.61	3.01	8.34
Males[a]	86–99	108–200	25–28	17–22	—	—	30
Females[a]	84–93	102–131	25–27	18–22	—	—	30–32

[a] Values given by Ali and Ripley (1973).

on alternate days, from day 0 (hatch day) to day 10. We recorded the number and duration of feedings by each parent, and the type and length (relative to adult bill size) of the food item were recorded when possible. Observations of fledglings and juveniles were made between May 21 and July 28, 1987. We noted the date and fledging sequence of the young when they left the nest. Thereafter, we recorded the location and activities of the young and of the parents, as well as the number and type of food items fed to the fledglings.

Data were tested for normality before statistical analyses were carried out.

RESULTS AND DISCUSSION

Morphological measurements and sexual dimorphism.—We caught, banded, and measured 37 adult shamas (20 males and 17 females). Measurements taken from two adult females and two adult males in the Waimanalo Experiment Station were included in the analysis. Males were significantly larger than females in all measurements (Table 1). Shamas on Oahu were smaller or tended to be near the low end of the range of measurements given for the native Indian population (*C. m. indicus*) of the species (Ali and Ripley 1973). Berger (1981) stated that the shama in Hawaii is about 22.9 cm long, while Ali and Ripley (1973) reported the bird to be 25.0 cm long in its native range. Unfortunately, neither source provides adequate data for statistical comparison. Environmental factors (e.g., diet, climatic factors), genetic drift, and factors associated with founder effect may have influenced this possible size reduction in the Hawaiian population.

Adult shamas are both sexually dichromatic and dimorphic, males be-

TABLE 2

NUMBER OF WHITE-RUMPED SHAMAS RECORDED DURING MONTHLY COUNTS AND THE NUMBER OF ACTIVE NEST BOXES IN MAKIKI VALLEY DURING 1986–1987

Month	Mean ± SE	Range	Number of active nest boxes
November	2.7 ± 0.42	1–5	0
December	3.0 ± 0.49	1–6	0
January	6.2 ± 0.83	1–10	0
February	3.2 ± 0.73	1–7	0
March	5.1 ± 0.35	3–7	8
April	4.2 ± 0.63	2–7	21
May	5.6 ± 0.37	4–8	6
June	3.0 ± 0.37	2–5	7
July	1.4 ± 0.27	0–3	4
August	2.1 ± 0.43	0–4	0
September	3.3 ± 0.37	2–5	0
October	2.1 ± 0.43	1–5	0

ing larger. Males have a glossy black body, head and tail, and a dark chestnut chest. The female is similarly colored, but relatively drab, being grayish black to brownish. The chest is much lighter in females (Berger 1981, Pratt et al. 1987), and some females we saw had a grayish chin. Both sexes have distinct white rump and outer tail feathers.

Seasonality.—Numbers of shamas recorded per station were greater during the months of January, March, April, and May, being highest (6.2 birds/station) in January (Table 2). Most shamas were heard, not seen, so low numbers are probably due to decreased singing activity rather than an actual decrease in the number of birds present. The greatest singing activity occurred in January and decreased thereafter. In captivity there is less singing with each successive nesting attempt (J. Mejeur, pers. comm.). Nest building and egg laying were first recorded in March. Nesting activity peaked in April, when there were 21 active nests (46% of all recorded nests), and then decreased through the months of May, June, and July. The lowest level of nesting activity (other than no activity) in July corresponded to the lowest mean number of shamas recorded per station count.

Other studies have shown avian breeding seasons to coincide with or follow periods of increased rainfall (Immelmann 1971) or increases in day length (Murphy and Haukioja 1986), either of which may be followed by an increase in food availability. The Oahu shama breeding season followed a relatively consistent annual period of high rainfall (Taliaferro

1959). We suspect increased rainfall (from November to April) is correlated with increased food abundance. Shamas in India breed from March to August (Ali and Ripley 1973) during the monsoon period.

Territory and song.—Male shamas were seen within their territories throughout the year. However, it is unknown whether males defend nest sites and mates throughout the year. Feeding, nesting, and care of young occurred almost entirely within the territory. Because females are cryptic during the nonbreeding season, we could not determine whether females remained in the territory during the nonbreeding season. Captive males are aggressive towards females during the nonbreeding season (Anon. 1982), suggesting that male and female home ranges may differ at this time.

The mean territory size of nesting pairs was 0.091 ± 0.009 ha (N = 17, range = 0.011–0.154 ha). Factors that could explain the large range in territory size include available food, suitable nest sites, vegetation cover, defensive behavior of territory holders, and size of territory holder. Some of these factors are discussed later. Habitat structure may have been important, as territories were found in heterogenous habitat, e.g., in dense thickets of *Hibiscus tiliaceaus,* as well as open forest. Territories usually had some open understory, which appeared to facilitate foraging for prey on the ground.

Male and female shamas usually vocalized within their territories. Both sexes (and fledglings) made a "Tck" call, usually in response to disturbance within the territory, or just before sallying for a prey item. Males sang a complex, melodius song, but females sang short songs only during the breeding season and when in the presence of male partners. In their discussion of the White-rumped Shama, Ali and Ripley (1973) reported singing from March to May, and breeding from March to August. In our population singing did not cease during the nonbreeding season (September–February) and male shamas responded to tape playbacks of song during the breeding (March–August) and non-breeding season, indicating Oahu shamas may defend territories throughout the year. J. Mejeur (pers. comm.) observed whisper song in captive shama during non-breeding periods. If territories are held all year, increased singing may be associated with mate attraction in shamas.

We were unable to observe shama courtship behavior, and it has been reported only for shamas kept in captivity (Domin 1978:98). Our observations indicate that the White-rumped Shama is a monogamous species. The usual length of the pair bond is unknown, but we found it could be at least two years.

Nesting.—Ali and Ripley (1973) reported that only female shamas build nests. In shamas that breed in captivity, the male appears to "scout"

TABLE 3

EGG, INCUBATION, AND FLEDGLING DATA FOR WHITE-RUMPED SHAMAS IN MAKIKI VALLEY, 1986–1987

	Length (mm)	Width (mm)	Mass (g)	Incubation period (days)	Nestling period (days)	Brood size	Number of fledglings
Mean	21.80	16.02	3.12	13.61	12.31	3.13	1.71
SE	±0.20	±0.09	±0.08	±0.18	±0.24	±0.19	±0.30
Range	—	—	—	13–15	11–13	1–4	1–4
N[a]	110	110	41	18	13	23	17

[a] N = number of eggs measured or number of nests for which incubation and nestling periods and numbers of eggs hatched or young fledged were recorded.

for nest sites, but the female selects the final site and builds the nest, while the male guards unused but apparently suitable sites in the territory (J. Mejeur, pers. comm.). The nest is located within a tree cavity or hollow of bamboo and padded with rootlets and leaves. Because females appear to be easily disturbed, nest building behavior was not documented during the course of this study.

Nests in nest boxes had a large base of leaves, 3–5 cm deep, on which a depression was made where the nest cup was placed. The cup was fashioned from a layer of petioles and lined with leaves. Nesting material included dried leaves, petioles, *Casuarina equisetifolia* needles, and pieces of fern, materials typically found in the territory.

During this study 32 nests were found, and 110 eggs were measured and weighed (all eggs were weighed within 24 h of laying time). These data, as well as incubation period, nestling period, hatching success and fledging success are summarized in Table 3 for all nests and eggs recorded during the study. No significant difference in body mass or tarsal length was detected between females that laid three-egg clutches and those that laid four-egg clutches (Table 4).

Clutch size.—Three- and four-egg clutches were the only clutch sizes recorded during the two breeding seasons of this study. More nests (55% or 18 nests) had four-egg clutches than three-egg clutches (45% or 14 nests). No significant differences in length, width or egg mass, were found between the two clutch sizes (Table 4). During the 1987 breeding season, 42% or eight nesting pairs laid a second clutch. Eggs of second clutches averaged 21.63 ± 0.41 mm in length and 16.13 ± 0.20 mm in width, and 2.89 ± 0.18 g in mass. There was no significant difference in mass or dimensions between eggs in first and second clutches (Table 4). Of the eight females that laid second clutches, six laid the same number of eggs and two laid a larger or smaller clutch. According to Mejeur (pers.

TABLE 4

FEMALE SIZE, CLUTCH SIZE AND SIZE OF EGG FOR WHITE-RUMPED SHAMAS BREEDING IN MAKIKI VALLEY, 1986–1987

	Adult female			Eggs	
	Mass (g)	Tarsus (mm)	Length (mm)	Width (mm)	Mass (g)
Three eggs					
Mean	27.04	25.67	21.49	15.99	3.07
SE	±0.76	±0.42	±0.37	±0.27	±0.16
N	7	7	7	7	7
Four eggs					
Mean	27.21	24.68	22.14	16.12	3.13
SE	±1.16	±1.03	±0.85	±0.57	±0.39
N	11	12	13	13	4
t-test value[a]	0.108[b]	0.720[b]	0.560[b]	0.170[b]	0.220[b]

[a] *t*-test compared values for body and egg measurements between three-egg-clutch females and four-egg-clutch females.
[b] Not significantly different, $P > 0.05$.

comm.) shamas breeding in captivity consistently laid five-egg clutches and would usually nest five times during the season, always in the same nest site.

One egg was laid each day with incubation commencing after, but on the same day as, the last egg was laid. Eggs usually hatched synchronously within a couple of hours, and in the morning. However there were several nests in which eggs hatched asynchronously. The elapsed time between fledging of the first brood and laying of the second clutch (i.e., the first egg of the second clutch) averaged 38 ± 1.87 days (range = 11–42, N = 5). At the nest where our activities caused the first brood to fledge prematurely, the second clutch was laid about 14 days after the incident.

The sizes of eggs from 19 clutches were compared according to the sequence in which they were laid using one-way analysis of variance (ANOVA). There were no significant differences in the length, width and mass, respectively of eggs among first, second and third eggs: $F_s = 1.84$, df = 66; $F_s = 0.37$, df = 66; $F_s = 0.24$, df = 44 (all $P > 0.05$).

Incubation.—The average length of the incubation period for all clutches pooled was 13.61 days (Table 3). The average incubation period for second clutches was less, being 13.0 days (SE = 1.0, N = 3) but the difference was not significant ($t_s = 1.43$, $P > 0.05$). The average length of the incubation period was 13.9 ± 0.3 and 13.3 ± 0.21 days for three-

TABLE 5

NESTING DATA ASSOCIATED WITH THREE- AND FOUR-EGG CLUTCHES OF THE WHITE-RUMPED SHAMA IN MAKIKI VALLEY, 1986–1987

Clutch size	Incubation period	Nestling period	Number hatched	Number fledged
Three eggs				
Mean	13.90	12.30	2.60	1.90
SE	±0.30	±0.25	±0.22	±0.35
Range	13–15	11–13	1–3	0–3
N	8	8	10	9
Four eggs				
Mean	13.30	12.10	3.50	2.15
SE	±0.21	±0.31	±0.19	±0.36
Range	12–14	11–14	1–4	0–4
N	13	10	18	13
t-test values	1.71 ns[a]	0.50 ns	3.05[b]	0.48 ns

[a] Ns = not significant, $P > 0.05$.
[b] Significantly different, $P < 0.05$.

and four-egg clutches, respectively, but this difference also was not significant (Table 5). Incubation periods for shamas in Hawaii were similar to those of captive birds (Anon. 1982), but longer than the 12 days reported by Ali and Ripley (1973). The difference in incubation period may be real, or the result of differences in measurement of the incubation period. Captive shamas incubated their five-egg clutches 14 to 14.5 days (J. Mejeur, pers. comm.), and hatching took place over a two-day period.

Although Berger (1981) suggested that both adults incubate, we found only females incubating. In addition, none of the ten adult males that were caught during the breeding season had a brood patch. Males flew to the nest box during the incubation period (29 instances noted), but not all males exhibited this behavior. Most of these visits occurred during the middle of the incubation period. Typically, the male would fly to the nest box and perch on the rim, look inside and then fly away. On one occasion the male entered the nest box and pecked at the nesting material before leaving. We never observed male shamas bringing food to the nest during the incubation period; however, J. Mejeur (pers. comm.) occasionally observed this behavior in captive-breeding males.

Attentive periods (the time that a bird spent on eggs) gradually increased up to the eighth day of incubation and then decreased lightly afterwards. Mean attentiveness during the incubation period ranged from

13.90 ± 4.75 minutes on day one of incubation to 30.83 ± 4.20 min on day six. One-way ANOVA indicated that differences in the length of attentive periods on different days of the incubation period were significantly different from one another: $F_s = 2.37$, df = 89, $P < 0.05$. Although sample sizes were small, we did find that attentive periods for females with four-egg clutches tended to be longer, but not significantly so, than those with three-egg clutches. In a study of the House Wren (*Troglodytes aedon*), Baldwin and Kendeigh (1927) found that periods of attentiveness and inattentiveness were quite regular in duration; however, during the last three days of incubation, attentiveness increased but the duration of inattentiveness remained the same. Similarly, Domin (1978) found attentiveness in captive shamas to increase late in the incubation period.

Eggs usually hatched during early morning, though some hatched after noon. The average number of eggs hatched from first clutches was 3.17 ± 0.20 (N = 23). Four-egg clutches hatched significantly more young (3.5) than three-egg clutches, which averaged 2.6 young (Table 5). Second clutches on average hatched 3.40 ± 0.24 young (N = 5). Thus females that laid a second clutch had about 30% greater reproducive success (measured as number of young hatched) than females laying a single clutch. Because results were based on a single breeding season, we could not determine the effects of female age on reproductive success. Sample size was too small (N = 4, one clutch did not hatch) to determine if production of second broods was correlated with territory size, male size, or other factors.

Predation was not a major factor in egg losses during the incubation period. Only one nest at the egg stage (2.56% of the total) was preyed upon, possibly by rats (*Rattus* spp.). Other potential predators on eggs are mongooses (*Herpestes auropunctatus*), which are common in Makiki Valley (pers. obs.), and feral cats (*Felis catus*).

Nestling period and parental care.—Nestlings hatched blind and naked but responded to tapping on the nest box by gaping and exposing a bright yellow target in their mouths. At two days of age, the outlines of wing feather tracts were visible, and pin feathers erupted through the skin at four days. At six days, the eyes began to open and young were able to make soft "pipping" sounds. At about eight days old, primary and secondary feathers broke through the feather sheaths and all other tracts were clearly visible. By age ten days, feathers in all tracts had broken through their sheaths, and the young had begun preening themselves.

The nestling period of first broods averaged 12.31 ± 0.24 days (N = 13), and for second broods averaged 11.80 ± 0.37 days (N = 5) but these were not significantly different ($t_s = 1.15$, df = 16, $P > 0.05$). There were no significant differences between three- and four-egg clutch-

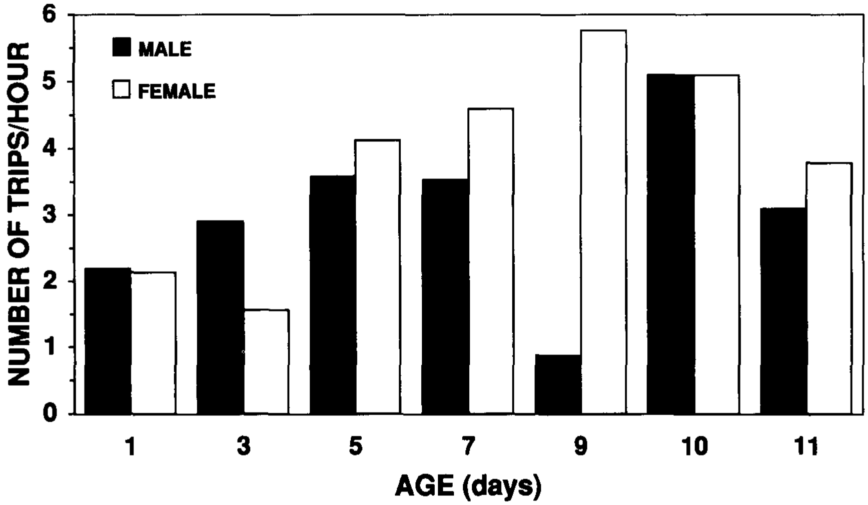

FIG. 1. Feeding trips made by adult White-rumped Shamas during the nestling period.

es in the length of the nestling period (Table 5). In captivity the nestling period is about 14 days (J. Mejeur, pers. comm.).

Observations of brooding behavior were made when nestlings were one to nine days old. Although both males and females removed fecal sacs from the nest, we observed only females brooding. Brooding ceased by the ninth day. Brooding averaged 11.77 ± 5.61 min per session at day one, then increased, averaging 17.14 ± 2.58 min per session on day three. Brooding decreased in subsequent days to 2.93 ± 1.23 and 1.13 ± 0.60 min per session on the fifth and seventh day, respectively.

Males fed nestlings more often than females (although not significantly more) when nestlings were one to three days old (Fig. 1). While females brooded, males delivered food to the female, who then fed the young, but only during the first five days of the nestling period. However, females tended to feed nestlings more often after day three. When young were ten days old, both parents fed young at approximately equal frequencies.

Two cases of cooperative breeding behavior were observed. At each of two nests, two different males were observed feeding young that belonged to a single female. At one nest when the single nestling hatched from a clutch of four eggs was nine days old both banded and unbanded males were seen feeding it. The female had been banded the previous day, so she could not have been confused with the second male. Both males were seen again feeding the nestling when it was 10 and 12 days old. There was no apparent aggression between the two males. A similar

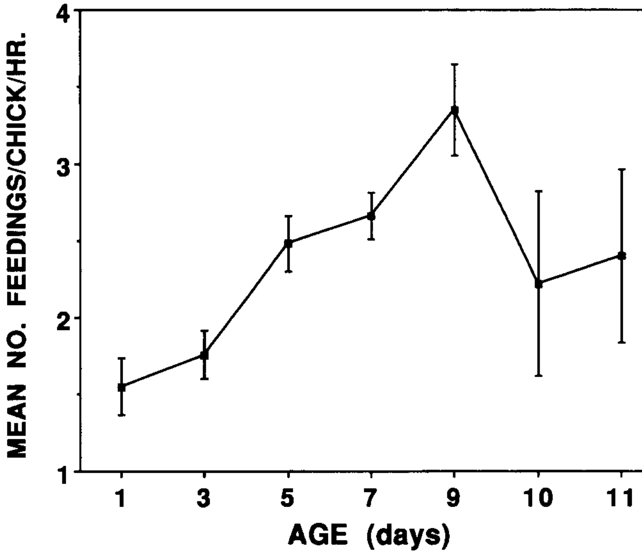

FIG. 2. Feeding rates of White-rumped Shama chicks. Vertical lines indicate ± 1 SE.

situation occurred at a nearby nest, but this time we observed aggressive behavior by the territorial male towards the intruder male. At this nest both parents were banded and the intruder male was not. Despite repeated attacks by the banded male, the unbanded male made repeated attempts to feed the young (he had food in his bill) and fed the young three times.

Feeding frequency increased as chicks got older until they were ten days old (Fig. 2). The subsequent decrease in feeding frequency may be associated with an actual reduction in nestling growth rate, as well as increased search time required to find food. The latter idea may be supported by the shift in food size during the mid- to late-nestling period (Fig. 3).

When young were newly hatched, parents fed mostly smaller food items. When young were five to nine days old, parents fed mostly larger food items. At five days of age, young were given larger foods (mainly earthworms) 55% of the time. At seven days of age young were given large foods 70% of the time. This amount decreased to 54% at nine days; then there was a shift to medium sized items. Because territories are quite small large food items may be substantially depleted by the time nestlings fledge. The types of food items fed to the young included adult insects (53%), earthworms (36%), unidentified adult arthropods (<8%), arthropod larvae or pupae (<3%), and skinks (<1%).

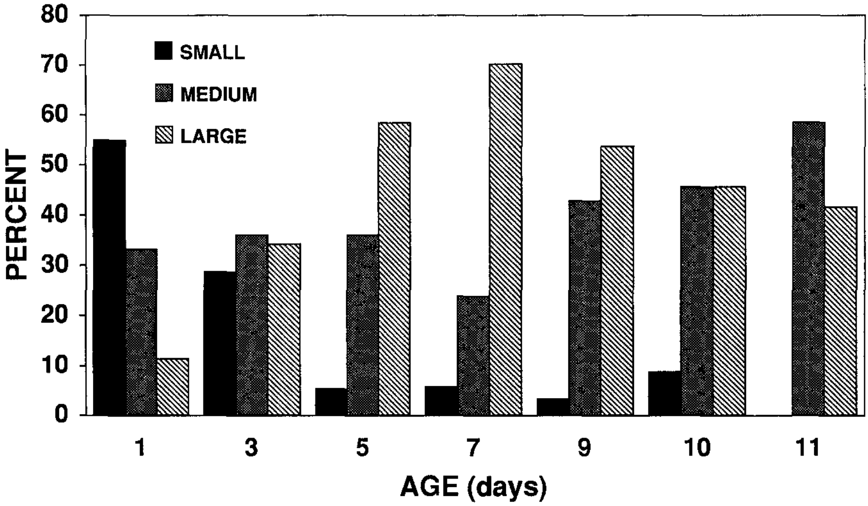

FIG. 3. Food size categories and age of White-rumped Shama nestlings. Small, medium, and large food items were smaller, approximately equal and larger, respectively, than the adult bird's bill (N = 209).

As Ali and Ripley (1973) reported for Indian shamas, both sexes on Oahu shared in feeding the young. In captive shamas, both sexes feed the young, but the female usually consumes or removes the fecal sacs (Anon. 1982). However, in this study both sexes were found to remove fecal sacs. Males removed fecal sacs approximately as often (53.3%, N = 107 observations) as females (46.7%). The parents swallowed the fecal sacs when the nestlings were young, or disposed of them away from the nest.

Nestling growth and survival.—Nestlings were measured on alternate days from the day of hatching to the tenth day (Figs. 4 and 5). The initial average mass of nestlings was 2.67 ± 0.09 g (N = 61). The average mass gain per day was 2.52 g until the eighth day when the rate decreased to 2.12 g per day. Average nestling mass gain between the eighth and tenth day was 0.64 g, or approximately 0.3 g per day. Mean nestling mass at ten days old was 22.32 ± 0.40 g (N = 53), 70.4% or 83% the weight of the mean weights of adult males or females, respectively.

The rapid mass gain of nestlings may be compared to the feeding rates of parents. The mass curve (Fig. 5) becomes asymptotic at the eighth day and corresponds to the lower feeding rates by the parents in subsequent days. The young may not require as much food during the few days before fledging because of a real reduction in growth rate. A prolonged nestling period, after asymptotic mass, is common among cavity nesters (von

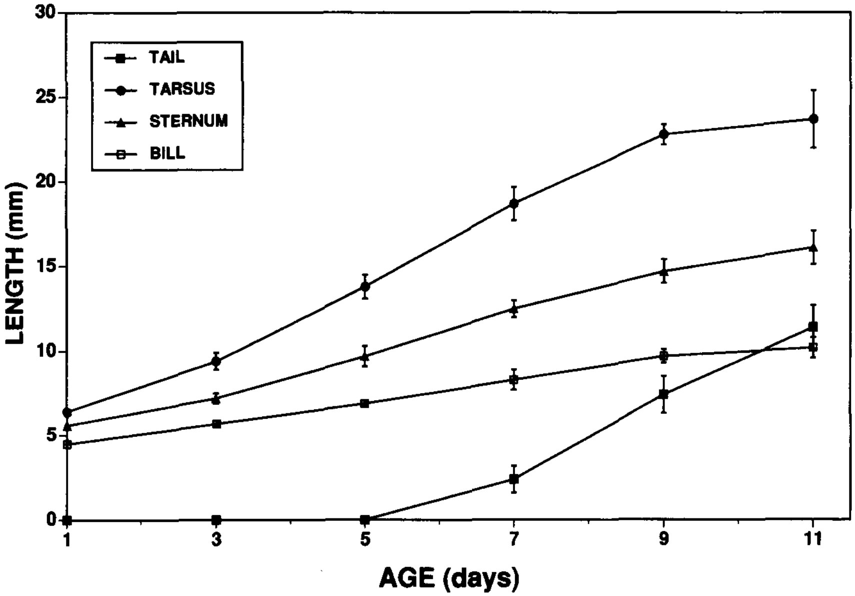

FIG. 4. Growth of tail, tarsus, sternum, and bill of White-rumped Shama nestlings of all broods combined. Vertical lines indicate ± 1 SE.

Haartman 1975). Freed (1988) found that tropical House Wrens (*Troglodytes aedon*) may remain in the nest at asymptotic mass for up to a week. Perhaps the feather development and maturation of both morphology and physiological processes known to occur at this time require less food (see Ricklefs 1984 for review).

We plotted nestling growth curves of tail, tarsus, sternum and bill (Fig. 4). Sternum length of newly hatched nestlings averaged 5.55 ± 0.01 mm (N = 61) and increased continually to 16.02 ± 0.16 (N = 42) at ten days of age. This length was about 72% or 79% of that of adult males or females, respectively. Tarsus length of newly hatched nestlings averaged 6.36 ± 0.13 mm (N = 61) and was 23.57 ± 0.82 mm (N = 42) at day ten. Tarsi of ten-day-old nestlings were about 91% or 95% the length of tarsi of adult males or females, respectively. Newly hatched nestlings' total bill length averaged 4.45 ± 0.05 (N = 61). At ten days of age nestling bill length averaged 10.27 ± 0.27 mm (N = 42), and measured 61% or 73% the size of adult male or female shamas, respectively.

Development of wing and tail feathers is shown in Figs. 4 and 5, respectively. The wing chord of newly hatched nestlings averaged 6.66 ± 0.09 mm (N = 61). This value actually is the length of the alula

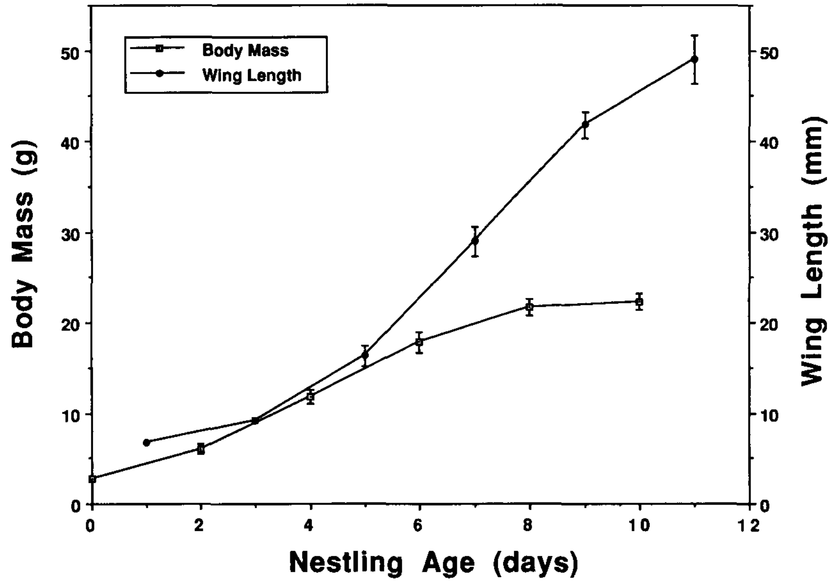

FIG. 5. Growth of wing and mass of White-rumped Shama nestlings of all broods combined. Vertical lines indicate ± 1 SE.

because nestlings are born naked. The wing chord length of ten-day-old nestlings averaged 48.78 ± 1.79 mm (N = 42), 54% or 58% of the wing length of adult male or female shamas, respectively. The tails of nestlings showed the most delayed development compared to the other parts measured. Tail feathers did not erupt from the feather tract until after the fifth day, and on the sixth day averaged 1.82 ± 0.12 mm (N = 37). At ten days old, nestling tail length averaged 11.25 ± 0.52 mm (N = 26), and 8% or 13% the length of the tail of adult male or female shamas, respectively.

Nestling survival from hatching until ten days old was 68.8%. Two nests (10.5%, N = 19 nests) lost all young. One nest with a brood of three was depredated after the eleventh day of the nestling period, and another nest with a brood of four lost all nestlings between the fourth and sixth day of the nestling period. Predation does not appear to be a major factor in nestling mortality. Young fledged when about 12 days of age. Fledging success of first broods aveaged 1.71 ± 0.30 young (N = 17). Second broods on average fledged 2.8 ± 0.45 young (N = 5) or 1.09 more young than the first broods, but this was not a significant difference.

Fledging.—Banded fledglings were observed within their natal territories up to 54 days after fledging. The last day that parents were observed to feed young was the 26th day after fledging. However, fledglings may remain on the territory for a longer period without care from their parents. On 11 June 1987, 26 days after the young of one nest had fledged the probable father of the fledgling came within two meters of a banded fledgling as both foraged on the ground. The fledgling did not beg from the male nor did the male attempt to feed the young bird. Four days earlier begging calls had been heard within the territory.

In his captive shamas, J. Mejeur (pers. comm.) observed that females were more likely to feed newly fledged chicks than those of the previously-fledged brood. He found that males, on the other hand, did most of the feeding of fledglings if the female was incubating a new clutch; he would continue to feed older fledglings even after the next brood fledged. Mejeur found that the fledgling period usually lasted about a month.

If newly mature shamas are unable to become part of the breeding population or to secure a territory, they may form flocks outside of defended breeding territories (this was never observed) or live solitarily and spend some time in other breeders' territories (Smith 1978). Because nesting sites may be limiting for this cavity-nester (van Balen et al. 1982, von Haartman 1957), these behaviors seem likely.

Reproductive success.—Although competition among hole-nesters for nesting sites may be intense, van Balen et al. (1982) suggested that their nesting attempts are usually more successful than those made by open-cupped or roofed nesters (about 10 to 20%; see Ricklefs 1969). Fledging success of all shama first broods was 65.7 ± 9.6% (N = 17). This percentage is comparable with fledging success of hole-nesters in North America (66.0%, Nice 1957, Ricklefs 1969), and greater than the 43.6% success reported for Costa Rica hole-nesting species (Skutch 1966).

Shamas that laid two clutches during the breeding season had greater fledging success than those that laid a single clutch, and parents that raised a second brood were able to fledge more young in relation to the number of eggs that hatched. The proportion of hatched young that fledged was larger in second broods (Mean = 0.832 ± 0.71, N = 5) than in first broods (Mean = 0.657 ± 0.097, N = 17) but not significantly so (Table 6). Survival rate of ten-day-old nestlings of all first broods was 77.7% but fledging rate was only 63.8%; whereas, the same age nestlings of second broods had a survival rate of 94.1% and a fledging rate of 82%. However, ten-day-old nestlings from second broods were significantly lighter than the average of those in first broods ($t_s = 1.96$, df = 41, $P > 0.05$). This suggests that there may be less food available within the territories of shamas raising second broods.

TABLE 6

REPRODUCTIVE SUCCESS OF SINGLE- AND DOUBLE-BROODED PAIRS OF WHITE-RUMPED SHAMAS IN MAKIKI VALLEY IN 1986–1987

	Mean % of eggs hatched	Mean % of eggs surviving to fledgling	Mean % of hatchlings fledged
All first broods	0.855 (23)[a]	0.495 (17)	0.657 (17)
Single brood pairs[b]	0.856 (18)	0.474 (13)	0.615 (13)
Double brood pairs	0.817 (5)	0.715 (5)	0.875 (5)
All second broods	0.950 (5)	0.790 (5)	0.832 (5)
Both broods combined[c]	0.850 (4)	0.770 (4)	0.906 (4)

[a] Sample sizes are in parentheses.
[b] These values represent total reproductive success for single-brooded pairs.
[c] These values represent total reproductive success for double-brooded pairs.

Shamas that raised two broods had a fledging success of 87.5% for the first brood. Total fledging success of pairs raising two broods (the mean number of young fledged from both broods divided by the mean number of young hatched) averaged 90.6 ± 0.9% (N = 4). However, this was not significantly different from the success rate of all first broods, possibly because sample sizes were small. The proportion of young fledged from second broods may be a reflection of parental age, parental physical condition, territory size and quality, or food abundance.

Many factors that promote higher reproductive success in birds have been documented. Perrins and McCleery (1985) studied reproductive success in Great Tits (*Parus major*) and found that age played an important role in terms of laying date, clutch size, number fledged, and number of offspring surviving to breed. They found that pairs with two older members had a higher reproductive success compared to pairs which had a first year member (male or female). Pairs with young males tended to lay later in the season, have smaller clutches, and have fewer young and survivors than pairs with older males. Pairs with young females tended to lay later and have smaller clutches than those with older females. In a study of the European Robin (*Erithacus rubecula*), Harper (1985) found that males with large territories were more likely to pair and tended to pair earlier than those defending small territories. In that study, female breeding success, based on the number of independent young, was positively correlated with the size of the territory. Finally, Perrins (1965) found that the incidence of second broods in Great Tits appeared to be related to food supply.

Reproductive success did not differ between shama pairs laying three- and four-egg clutches. Territory size of three- and four-egg pairs was not significantly different. Food abundance within the territories at the time of egg laying or during the nesting period might explain differences, but we have no data on this factor. Shama pairs raising two broods tended to be early nesters, laying the first clutch in April, whereas eggs of single-brooded pairs were laid between the beginning of May and mid-June.

Number of clutches rather than clutch size per se appears to be important in White-rumped Shama reproductive success. Our study suggests that individuals with two broods realize greater reproductive success per breeding season. An assumption underlying this conclusion is that the fledged progeny of pairs raising two broods have equal (or greater) survival in comparison to young of parents raising one brood. Though double-brooded pairs appear to have greater fitness in a single season, they must increase reproductive effort and may thereby reduce their future reproductive potential (Williams 1966). However, lifetime reproductive success of single- and double-brooded pairs must be determined before any definitive conclusion can be made.

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