

THE BREEDING BIOLOGY OF AN ENDANGERED HAWAIIAN HONEYCREEPER, THE LAYSAN FINCH¹

MARIE P. MORIN²

Department of Zoology, University of Hawaii at Manoa, Honolulu, HI 96822

Abstract. From 1986 to 1988 the breeding biology of an endangered Hawaiian honeycreeper, the Laysan Finch (*Telespiza cantans*), was studied on the coral island of Laysan in the Hawaiian Archipelago.

Laysan Finches are apparently monogamous. Pairs defend mates and nest sites, but not feeding territories. Only the female constructs the nest and incubates. The breeding season is prolonged, but there is yearly variation in onset. Pairs can have more than one clutch per year.

The average clutch size was 3.19 eggs. The modal incubation period was 16 days. One-third of all eggs laid disappeared, probably due primarily to intraspecific predation. Eggs hatched asynchronously in the order laid. Chicks fledged at 22–26 days of age, and were dependent for at least three additional weeks.

Weather affected reproductive success. A severe storm in 1986 caused almost total mortality of eggs and chicks, regardless of clutch size. Later in that same year, fledglings per nest increased as clutch size increased. During the dry 1987 field season, the onset of breeding was delayed, mean egg weight decreased, the number of malformed eggs increased, and clutches tended to be smaller.

Although in good years four-egg clutches produced more fledglings per nest than smaller clutches, in poorer years three-egg clutches produced at least as many or more fledglings per nest than larger clutches. In this fluctuating environment, a modal clutch size of three apparently has been selected for, possibly because it yields the highest average number of offspring per nest during both good and poor years.

Key words: *Laysan Finch; Hawaiian honeycreeper; Drepanidinae; Telespiza cantans; breeding biology; endangered.*

INTRODUCTION

The Laysan Finch, *Telespiza cantans* (Wilson 1890; Olson and James 1986), is an endangered member of an endemic Hawaiian group (Fringillidae: Drepanidinae) called the Hawaiian honeycreepers (AOU 1983). This group is known for its spectacular adaptive radiation, but unfortunately is noted also for its high proportion of endangered or extinct taxa (U.S. Fish and Wildlife Service 1984, Freed et al. 1987, Scott et al. 1988).

The breeding biology of Hawaiian honeycreepers in general is poorly known, although considerable progress has been made in the past 30 years (Berger 1969, 1970; Berger et al. 1969; Eddinger 1970; van Riper 1978, 1980; Scott et al. 1980; Sakai and Johanos 1983; Collins 1984; Kern and van Riper 1984; Freed et al. 1987b; Freed 1988; Pletschet and Kelly 1990).

The breeding biology of Laysan Finches has been frequently mentioned but little studied (Rothschild 1893–1900, Fisher 1903, Dill and Bryan 1912, Kramer 1959, Woodside 1961, Crossin 1966, Ely and Clapp 1973, Sincock and Kridler 1977, Conant 1985), mainly because of the remoteness of the present distribution and the unusually short visits by ornithologists to the refuge islands where they occur. The current natural distribution is on the remote, uninhabited Pacific island of Laysan in the Hawaiian Archipelago; a small introduced population occurs at Pearl and Hermes Reef. Fossil evidence confirms that they also occurred prehistorically on the islands of Oahu and Molokai (Olson and James 1982, James and Olson 1991). They are non-migratory.

The original flora and fauna of Laysan were highly endemic (Lamoureux 1963, Newman 1988). Originally, the fauna was composed of 17 species of seabirds, the green sea turtle, the Hawaiian monk seal, various migratory shorebirds, five species of endemic land birds, and numerous native terrestrial invertebrates (Ely and Clapp 1973).

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² Present address: Kaloko-Honokohau National Historical Park, 73-4786 Kanalani St., #14, Kailua-Kona, HI 96740.

There is no evidence that prehistoric Polynesians ever inhabited Laysan Island. The island was mined extensively for guano from about 1890 until 1910. Poaching for seabird feathers continued intermittently until at least 1915 (Ely and Clapp 1973). By 1903, rabbits had been introduced as a food source for the guano miners. Because reptilian predators and terrestrial mammals are not present on Laysan, the rabbit population increased quickly, causing almost total destruction of the vegetation. One of the three endemic plants, three of the five endemic land birds, and a number of terrestrial invertebrates became extinct (Butler and Usinger 1963, Ely and Clapp 1973). The Laysan Finch was the only passerine that survived the ecological disaster, which ended in 1923 when the last rabbits were killed. The post-1923 Laysan ecosystem, although still mostly composed of native species, differs from the original ecosystem. Non-native plants and invertebrates have been introduced over the past 100 years, undoubtedly affecting the native species. Some introduced species may provide new food sources for the Laysan Finch, but may also threaten the regeneration of other important native species (Morin and Conant 1990).

The intent of this research was to describe the breeding ecology of a poorly known, endangered Hawaiian honeycreeper, with the special focus of assisting in the conservation of this species in its native, closed ecosystem. Other closely related, finch-billed Hawaiian honeycreepers, such as the Palila (*Loxioides bailleui*) and the Nihoa Finch (*Telespiza ultima*) are much rarer than the Laysan Finch. It is hoped that information from this paper will contribute to understanding these rarer species, as well as insular passerines in general.

STUDY AREA AND METHODS

Laysan Island is located 1,506 km northwest of Honolulu (25°46'N, 171°45'W), and is part of the Northwestern Hawaiian Islands National Wildlife Refuge. The island is about 2.9 km long and 1.7 km wide, with a maximum elevation of 10.7 m above sea level. The central portion is covered with a shallow, hypersaline lake (Fig. 1). Although there is no standing fresh water, there are a few fresh water seeps along the lake shore (Ely and Clapp 1973, Morin 1987a). Only about 187 (47%) of the island's 397 ha are covered with vegetation; the rest is open sand and lake. Because of its latitude, Laysan has a more temper-

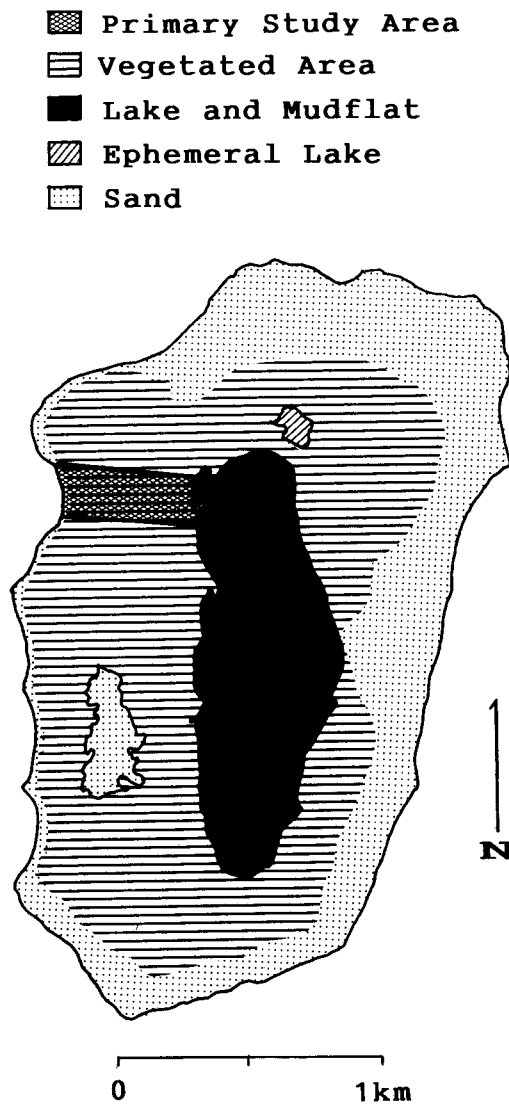


FIGURE 1. Map of Laysan Island showing primary study area.

ate climate than the inhabited main Hawaiian islands. Although extreme weather conditions are more common during the winter months, heavy rain and high wind may occur at any time (Table 1 and Fig. 2).

Five vegetation associations occur more or less concentrically around the lake, from outermost to innermost, as follows: *Scaevola* shrub; *Eragrostis* bunchgrass; *Ipomoea-Boerhavia-Sicyos* viney; *Pluchea* shrub; and *Sesuvium-Heliotropium-Cyperus* wetland associations. Although

TABLE 1. Average daily maximum and minimum temperature (°C) and average daily wind speed (km/hr). *n* equals number of days with data.

	1986	1987	1988
March			
Ave. max. temp.	—	—	27.5 (<i>n</i> = 27)
Ave. min. temp.	—	—	19.6 (<i>n</i> = 27)
Ave. wind speed	14.8 (<i>n</i> = 25)	—	11.0 (<i>n</i> = 21)
April			
Ave. max. temp.	—	24.0 (<i>n</i> = 22)	28.0 (<i>n</i> = 28)
Ave. min. temp.	—	19.4 (<i>n</i> = 22)	20.7 (<i>n</i> = 29)
Ave. wind speed	15.1 (<i>n</i> = 30)	14.5 (<i>n</i> = 22)	11.2 (<i>n</i> = 28)
May			
Ave. max. temp.	26.2 (<i>n</i> = 15)	24.1 (<i>n</i> = 31)	27.9 (<i>n</i> = 29)
Ave. min. temp.	21.6 (<i>n</i> = 15)	19.8 (<i>n</i> = 31)	22.3 (<i>n</i> = 29)
Ave. wind speed	14.4 (<i>n</i> = 17)	12.4 (<i>n</i> = 31)	9.9 (<i>n</i> = 29)
June			
Ave. max. temp.	28.4 (<i>n</i> = 30)	26.5 (<i>n</i> = 30)	31.7 (<i>n</i> = 29)
Ave. min. temp.	22.4 (<i>n</i> = 30)	21.8 (<i>n</i> = 30)	23.8 (<i>n</i> = 29)
Ave. wind speed	15.7 (<i>n</i> = 30)	9.7 (<i>n</i> = 30)	8.5 (<i>n</i> = 29)
July			
Ave. max. temp.	29.9 (<i>n</i> = 31)	29.6 (<i>n</i> = 31)	32.0 (<i>n</i> = 31)
Ave. min. temp.	23.8 (<i>n</i> = 31)	23.9 (<i>n</i> = 31)	24.3 (<i>n</i> = 31)
Ave. wind speed	15.5 (<i>n</i> = 31)	7.7 (<i>n</i> = 31)	15.5 (<i>n</i> = 30)
August			
Ave. max. temp.	—	30.6 (<i>n</i> = 31)	32.5 (<i>n</i> = 30)
Ave. min. temp.	—	24.8 (<i>n</i> = 31)	24.0 (<i>n</i> = 30)
Ave. wind speed	14.5 (<i>n</i> = 2)	8.8 (<i>n</i> = 31)	9.6 (<i>n</i> = 30)
September			
Ave. max. temp.	—	29.8 (<i>n</i> = 12)	—
Ave. min. temp.	—	23.6 (<i>n</i> = 12)	—
Ave. wind speed	—	10.1 (<i>n</i> = 11)	—

Newman (1988) recently detailed eight vegetation associations, mine are more similar to those described by Lamoureux (1963). I have omitted his ephemeral *Nama* beach association (where finches were seldom seen) and added the *Pluchea* association; the latter is a non-native shrub association that was not present in 1961.

From 1986 to 1988, representative areas from each of these vegetation types were searched for nests. In 1986, nest studies were concentrated in the northern third of the island, whereas in 1987 and 1988 they were restricted to the northwestern portion of the island (Fig. 1). I concentrated my efforts in these areas not only to reduce time spent walking from one area to another, but also to reduce the likelihood of accidentally collapsing the many procellariid nest burrows.

GENERAL MEASUREMENTS

Three field seasons were spent on Laysan: February to August 1986, April to July 1987, and

May to August 1988. For five or six months each year, daily rainfall and daily maximum and minimum temperatures were recorded. Wind speed (km/hr) and direction were recorded once daily at dawn in camp.

A total of 1,106 adult, subadult, and nestling finches were banded. In addition to morphological measurements, finches were weighed to the nearest 0.5 g, and age, sex, stage of molt, presence or absence of a brood patch, and status of the cloacal protuberance were recorded. Accumulation of fat in the furcular region was estimated on a scale of 0 to 4, where 0 represented no fat present and 4 represented a convex pad of fat.

Each bird was banded with a unique sequence which included a numbered U.S. Fish and Wildlife Service (USFWS) aluminum band and plastic colored leg bands. Birds that were banded and measured were caught in the northern one-third of the island; most were captured in the primary study area (Fig. 1).

NEST VISITATION; EGG AND CHICK MEASUREMENTS

Nests were located after observing specific adult behaviors in an area or locating a female late in the season who had not yet begun her post-breeding molt. Nests of unknown initial clutch size were sometimes discovered by hearing the chicks beg. Most nests were located fortuitously during random walks made while feeding observations were being recorded (unpubl. data). Some nests were found by methodically searching through *Eragrostis* clumps. Although this method was much less productive, it was employed especially during the 1988 field season, because I arrived on Laysan after the peak of nest building.

At the end of the 1986 field season, 10 *E. variabilis* clumps containing nests with banded pairs that had produced young were marked so that they could be located in following years. Another 11 such bunchgrass clumps were marked in 1987.

Located nests were usually checked daily each morning until the clutch was complete, again on the 10th and 15th day after the first egg was laid, and thereafter daily until the clutch had hatched. Each egg was uniquely numbered within 24 hr after being laid. If the nest was located after eggs were laid, it was checked daily, or every other day, until the eggs hatched. Eggs in these nests were marked in order to track individuals, but were excluded from analyses requiring known laying order, clutch size, or egg age. Egg lengths and widths were measured to 0.1 mm with calipers, and eggs were weighed to 0.1 g with a Pesola scale. Only first-day egg weights were used in analyses. Over the three years, most measures were from May and June.

Newly hatched chicks were marked with different colors on the dorsal down with felt-tip pens so that individuals from known eggs could be identified. If the female parent was unbanded, an attempt was made to capture, band, and measure her just after the last or next-to-last chick had hatched, when she was easy to capture on the nest. Chicks/eggs were always covered with a light cotton cloth or porous plastic lid while the female was quickly banded.

When the hatching order of chicks was not known, the chicks were not included in hatch-order analyses. New chicks were initially measured on the first, second, and/or third day of life. Chicks were measured every other morning

thereafter until approximately 11 to 14 days of age, by which time they had been uniquely leg-banded. Nest checks and egg or chick measurements were not made during heavy rain or high winds.

The following measurements were made on chicks: unflattened right wing chord, right tarsal length, beak depth, beak width, beak length, and sternum length, all measured to the nearest 1.0 mm. Weights were taken to 0.1 g with a Pesola scale. These weights and measures will be described in detail elsewhere (Morin and Conant, unpubl. data). In 1987, detailed observations of feather emergence and chick development were made on five chicks.

FATES OF EGGS AND CHICKS

Nests were checked every few days (even after chicks were no longer being measured) to determine the fate of offspring and the age of fledging. The definitions of the 17 possible fates are summarized in Table 2. Fates are not necessarily mutually exclusive, but represent a "best guess" based on the evidence. However, each egg/chick was assigned only one fate.

All data were statistically analyzed using routines from the personal computer Statistical Analysis System, version 6.03 (SAS 1988).

RESULTS

WEATHER

Daily air temperatures ranged from a minimum of 13.3°C to a maximum of 36.1°C (Table 1). Recorded wind speeds ranged from 0 to 48 km/hr, although storms with considerably higher wind speeds beyond our measurement capability occurred. Daily precipitation ranged from 0 mm to a high of 152 mm. Based on our rainfall data, as well as observations of vegetation status, 1986 could be considered an unusually wet year, 1987 a drought year, and 1988 an intermediate, possibly more representative year (Fig. 2). Although not included in this paper, qualitative observations of plant phenology and finch feeding patterns indicated reduced food abundance during the 1987 breeding season (Morin and Conant, unpubl. data).

PAIR FORMATION AND MAINTENANCE

Laysan Finches exhibit delayed plumage maturation; males do not usually reach full adult plumage until their third year (Banks and Laybourne 1977). All males seen in banded, breeding

TABLE 2. Abbreviations and descriptions of egg fates.

Fate	Description
CHICK DEFECT/DISEASE	Chick died of injury, defect, or disease before it fledged.
CHICK DEAD IN NEST	Chick died in nest prior to fledging from unknown causes.
CHICK DEAD OUTSIDE NEST	Chick found dead outside nest prior to fledging from unknown causes.
CHICK STARVED	Chick starved to death (i.e., did not thrive or was neglected and thin) before it fledged.
CHICK DISAPPEARED	Chick was seen after hatching, but chick later disappeared without a trace.
CHICK FLEDGED	Chick apparently fledged.
CHICK NEVER SEEN	Egg apparently hatched (seen during pipping) but chick was never seen.
EGG DROWNED	Egg drowned due to rain or flooding.
EGG CRACKED/PECKED/HOLES	Egg found cracked or with holes from predation or mechanical damage prior to hatch "due" date.
EGG ADDLED/INFERTILE	Intact egg seen a day or more past its hatch "due" date and nest was not abandoned.
EGG ABANDONED	Intact egg seen a day or more past the day when the nest was apparently abandoned.
RESEARCHER DAMAGE	Egg did not hatch due to damage or disturbance by researcher.
EGG DISAPPEARED	Egg apparently did not hatch and disappeared; shells or yolk may or may not have been found.
NEST DESTROYED	Nest destroyed by seabirds, other finches, weather, or other mechanical damage.
EGG DEFECTIVE	Egg was misshapen or not of normal composition.
DIED PIPPING	Egg appears to have died during pipping; these eggs are not considered to have hatched.
UNKNOWN	Unknown if egg hatched, or if chick fledged.

pairs on Laysan had adult (after-second-year or ASY) plumage. However, Conant (pers. comm.) has seen second-year males paired and apparently breeding in the introduced population at Pearl and Hermes Reef.

During the pairing and nest building period, males sang loudly from atop vegetation, usually the bunchgrass *E. variabilis*, but sometimes *Scaevola* or *Pluchea* shrubs. For all three years, 8 March 1986 was the earliest date male singing was recorded, and 26 March 1986 was the earliest date pair-formation was recorded. The earliest nest building activity (female carrying grass) was seen on 19 March 1986.

Monogamy was the only breeding system observed. Once a pair had formed and a nest was under construction, the mates were either seen only together or each alone ($n = 44$ different pairs with known nest sites). A minimum of nine banded pairs were resighted in subsequent years, indicating at least some year-to-year mate fidelity. In at least 12 cases, one or both members of a pair were seen reneesting within the same season. Only once were both members of a previously identified pair seen together at a reneest

within the same season. More typically, only one member of a pair was ever seen at the first or second nest, or one member of the pair was unbanded, so that positive pair identification was impossible. Repairing within a season was never observed. However, three individual birds repaired between seasons; two had spent two consecutive seasons with the same partner, but in the third season were seen with a new partner. At least two of these three reparings probably represent replacement after the death of the previous partner, since the missing partner was not resighted. Because banded finches were seldom seen more than 0.8 km from where they had been banded (Morin, unpubl. data), it is probable that these missing mates would have been seen if they were alive.

The male frequently regurgitated food to his mate during courtship and during the laying and incubation period. The females quivered their wings while soliciting feeding with vocalizations similar to those of fledglings begging for food. Both sexes were seen singing and performing wing and tail "flips" near each other. (The wings were rapidly spread in and out and the tail was rapidly

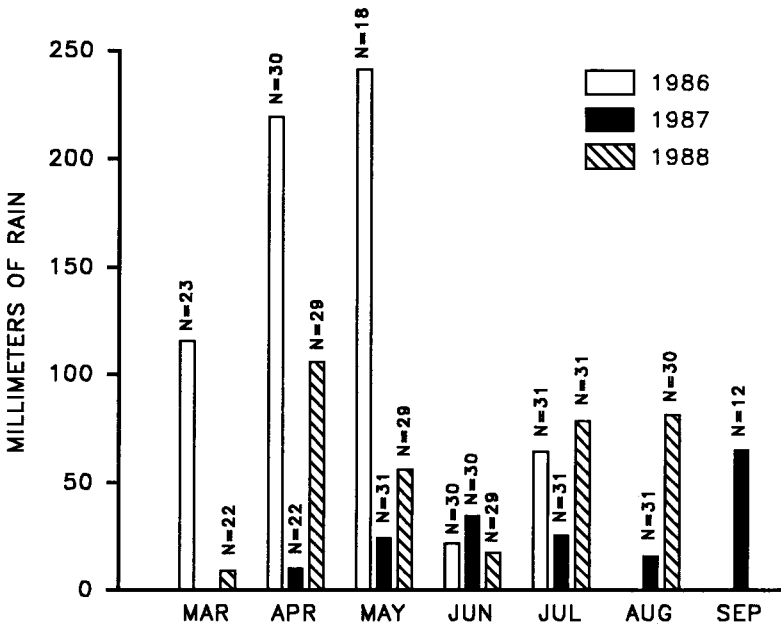


FIGURE 2. Minimum monthly rainfall (millimeters): n indicates the number of days with data. Where no n is shown, no data were collected.

flipped up and down.) The role of this display is not understood. During April 1987 (pre-breeding), I observed that females appeared to be soliciting males with these displays, but were often ignored. Both sexes appeared to guard their mates and vigorously chased intruders. Several times males were actually seen fighting. Fighting was often preceded by a "face off" display, where the males crouched face-to-face on the sand, raised their dorsal feathers and rump, and made movements toward each other with open beaks. Once, a female chased one male away and then begged from the remaining male, who then attempted to mount her.

DURATION OF THE BREEDING SEASON

The breeding season is long, and varies somewhat in duration and annual onset. Renesting appears to be common. In all three years, the earliest nest located with eggs was found on 2 April 1986 and the latest eggs were reported on 13 August 1988.

No hatch-year birds were present at the beginnings of the 1986 and 1987 field seasons. Between February and August 1986, eggs were found from 2 April until at least 26 July. Between April and July 1987, the first nest was found under

construction on 7 May. The first eggs were not found until 13 May (over a month later than in 1986), the first known-age egg was laid on 17 May (Fig. 3), and eggs were laid until at least July 13.

In 1988, fledged hatch-year birds were observed on 16 May; this indicated that eggs had been laid at least 45 days earlier, or by 2 April. The last 1988 eggs were seen on 13 August.

For all three years combined, egg laying peaked during mid to late May ($n = 491$ known-age eggs), and this appeared to be true for each separate year (Fig. 3). In 1986, a secondary peak occurred in April. In 1988, a secondary peak must have also occurred in April or earlier, because fledged hatch-year birds were already present in May. In 1987, only one breeding pulse was detected during my three and one-half month field season. However, other peaks may have occurred unobserved later in the year.

NEST SITUATION AND DESCRIPTION

Nests occurred almost exclusively in the bunchgrass *E. variabilis*; more detailed descriptions of nest characteristics, locations, and substrates have been presented elsewhere (Morin and Conant 1990, Morin 1992). Almost all nests occurred in

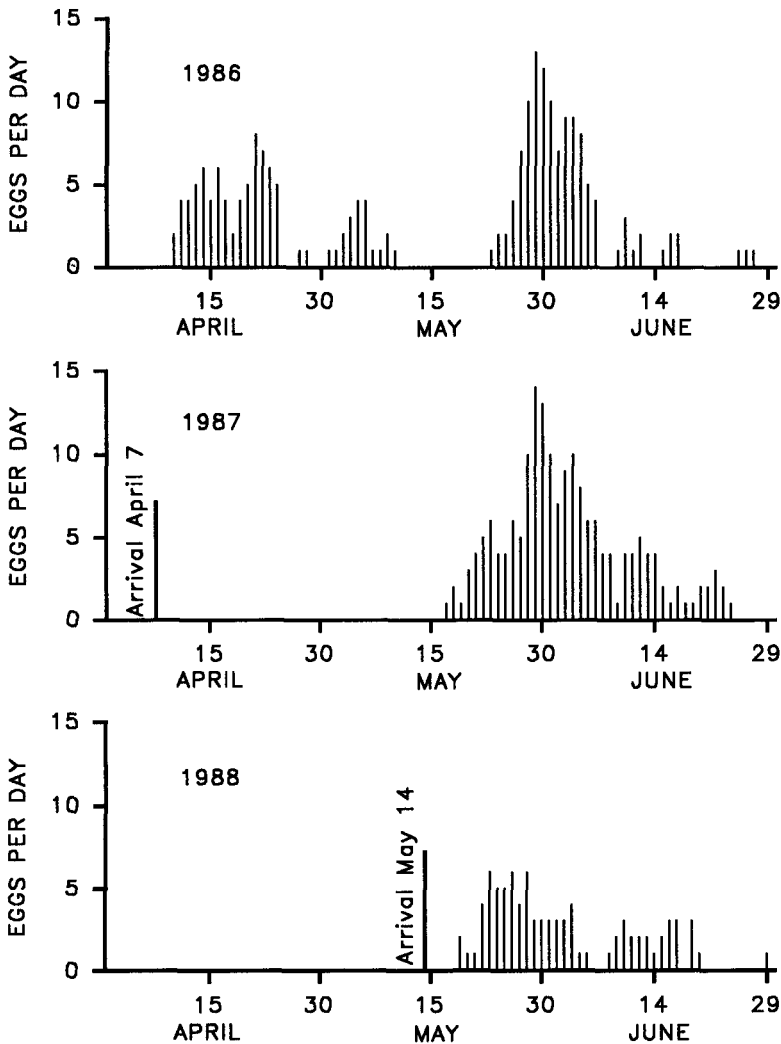


FIGURE 3. Temporal distribution of egg laying. See "Duration of the Breeding Season" under Results for latest egg laying dates in each season.

the *Eragrostis* or *Ipomoea-Boerhavia-Sicyos* vegetation associations where the bunchgrass primarily occurs. Nests were usually in close proximity to one another; this is possible because the finches do not defend traditional nesting territories. Infrequently, more than one complete or partially constructed nest was found in a single clump, but never two simultaneously active nests.

WITHIN- AND BETWEEN-YEAR NEST SITE FIDELITY

In 1987, only one of the ten marked *Eragrostis* clumps from 1986 (that had a successful nest and both members of the pair banded) was reused as

a nest site, but it was used by a different pair. Seven of the clumps did not contain any nests, and the remaining two had collapsed. (Collapsed clumps were mostly dead and had fallen into pits formed when the sand beneath them was undermined by burrowing procellariid seabirds and weakened by the effects of rain and wind.) None of the banded pairs nested in exactly the same staked clump as the previous year.

The same ten clumps from 1986 and another ten clumps from 1987 were relocated in 1988. Thirteen of these clumps were collapsed or collapsing and were unsuitable as nest sites. Only one of the remaining seven clumps (a 1987 nest

site) contained an active nest in 1988, but the female was not the 1987 female, and the 1988 male was never sighted.

Based on data from all three years, six pairs (out of 44 different pairs where both members were banded *and* the nest sites were known) were verified nesting with the same mate for two consecutive years in nearby *Eragrostis* clumps. One pair built 1986 and 1987 nests only 3 m apart. More typically, only one member of a pair was positively identified at a nest (the mate was either not seen or was unbanded). Even for these individuals, the subsequent year's nest could often be found by looking near the previous year's nest.

Within the same year, limited anecdotal evidence suggests that re-nest(s) tend to be near each other, or even in the same nest cup. One 1988 banded pair had two unsuccessful nests before their third nest produced two fledglings; the first two nests were 34.6 m apart and the final nest was 56.5 m from the second nest. In 1987, a banded female re-nested in her original nest cup after her first clutch of four failed, but I left Laysan before I could determine the fate of her second clutch of three eggs. In 1986, a banded female reused her original nest cup after she successfully fledged a chick, but her second brood failed when the chicks starved.

NEST CONSTRUCTION AND ADULT BEHAVIOR AT THE NEST

It is not clear who chooses the nest site, but prior to nesting, females were frequently seen running on the ground, with the male in close pursuit. A female would quiver her wings in front of a clump of *E. variabilis* before climbing in and investigating it. She did this repeatedly with a series of clumps, giving the appearance of searching for a nest site. Once selected, the nest site might be guarded by both sexes, but a larger territory was not defended. Relative to their nests, pairs foraged both near and far away, but did not defend foraging areas. Foraging occurred in all vegetation types, although some spots appeared to be especially popular foraging "commons." Factors such as plant and insect availability, proximity to researcher tents (i.e., food crumbs), fresh water availability, the distribution of seabird nests, and the density of finch nests probably affected foraging patterns.

Only female Laysan Finches were seen carrying nesting material to the nest, although a female was sometimes followed by her mate dur-

ing the nest building. Nest construction generally took two to seven days. Nests were often located after partial construction, making construction time difficult to calculate. The construction of two nests appeared to take at least 27 and 29 days, but these were abandoned during early construction and activity was resumed much later. Since the pairs for both nests were unbanded, it is possible that different pairs finished the nests.

After a nest seemed completed, the pair frequently left the site for several days, presumably to forage. After such an absence, the female was often found sitting in the empty nest cup in an incubating position; her first egg was almost always found the next morning. Generally, females appeared to begin daytime incubation as soon as the first egg was laid. On one occasion, a nest was checked the night (22:00 hours) the first egg was laid; the female was not found on the nest. However, she was asleep on the nest the next night at the same time, after she had laid her second egg. Based on three night observations of a nest from 1987, the female brooded the chicks at night until they were at least 17 days old. The male was not seen during these nocturnal visits.

Males do not have brood patches and only females were seen incubating. During egg laying, incubation, and early brooding, females seldom left the nest site and were fed by male regurgitation. When a male came to feed his mate, she usually left the nest and was fed by him nearby (within 3 m). Both males and females appeared disturbed if such feedings were observed, and positioned themselves so that my view was blocked by vegetation. If a female appeared to notice me when she was returning to the nest after a feeding bout, she usually would move to *Eragrostis* clumps that did *not* contain her nest. I sometimes found nests by going to the clump avoided by the female.

When nesting was at its peak, females were seen less frequently because of their incubation schedules. At this time, adult males were unusually abundant in camp and were easily caught in food-baited traps and at water stations during dry conditions. Some of the male foraging for food and water occurred at a frenzied pace after the eggs had hatched. The females did not substantially help with feeding the chicks until they were several days old. Even then, males seemed to do most of the feeding. Both males and females fed the young by regurgitation.

Fecal sacs were removed by both parents, and

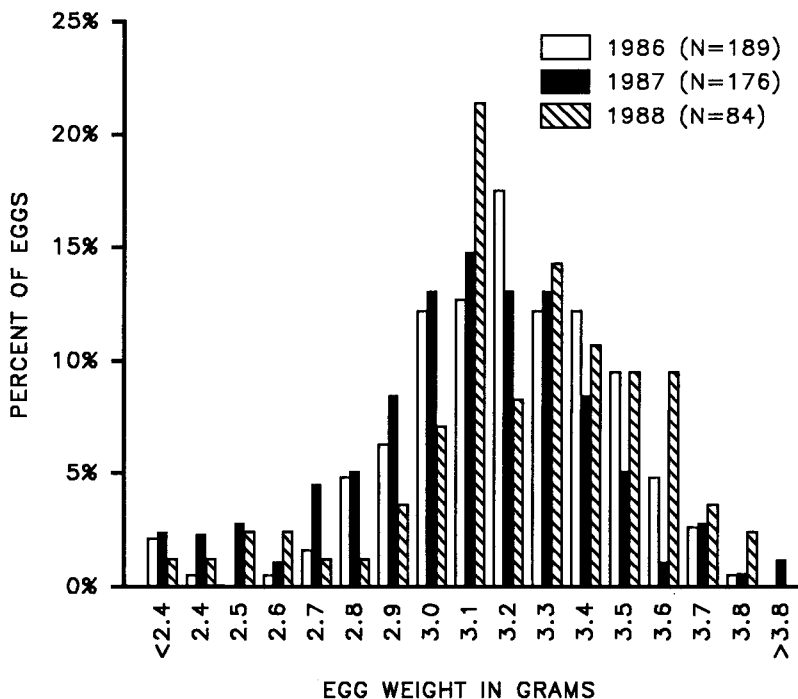


FIGURE 4. Distribution of fresh egg weights during three years: *n* indicates number of eggs.

were sometimes seen being carried away from the nest. This behavior persisted until the chicks were at least 16 days old, decreasing as the chicks aged. By the time the chicks had fledged, there were often feces all around the rim of the nest, which had become flattened due to the activity of the chicks.

EGG CHARACTERISTICS AND LAYING INTERVAL

Laysan Finch eggs resembled other Hawaiian honeycreeper eggs in coloration and spotting; they were a light cream color with maroonish-brown speckles, often more heavily concentrated on the wide end of the egg (Berger 1972, pers. observ.) One egg was laid daily, apparently within a few hours of sunrise, until the clutch was complete. Very infrequently, a day was skipped during the egg-laying process.

The average egg length was 2.21 cm ($n = 568$, $SD = 0.109$) and average egg width was 1.65 cm ($n = 568$, $SD = 0.064$). Using Hoyt's (1979) equation, the average Laysan Finch egg volume was 3.07 ± 0.06 ml.

The average mass for an egg 24 hours old or

less was 3.16 g ($n = 449$, $SD = 0.330$); only fresh egg masses were used in analyses (Fig. 4). The smallest and largest fresh egg masses that yielded viable fledglings were 2.4 g ($n = 2$) and 3.7 g ($n = 2$).

The mean fresh egg mass per clutch differed significantly among the three years of this study (Kruskal-Wallis: $\chi^2 = 6.43$, $P = 0.04$). The 1986 mean was 3.17 g ($n = 40$ nests, $SD = 0.295$, mode 3.2), the 1987 mean was 3.10 g ($n = 51$ nests, $SD = 0.245$, mode 3.1), and the 1988 mean was 3.24 g ($n = 22$ nests, $SD = 0.281$, mode 3.1). Mean egg mass per clutch for 1987 and 1988 were significantly different at the 0.05 level (Tukey test).

In 1986, mean egg mass increased with increasing clutch size (Fig. 5). The mean egg from a four-egg clutch in 1986 was significantly heavier than the mean egg from a three-egg clutch (Mann-Whitney: $Z = 2.273$, $P = 0.023$). In the drought year of 1987, the trend was reversed; eggs from three-egg clutches were significantly larger than those from four-egg clutches (Mann-Whitney: $Z = -2.776$, $P = 0.006$). However, in 1988, there was no significant difference between

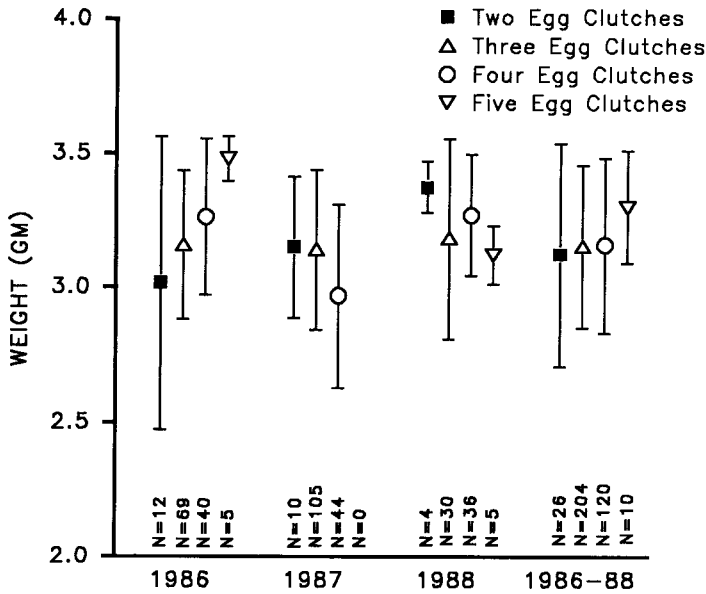


FIGURE 5. Mean fresh egg weights and standard deviations in relation to clutch size by year: *n* indicates number of eggs.

the eggs' masses from three- and four-egg clutches, perhaps because of the small sample sizes (Mann-Whitney: $Z = -0.597$, $P = 0.550$).

A two-factor unbalanced analysis of variance was performed on ranked fresh egg masses from three- and four-egg clutches only. Year, clutch size, and the interaction of year and clutch size were specified as the model effects. Type III partial sums-of-squares indicated that only year, and the interaction of year with clutch size, significantly affected egg mass ($F = 5.21$, $P = 0.006$ and $F = 5.63$, $P = 0.0002$, respectively).

The body mass of the parent female ($n = 26$) was not correlated with the mean fresh egg mass nor the total egg mass for her clutch (Pearson Correlation Coefficient: 0.079, $P = 0.703$ and 0.137, $P = 0.505$, respectively).

In 1987, three nests each had at least one defective egg with an unusually thin shell and an oversized air cell. None of these hatched. Another 1987 clutch that failed to hatch consisted of two tiny eggs weighing only 0.9 and 2.0 g.

CLUTCH SIZE, FEMALE CONDITION, AND BROODS PER YEAR

For clutches of known size, three eggs were the mode for all three years ($n = 166$; Fig. 6), and 3.19 eggs was the overall mean (SD = 0.696). Although close to significant, there was no dif-

ference among the years in the mean clutch sizes at the 0.05 level (Kruskal-Wallis: $\chi^2 = 5.531$, $P = 0.063$). In 1986, the mean clutch was 3.17 eggs ($n = 75$, SD = 0.742, range 1-5), in 1987 it was 3.08 eggs ($n = 61$, SD = 0.557, range 2-4), and in 1988 it was 3.47 eggs ($n = 30$, SD = 0.776, range 2-5).

However, clutch size varied significantly with the amount of female furcular fat (G-test, $G(\text{adj.})$

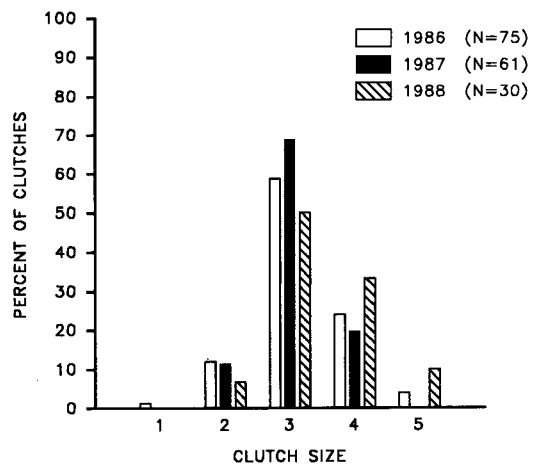


FIGURE 6. Distribution of clutch sizes by year: *n* indicates number of clutches.

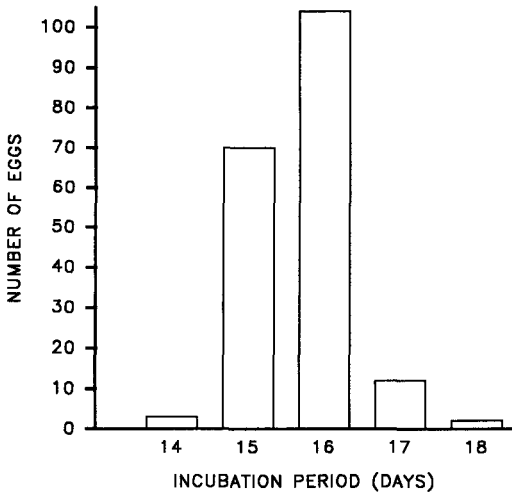


FIGURE 7. Incubation periods in days for 191 eggs from 1986 to 1988 combined.

= 4.019, $P < 0.05$, $n = 43$ nests). Females with a furcular fat status of one or two had more clutches of two or three eggs than clutches of four or five eggs (15 vs. 6), whereas females with the higher fat status of three or four had fewer clutches of two or three eggs and more clutches of four or five eggs (9 vs. 13). Females with a furcular fat status of two or lower composed 31% (5 of 16) of this sample in 1986, 65% (13 of 20) of this sample in 1987, and 43% (3 of 7) of this sample in 1988.

The mean female parent mass for 1986 was 32.5 g ($n = 16$), for 1987 it was 34.0 g ($n = 19$), and for 1988 it was 33.5 g ($n = 6$). These masses did not differ significantly among the three years (ANOVA, $P = 0.438$). However, the 1987 females had a large standard deviation (4.35 vs. 2.31 in 1986 and 1.34 in 1988), indicating much variability among their masses.

Based on the average egg mass (3.16 g) and average clutch size (3.19 eggs), the estimated average clutch mass is 10.1 g. This is approximately 31% of the mean adult female body mass of 32.7 g (based on $n = 120$ females three years old or older). The maximum clutch size of five, with an estimated clutch mass of 15.8 g, is only 48% of the mean adult female body mass. This production is much less than the 95% to 110% of female body mass reported for clutch weights in 10 species of fringillids (Amadon 1943, Rahn et al. 1975).

Finches are capable of raising at least two

broods a year, although it is uncertain what proportion of the pairs actually do so. Twelve banded birds (eight individuals and two pairs) were known to have laid at least two clutches within a single year. Of these, four of the birds (two individuals and one pair) fledged at least one chick from both their first and second clutches. One pair failed in both their first and second nest attempt, but fledged young from their third nest.

DURATION OF INCUBATION

Mean incubation period was 15.7 days ($n = 191$, $SD = 0.662$) and the mode was 16 days (Fig. 7). The three eggs with 14-day incubation periods were each laid after the female had apparently skipped a day during egg-laying. These eggs may have been laid later in the day after I checked the nest (in which case they hatched after 15 days of incubation).

The mean incubation period shortened from the first laid egg to the last: the average length of incubation for the first egg was 16.2 days ($n = 55$; $SD = 0.631$), for the second egg was 15.6 days ($n = 59$; $SD = 0.522$), for the third egg was 15.4 days ($n = 57$; $SD = 0.593$), and for the fourth egg was 15.3 days ($n = 19$; $SD = 0.582$). These incubation periods differ significantly (Kruskal-Wallis: $\chi^2 = 45.40$, $P = 0.0001$). The single fifth egg on which I had complete data had an incubation period of 16 days. Using the average egg mass and Rahn and Ar's (1974) equation, the Laysan Finch incubation period is predicted to be 15.4 days.

HATCHABILITY, HATCHING SUCCESS, AND HATCHING ORDER

For all three years combined, 40.6% of all eggs laid in known-size clutches hatched; hatchability was similar for each year (Table 3). The low hatchability is due to the large number of eggs that disappeared from the nest.

If nest success is measured as the percent of nests that hatch at least one egg (Hensler 1985), then the overall success was 56.4% for the three years combined ($n = 166$). However, success varied among different time periods within a year. For April 1986 nests, the success rate was only 22.2% ($n = 27$), probably because of the adverse weather conditions in April and early May of that year. For clutches laid after April in 1986, nest success was 62.5% ($n = 48$). The data from 1987 and 1988 (gathered in May and June) showed similar success rates of 62.3% ($n = 61$)

TABLE 3. Hatchability, defined as (number of eggs hatched/number of eggs laid) \times 100, and hatchling survival, defined as (number of fledglings/number of hatchlings) \times 100, for Laysan Finch eggs from known-size clutches.

Year	No. of eggs laid	No. hatched	No. fledged	Hatchability	Hatchling survival
1986	238	94	65	39.5%	69.1%
1987	188	80	56	42.6%	70.0%
1988	104	41	28	39.4%	68.3%
Overall	530	215	149	40.6%	69.3%

and 63.3% ($n = 30$), respectively. The percent of nests in which all eggs hatched was 18.7% (31 of the 166 nests from all three years).

In a few nests, eggs hatched almost synchronously (within 24 hours), but hatching was usually spread over 2 or more days, with eggs hatching in the order laid (Morin and Conant, unpubl. data). Only one out of 151 eggs hatched out of sequence.

NESTLINGS, FLEDGLINGS, AND POST-FLEDGING DEPENDENT PERIOD

At hatching there is light grey down on the capital, spinal, femoral, alar, humeral, and part of the ventral feather tracts. There is no obvious down on the crural or caudal tracts. Chicks have yellow flanges and bill, and the inside of the gape is lavender with patches of red on the palate.

Chicks develop slowly compared to temperate passerines. Pin feathers begin to emerge at 4 days of age, and feathers begin to unsheathe in most tracts when nestlings are 10 days of age or older (Tables 4, 5).

Because of asynchronous hatching, there was usually a size hierarchy within a clutch: the older chicks were almost always larger. Size differences persisted until the chicks approached fledging. Chicks abandoned the nest prematurely if handled after 14 days of age, but they appeared to later regroup outside the nest after such a disturbance.

Chicks left the nest cup gradually, and spent progressively more time perched on the nest rim as they aged; older chicks did so earlier than younger chicks. Infrequently, after a disturbance, chicks moved from the nest clump to a nearby clump before the normal fledging age. Fledging was a gradual process; I defined a "fledged" chick as one that no longer associated mainly with the nest, even though it still may have frequented

TABLE 4. Development of feather tracts in Laysan Finch nestlings.

Tract	Age (days)													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
SPINAL														
ALAR														
VENTRAL														
CAUDAL														
CAPITAL														
HUMERAL														
FEMORAL														
CRURAL														

..... Pin feathers appear.
 - - - - - Pin feathers unsheathing.

the nest's bunchgrass clump. Chicks usually fledged between 22 and 26 days of age ($n = 37$), but a few unusually small ones took longer. For seven to ten days after fledging, chicks stayed in or near a bunchgrass clump, *Scaevola* shrub, or a *Pluchea* shrub (either the nest's clump or a clump or shrub within 10 m of it). During this period, the parents left the fledglings hidden and called them out of hiding with contact calls when they returned to feed them. Fledglings at this age retained the obvious yellow bill flanges and had a peculiar, fluttery, bat-like flight. Fledglings were seen more and more frequently thereafter, openly following and begging from a parent. Male parents were followed as often as female parents, or more so. The parents sometimes split the brood, possibly because at this stage the parents often foraged separately.

After fledging, the chicks depended on their parents for at least three weeks. Fledglings of 40 days or older were commonly seen begging from adults, although parental feeding declined as the chicks aged. The oldest known-age fledgling seen being fed by a parent was 45 days old. Fledglings occasionally begged from non-parent adults, but I saw a banded fledgling being fed by such a bird only once. Fledglings were observed watching and then sampling the same plant or plant part that the parent had just eaten. However, they probably also learned what to eat by trial and error. I saw several hatch-year birds trying to crack small bits of plastic marine debris, some-

TABLE 5. Developmental patterns in young Laysan Finches.

Developmental characteristic	Age (days)															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
OPENING OF EYES	SHUT			OPENING			FULLY OPEN									
GRASPING	NOT ABLE TO GRASP						GRASPING DEVELOPED									
FEAR RESPONSE	NO COWERING												RUN AWAY			
ABILITY TO STAND	UNABLE TO STAND				SOME STANDING				STANDING WELL							
COLOR OF BEAK	YELLOW			TRANSITIONAL				BLACKISH								
PREENING	NONE SEEN UP TO DAY 16															
WING FLAPPING	NONE SEEN UP TO DAY 16															

times even fighting over especially attractive pieces (small, round pieces seemed to be favored). At 40 or more days of age, fledglings regularly fed themselves, either alone or in the company of hatch-year birds other than their siblings.

By three months of age, a few banded hatch-year birds had moved as far as 0.8 km or more within a single day. The yellow bill flanges were no longer obvious at a distance after the fledglings were about two and one-half months of age.

EGG AND CHICK MORTALITY

Overall, 69.3% of all eggs that hatched survived to fledge. Hatchling survival was similar during each of the three years (Table 3).

The mean numbers of hatchlings and fledglings per nest for each clutch size for the four breeding peaks are shown in Fig. 8. The year 1986 has been separated into early and late seasons, since weather during the early season (Fig. 2) had a devastating effect on egg and chick survival, regardless of clutch size. In contrast, the late 1986 season showed an increase in hatchlings and fledglings per nest with an increase in clutch size. During the drought year of 1987, all the two-egg clutches failed, and the four-egg clutches did no better than the three-egg clutches. Except for the biggest clutches (five-egg clutches),

1988 showed moderate increases in the mean hatchlings and fledglings per nest with increasing clutch size.

Female parents with a fat status of one or two produced a mean of 1.3 fledglings per nest ($n = 19$ nests), whereas females with a fat status of three or four produced a mean of 2.1 fledglings per nest ($n = 20$ nests). These two fledgling rates are at the borderline of being significantly different (t -test: $t = 2.018$, where $P = 0.05$ corresponds to $t = 2.026$). However, females with lower fat status also had fewer eggs per clutch than females with higher fat status.

The two most common fates for eggs from known- and unknown-size clutches in all three years combined were EGG DISAPPEARED (24.9% or 208) and CHICK FLEDGED (34.0% or 284) (Tables 6, 7, 8). Four of the 284 fledged chicks are known to have died later in the same field season. Most of the eggs in the EGG DISAPPEARED category probably belong in the more specific categories of EGG CRACKED/PECKED/HOLES and DIED PIPPING (Table 2), but could not be so assigned due to lack of evidence.

Because of underestimation bias associated with nests found after a clutch was completed or found during the chick stage (Mayfield 1975, Hensler 1985), such nests have been eliminated

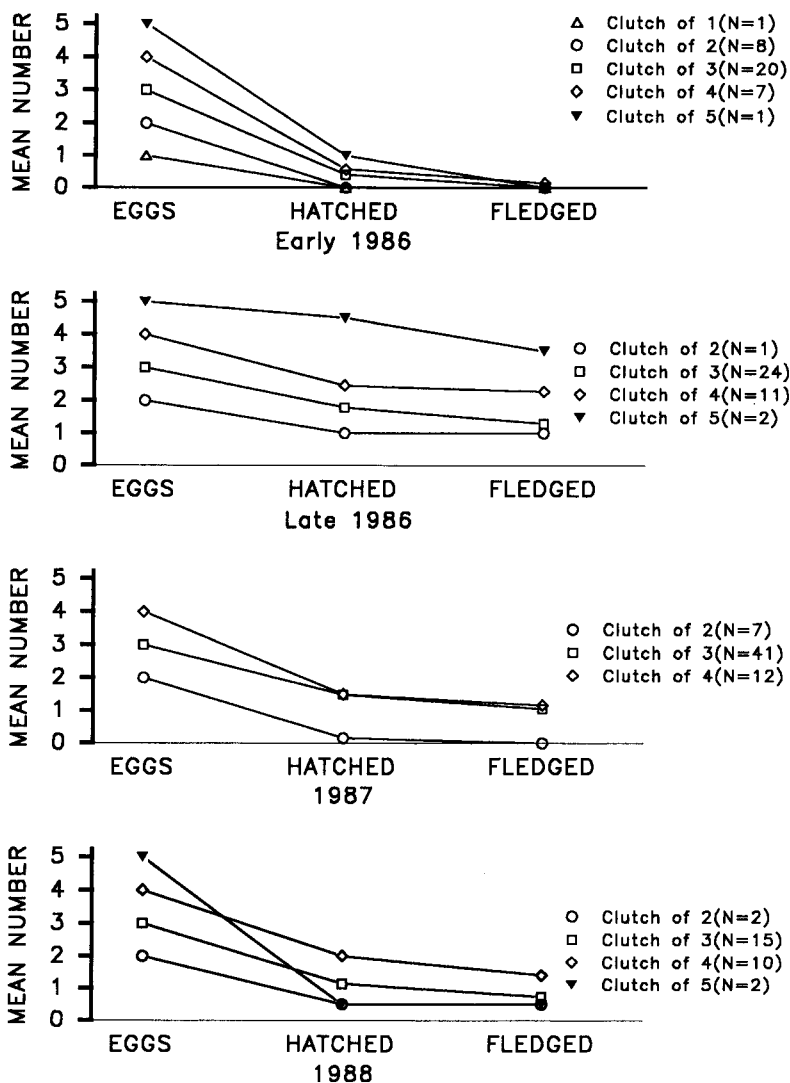


FIGURE 8. Mean number of hatchlings and fledglings per nest for each clutch size in each reproductive period: n indicates number of clutches.

from the analyses which follow, unless otherwise stated. Only nests with known-size clutches are included, where all eggs were marked as they were laid. The few clutches of five were included as known-size clutches because five eggs appears to be the maximum clutch size. The fates of eggs and chicks from nests of unknown initial clutch size are summarized in Table 6.

For all three years combined, fates of eggs from known-size clutches were primarily EGG DISAPPEARED 33.0% ($n = 175$), CHICK FLEDGED 28.1% ($n = 149$), and EGG AD-

DLED 10.2% ($n = 54$). The other 14 fates each accounted for less than 4% of the total 530 eggs from known-size clutches. For each year taken separately, egg fates from known-size clutches were also primarily EGG DISAPPEARED and CHICK FLEDGED (Table 7). However, of the 83 eggs from known-size clutches laid in the early 1986 season, 47 (57%) disappeared, 35 (42%) suffered various other fates, and only 1 (1%) fledged a chick. This subset of eggs also accounted for 13 of the 18 EGG ABANDONED, 6 of the 10 CHICK STARVED, and 6 of the 10 EGG

TABLE 6. Number (*n*) and percent (%) of the most common fates for eggs from unknown-size clutches in each of three years.

Clutch size	Year	Fate						Total	
		Egg disappeared		Chick fledged		Other		<i>n</i>	%
		<i>n</i>	%	<i>n</i>	%	<i>n</i>	%		
At least 1 egg	1986	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)
	1987	1	(25.0)	1	(25.0)	2	(50.0)	4	(100.0)
	1988	0	(0.0)	7	(50.0)	7	(50.0)	14	(100.0)
At least 2 eggs	1986	0	(0.0)	1	(50.0)	1	(50.0)	2	(100.0)
	1987	4	(28.6)	0	(0.0)	10	(71.4)	14	(100.0)
	1988	0	(0.0)	14	(53.9)	12	(46.2)	26	(100.0)
At least 3 eggs	1986	13	(33.3)	9	(23.1)	17	(43.6)	39	(100.0)
	1987	7	(21.2)	9	(27.3)	17	(51.5)	33	(100.0)
	1988	6	(9.1)	43	(65.2)	17	(25.8)	66	(100.0)
At least 4 eggs	1986	1	(5.0)	10	(50.0)	9	(45.0)	20	(100.0)
	1987	0	(0.0)	9	(45.0)	11	(55.0)	20	(100.0)
	1988	1	(1.5)	32	(47.1)	35	(51.5)	68	(100.0)
Total number of eggs		33		135		138		306	

CRACKED/PECKED/HOLES for that entire year (Table 7).

When the egg fates of known-size clutches were combined for all years ($n = 530$), there was a tendency for the percent of eggs with the fate EGG DISAPPEARED to decrease as the clutch size increased (Table 8). In contrast, there was a tendency for the percent of eggs with the fate CHICK FLEDGED to increase as the clutch size increased. After the single clutch of one egg was omitted, success (fledged versus nonfledged eggs) was not independent of clutch size ($G = 14.702$, $P = 0.002$). However, for only the three- and

four-egg clutches, and only the three-, four-, and five-egg clutches, fledging success was independent of clutch size ($G = 2.266$, $P = 0.132$; and $G = 2.272$, $P = 0.321$, respectively). Two-egg clutches had significantly lower fledging success.

In 1986, the percent of eggs producing fledglings increased as the size of the clutch increased (Fig. 9). This was the only year when an egg's prospect for fledging success was associated with clutch size for three- and four-egg clutches ($\chi^2 = 44.67$, $P < 0.001$); a higher percent of eggs from four-egg clutches produced fledglings. In the dry year of 1987, no five-egg clutches were found,

TABLE 7. Number (*n*) and percent (%) of fates for eggs from known-size clutches in each of three years.

Fate	1986		1987		1988	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Egg disappeared	82	(34.5)	56	(29.8)	37	(35.6)
Chick fledged	65	(27.3)	56	(29.8)	28	(26.9)
Egg addled	15	(6.3)	29	(15.4)	10	(9.6)
Egg abandoned	18	(7.6)	1	(0.5)	2	(1.9)
Egg cracked/pecked/holes	10	(4.2)	3	(1.6)	5	(4.8)
Chick starved	10	(4.2)	4	(2.1)	0	(0.0)
Chick dead in nest	5	(2.1)	10	(5.3)	2	(1.9)
Chick defect/disease	2	(0.8)	3	(1.6)	5	(4.8)
Nest destroyed	7	(2.9)	3	(1.6)	5	(4.8)
Chick disappeared	8	(3.4)	5	(2.7)	3	(2.9)
Chick never seen	2	(0.8)	0	(0.0)	1	(1.0)
Egg defective	1	(0.4)	7	(3.7)	0	(0.0)
Chick dead outside nest	1	(0.4)	2	(1.1)	2	(1.9)
Researcher damage	4	(1.7)	1	(0.5)	1	(1.0)
Egg drowned	4	(1.7)	0	(0.0)	0	(0.0)
Died pipping	1	(0.4)	6	(3.2)	0	(0.0)
Unknown	3	(1.3)	2	(1.1)	3	(2.9)
Total eggs	238	(100)	188	(100)	104	(100)

TABLE 8. Number (n) and percent (%) of the most common fates for eggs from all known-size clutches in 1986, 1987, and 1988.

Fate	Clutch size									
	One		Two		Three		Four		Five	
	n	%	n	%	n	%	n	%	n	%
Egg disappeared	1	(100.0)	27	(75.0)	99	(32.7)	39	(24.4)	9	(30.0)
Chick fledged	0	(0.0)	2	(5.6)	84	(27.7)	54	(33.8)	9	(30.0)
Egg addled	0	(0.0)	2	(5.6)	26	(8.6)	26	(16.3)	0	(0.0)
Egg defective	0	(0.0)	2	(5.6)	3	(1.0)	3	(1.9)	0	(0.0)
Egg abandoned	0	(0.0)	0	(0.0)	17	(5.6)	4	(2.5)	0	(0.0)
Egg cracked/pecked/holes	0	(0.0)	2	(5.6)	8	(2.6)	5	(3.1)	3	(10.0)
Chick disappeared	0	(0.0)	0	(0.0)	14	(4.6)	1	(0.6)	1	(3.3)
Other	0	(0.0)	1	(2.8)	52	(17.2)	28	(17.5)	8	(26.5)
Total number of eggs (n)	1	(100.0)	36	(100.0)	303	(100.0)	160	(100.0)	30	(100.0)
Total number of clutches	1		18		101		40		6	

and no two-egg clutches produced fledglings. In the 1987 three-egg clutches, 33.3% of the eggs produced fledglings, whereas only 29.2% of the four-egg clutches did so (Fig. 9). In 1988, four-egg clutches had the higher percent of eggs that produced fledglings (35.0% vs. 24.4% for eggs from three-egg clutches).

Of the 165 known-size clutches from all three years, 149 fledglings were produced, yielding an overall average of 0.90 fledglings per nest. Of these 149 banded fledglings, only five have been seen again a year or more later. All five of these birds were from four-egg clutches. An additional five individuals from the total 135 banded fledglings from unknown-size clutches have also been seen a year or more later. Therefore, survival for the first year was at least 3.5% (10 out of 284).

DISCUSSION

WEATHER AND REPRODUCTION

Laysan Island has a fairly simple ecosystem that experiences wide fluctuations in temperature, moisture, and wind. These factors alter the quality and quantity of vegetation available to finches as food either indirectly (e.g., by regulating plant growth) or directly (e.g., by burying vegetation under sand during wind storms or flooding vegetation when the lake receives large amounts of rain).

Laysan Finches are omnivores and eat some part of almost every plant on the island, as well as invertebrates, carrion, and eggs. Finch feeding probably has a significant effect on many of the plant species and other animals, especially when finch populations are high (pers. observ.). However, their usual diet does not buffer the finches

from some effects of weather. Adverse weather may cause almost total nest failure. In April and May of 1986, Laysan received over 218 mm and 241 mm of rain, respectively (Fig. 2). The rain raised the lake level at least 0.3 m and caused extensive flooding, which extended into three of the plant associations where finches regularly foraged (*Pluchea* and *Sesuvium-Heliotropium-Cyperus*) or nested (*Ipomoea-Boerhavia-Sicyos*). Several early nests were completely destroyed by flooding. Even more destructive were the winds that accompanied these storms. Many of the ear-

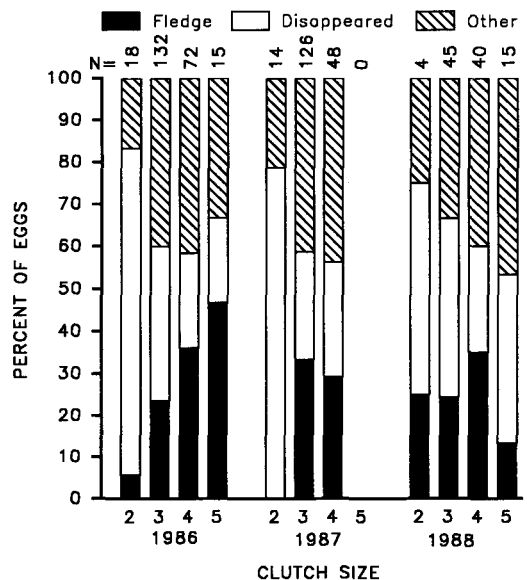


FIGURE 9. Fates of eggs in known-size clutches by year: n indicates number of eggs.

ly nests had normal chicks that apparently starved to death. Not only did rain and wind during these storms appear to stress the young chicks thermally (e.g., chicks were cool to the touch), but the parents seemed unable to feed them adequately during such conditions. From the 83 eggs laid in known-size clutches in early 1986, only one chick fledged. More than half of the eggs disappeared, and most of the rest were abandoned, were found with holes (e.g., pecked eggs), or the chicks were found starved.

Laysan Island experienced a dry 1987 (Fig. 2), and weather again influenced finch reproduction. The level of the lake was low; sections of the lake bed were dry and exposed. Various observations of vegetation, as well as total reproductive failure by the Laysan Duck, further confirm that 1987 was a drought year (pers. observ.; A. Marshall, pers. comm.). The native vine (*Sicyos maximowiczii*), an important finch food source, decreased in abundance relative to 1986. Another important finch food, *Portulaca* spp., which was abundant in 1986, was absent until after a mid-June rain in 1987, when it began sprouting. In many of the areas that were flooded the previous year, the vegetation had not yet recovered, so potential finch foraging areas were reduced in quality and also quantity. Of the three years studied, only in 1987 did the finches not attempt to breed early in the season. The highest percent of addled and defective eggs, eggs that died during pipping, and chicks that died in the nest from unknown causes also occurred in 1987 (Table 7). Since relative humidity affects water loss from eggs, thus affecting hatchability (Drent 1975), the addled eggs and chicks that died pipping may have been partially a result of the dry conditions, as well as nutritional limitations.

Seven of the eight defective eggs from all three years occurred in 1987. The defects of these eggs (unusually small size or malformed shell and contents) suggest nutritional deficiencies. The mean mass of eggs in 1987 was also significantly lower than in the other years. Usually females under nutritional constraints lay relatively smaller eggs (O'Connor 1984), and birds lay larger eggs when food is abundant (Ewald and Rohwer 1982, Briskie and Sealy 1990).

The mean clutch size in 1987 was the smallest of the three years. No five-egg clutches were found in 1987, although they were found in both 1986 and 1988. This possible reduction in clutch size

may have also been a response to nutritional stress caused by the drought. In 1987, 65% of the female parents (from known-size clutches where female fat status was known) had a fat status of two or less. If fat indicates female condition, as is commonly believed (Murton and Westwood 1977, Rogers 1991), and as egg mass data from this study suggest, then 1987 was the year when females were in worst condition.

The low population estimate of $5,201 \pm 1,211$ birds made in May 1988 (Morin 1988, Morin and Conant in press), further supports the view that 1987 was a poor year for reproduction and subsequent recruitment. May estimates for 1986 and 1987 were $10,333 \pm 1,796$ and $10,911 \pm 1,769$, respectively (Morin 1986, 1987b).

Baldwin (1953) reported adverse effects on breeding of other Hawaiian honeycreepers during stormy, wet periods; hard rains caused nest destruction, abandonment, and lowered production of young. The effect of adverse weather on breeding has been well documented in the Large Cactus Finch (*Geospiza conirostris*) in the Galapagos Islands (Grant and Grant 1989); unpredictable weather and its effect on environmental conditions and food supply exert selection pressures on its breeding strategy. It is probably also true for Laysan Finches that unpredictable weather has a major influence on their breeding success every year. This in turn affects the population size, and may partially explain the wide population fluctuations that have been documented over the past two decades (Dennis et al. 1991).

LAYSAN FINCH BREEDING STRATEGY

Like the Large Cactus Finch (Grant and Grant 1989), the Laysan Finch seems to have a breeding biology that has both temperate and tropical characteristics. Unlike temperate passerines, breeding condition is not regulated only by photoperiod, but is at least influenced, if not induced, by food supply. During the 1987 drought, for example, breeding did not begin until May, a full month or more later than in the other two years. Food availability as a proximate control over the onset of reproduction has also been observed in other fringillid finches (Newton 1973). Under optimal environmental conditions, it seems feasible that Laysan Finches could breed almost year round. Indeed, a captive female Laysan Finch held in the Honolulu Zoo during 1989 had

a brood patch and an attending male during November (pers. observ.).

On Laysan Island, the males do not breed until they are at least two years old (pers. observ.). Such delayed maturity generally occurs when adult annual survival exceeds about 60% (Murton and Westwood 1977). In spite of high adult survival, survival between hatching year and second year appears to be low; only 3.5% of banded chicks that fledged were resighted a year or more later. The probability of resighting a banded bird is rather high, since dispersal of banded finches away from the banding sites is low (unpubl. data). Therefore, it is more likely that banded fledglings died rather than dispersed to a distant area.

In an unpredictable environment, the probability of fledging young can be increased by spreading reproduction over a long breeding season with the potential for multiple broods and by having a long reproductive lifetime (Murton and Westwood 1977). Laysan Finches qualify under both of these criteria.

Laysan Finch eggs are lower in mass than would be expected from adult body mass (Rahn et al. 1975). Using the mean Laysan Finch egg mass of 3.16 g, and a mean female body mass of 32.7 g (for $n = 120$ females three years old or older, banded on Laysan Island; unpubl. data), the proportionality coefficient (a) is estimated as 0.300. This is considerably less than the value of 0.413 which Rahn et al. (1975) compiled for 13 other species of fringillids. A low clutch mass (an estimated average 30% of the mean adult female mass) may be adaptive in an unpredictable environment. If the female does not deplete all her reserves on any one nesting attempt, she can remain ready to renest quickly if necessary.

Laysan Finches are monogamous within any year, and display at least some year-to-year pair and site fidelity. These are reproductive features that can be expected in long-lived species when both parents are needed to raise the young successfully (e.g., for defense against predation: Oring 1982, Freed 1986), when previous experience increases reproductive success (O'Connor 1984), or when opportunities to acquire new mates are limited (Freed 1987). Year-to-year nest-site fidelity focused on a relatively small area, but was not confined to a single *Eragrostis* clump. This flexibility in specific site selection may be adaptive, since my limited data on individually marked clumps show that they have a rather high

turnover rate. However, the finches' familiarity with a general area should increase their foraging efficiency, because they will know where food was located in the past.

Laysan Finches do not maintain a type 1 territory, but only defend the nest, nest substrate (*E. variabilis*), and their mates. These behaviors decrease the likelihood of extra-pair copulation and nest parasitism, which I have never observed. Nest parasitism seems unlikely, since females seldom leave their nests once laying begins. However, male parents were frequently absent from the nest site while foraging and had ample opportunity to copulate with females other than their mates.

The lack of a feeding territory is probably related to the scattered temporal and spatial distribution of potential food, as well as the distribution of bunchgrass, the preferred nest substrate. Some of the best feeding areas contained few or no nest substrates; conversely, the second-best nesting area was nearly a monoculture of bunchgrass. The preferred breeding area contained nest substrate plants, as well as a variety of important finch foods, and possibly conferred some microhabitat protection from the elements (Morin 1992).

MORTALITY, ASYNCHRONOUS HATCHING, AND OPTIMAL CLUTCH SIZE

The bias inherent in survival and mortality estimates based on nests found after laying has commenced, or nests found with chicks, has been much discussed in the literature. Briefly, such nests give an overestimate of survival and an underestimate of mortality for offspring. The Mayfield Method and various other modifications have been suggested to correct such nest data (Mayfield 1975, Hensler and Nichols 1981, Bart and Robson 1982, Hensler 1985). In this study, many nests were found before laying began (the "known-size clutch" nests), so that individual eggs and subsequently chicks could be marked and their ultimate fates identified. Comparing unknown-size clutches (Table 6) with known-size clutches (Table 8) demonstrates how uncorrected data from unknown-size clutches inflate the fledging rate and seriously underestimate the number of eggs lost. Also, the number of nests of unknown-size clutches is not representative of the true clutch size distribution. The uncorrected data of Table 6 suggest that there

were relatively fewer three-egg clutches than there actually were (Table 8), and that there were relatively more four- or five-egg clutches in the unknown-size clutches. These discrepancies may be explainable if nests with more nestlings (e.g., four chicks) are noisier and therefore easier to find, or if eggs from larger clutches have better survival.

Death before fledging is the most likely outcome for a Laysan Finch egg. Approximately one-third of all eggs from known-size clutches in any year fledged a chick. The most common fate for the rest of the eggs was to "disappear." Laysan has no mammalian or reptilian predators. Predation on fledglings by Great Frigatebirds (*Fregata minor palmerstoni*) is probable, and egg or chick predation by migratory Bristle-thighed Curlews (*Numenius tahitiensis*) and Ruddy Turnstones (*Arenaria interpres*) is possible, although I have never witnessed it. Walker (1961) has reported seeing a curlew carrying a freshly killed Laysan Finch. Intraspecific egg predation has previously been reported (Dill and Bryan 1912). Many of the eggs in the EGG DISAPPEARED category may have been intraspecifically depredated (Table 7). On one occasion, I saw an unbanded finch eating the contents of a finch egg while carrying it away from one of the study nests. This predation may be a case of interference competition, whereby potential competitors are removed (O'Connor 1984).

In principle, the hatching asynchrony of Laysan Finch eggs seems consistent with the brood reduction model in an unpredictable environment (O'Connor 1984). If the future environment is not predictable at the time an egg is laid, brood reduction (the selective starvation of younger, smaller chicks) may occur during poor conditions. In this way, at least some of the clutch may survive (Lack 1954).

However, my data do not consistently support the brood reduction model, although it may be applicable during some years. During the late 1986 season, a higher percent of eggs from bigger clutches actually fledged than those from smaller clutches (Figs. 9, 10). The 1987 data may appear to support brood reduction, since a lower percent of eggs from four-egg clutches fledged chicks than eggs from three-egg clutches. If brood reduction occurs only in some years, a drought year (like 1987) with limited food would be a likely time to expect it. During 1987, egg weights were also significantly lower in four-egg clutches than in

three-egg clutches (Fig. 5). However, the mean number of hatchlings per nest was the same for both clutch sizes (Fig. 8), suggesting that egg size (and therefore indirectly brood size) may be adjusted by the female's ability to form viable eggs in relation to her nutritional status.

Several studies have shown that nestling survival is related to initial egg size. Slagsvold et al. (1984) found that eggs that did not hatch were significantly smaller than those that did. This could explain why the 1987 four-egg clutches, which had significantly smaller egg weights than the 1987 three-egg clutches, did so poorly (Fig. 8). During 1988, a year that seemed intermediate in both food availability and rainfall (Fig. 2), four-egg clutches had a higher fledging rate than three-egg clutches (Figs. 8, 9). The 1988 mean egg mass from four-egg clutches also tended to be heavier than the mean from three-egg clutches (Fig. 5). These fledging trends are not surprising if the relationship of mean egg mass between three- and four-egg clutches in the different years are reexamined.

Why is the overall modal clutch size three eggs, when in two out of the three years (1986 and 1988) there tended to be a higher percent of eggs from four-egg clutches that produced fledglings? If 1987 was a poor year due to the drought, it may be that the optimal clutch size in a poor year (three eggs) is smaller than the optimal clutch size in good years (four or five eggs; Figs. 8, 9). In late 1986 and all of 1988, the average three-egg clutch fledged 1.29 and 0.73 chicks per nest, respectively. The average four-egg clutch in late 1986 fledged 2.27 chicks per nest, and in 1988 1.4 chicks per nest. In contrast, three-egg nests in 1987 fledged 1.0 chick per nest, and four-egg nests fledged only 1.2. The advantage to the parents for expending the extra energy for the fourth egg in 1987 appeared to be minimal; however, it did not appear to decrease their immediate fitness. As discussed earlier, Laysan Finch females lay a smaller total egg mass per clutch (less than 50% of female body weight) than the 100% of female body weight expected (Amadon 1943, Rahn et al. 1975), so laying an extra egg may represent a relatively small investment. However, in good years, there is an advantage to laying a larger clutch, because more fledglings per nest attempt will be produced (Fig. 8).

A similar situation has been described by Boyce and Perrins (1987) for Great Tits in a fluctuating environment. They suggested that in the long run

it is advantageous for tits to lay clutches smaller than the largest possible clutch size. This strategy may be illustrated in the Laysan Finch by the fledging success in clutches of five. During a good breeding season (late 1986), the two five-egg clutches were the most productive, but during a representative year (1988), fledging success in the two five-egg clutches was as poor as the success from two-egg clutches (Fig. 8). Murton and Westwood (1977) believed that the optimal clutch size is always smaller than the largest possible clutch size, and that the most frequent clutch size is that which on the average gives the most survivors. Although there may be selection on Laysan Island against four- and five-egg clutches in the poorest years, counter selection during the best years probably keeps the clutch size from stabilizing at three. This suggests that demanding environmental conditions (e.g., droughts) may be a fairly common occurrence.

Although there are only anecdotal supporting observations, it seems likely that high ambient temperatures, intense isolation and low wind speed may sometimes cause such extreme ground level heating of the sandy Laysan substrate that bigger broods with older nestlings may become seriously heat stressed. Several times chicks were seen panting in crowded nests, and upon being handled, were found to be unusually warm. It seems likely that occasional heat stress also places an upper limit on clutch size, at least in some years. Although Laysan is rather desert-like, the finch has apparently not evolved unusual heat tolerance (Weathers and van Riper 1982), even though it has a reduced basal metabolic rate and reduced evaporative water loss, which are both adaptations associated with dry environments.

COMPARISON WITH OTHER HAWAIIAN HONEYCREEPERS

Laysan Finches are grouped taxonomically with the other finch-billed Hawaiian honeycreepers. The Nihoa Finch is certainly the most closely related, but little is known about its breeding biology. Recently it has been suggested that another honeycreeper, the Palila (*Loxioides bailleui*), is congeneric with the Laysan Finch (Johnson et al. 1989). The breeding biology of the Palila (van Riper 1978, Pletschet and Kelly 1990) and the Laysan Finch are similar in many aspects. Both species have: (1) long breeding seasons apparently tied to food resources as well as photoperiod, (2) courtship (and chick) feeding by

regurgitation, (3) mate and nest guarding rather than traditional territory defense, (4) year-to-year nest area fidelity, (5) female-only incubation, (6) similar incubation length, (7) similar age at fledging, and (8) an extended period during which the fledglings are dependent on their parents (about a month). The species differ in modal clutch size (two eggs for Palila and three for Laysan Finch), degree of nest sanitation (Laysan Finches remove fecal sacs for a larger proportion of the nestling phase), and participation in nest construction (only female Laysan Finches construct the nest, whereas Palila of both sexes do so; van Riper 1978). Other than the Hawaii 'Akepa (L. Freed, pers. comm.), the Laysan Finch is the only Hawaiian honeycreeper for which the female alone is reported to construct the nest. In this regard, only the Hawaii 'Akepa and the Laysan Finch (and possibly the extinct Greater Koa-finch, *Rhodacanthis palmeri*; Perkins 1903) are known to be similar to the cardueline finches. However, the considerable plasticity in life history parameters of avian taxa makes life history a weak source of evidence for phylogenetic classification.

The phylogenetic relationships among the Hawaiian honeycreepers are still unclear, as are many aspects of their biology. Stochastic weather events and predation are probably the two major factors currently limiting Laysan Finches, in contrast to most of the other Hawaiian honeycreepers, whose populations are limited primarily by past and present human activities.

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