LAYSAN FINCH NEST CHARACTERISTICS, NEST SPACING AND REPRODUCTIVE SUCCESS IN TWO VEGETATION TYPES[1]

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Abstract. The typical Laysan Finch (*Telespiza cantans*) nest on Laysan Island is composed primarily of the bunchgrass *Eragrostis variabilis,* and is hidden from view within a bunchgrass clump. About one-third of the nests have two or more plants species in the nest substrate and canopy. Nests are usually in the lower two-thirds of the bunchgrass clump, and in the lee of the prevailing winds. The dimensions of nests and nest substrates were compared between the predominant vegetation associations: bunchgrass and viney. Almost all nests occurred in these two associations. Nests in the bunchgrass association had more of their canopies composed of a single plant species, had substrates with greater maximum heights, had more cover over the nest cups, and had wider outer nest diameters. Nine other nest and nest substrate variables showed no difference between the two vegetation types, nor did clutch size and fledging success differ significantly, although evidence suggested that fledging success may differ for early (or late) season nesters.

Nearest-neighbor distances of simultaneously active nests were larger in the bunchgrass association than in the viney, and nest densities were approximately half. Nests were relatively more aggregated in the viney association. The viney association occupies half as much total area as the bunchgrass association, but it appears to be the most productive per unit area for nesting. The rapid invasion over the past 29 years by a non-native bush (*Pluchea indica*) into this important vegetation association warrants further study into the possibility of vegetation control.

Key words: Hawaiian honeycreeper; Laysan Finch; Drepanidinae; nest-site selection; nest density; nearest-neighbor distance; non-native vegetation; endangered species.

INTRODUCTION

The Laysan Finch (*Telespiza cantans*) is an endangered, endemic Hawaiian honeycreeper that currently occurs naturally only on the uninhabited, 187-hectare island of Laysan in the Hawaiian Archipelago. Although this population has extreme fluctuations (Dennis et al. 1991, Morin 1991), the average population size is about 10,000 (USFWS 1984). A much smaller, introduced population also occurs on Pearl and Hermes Reef, but that population was not a part of this study.

Laysan Finches defend nest sites during breeding but do not defend larger foraging territories. Therefore, nests can be close together and birds forage near other nests. In a previous paper (Morin and Conant 1990), it was documented that on Laysan Island the finches show a striking dependence on a single plant species, the bunchgrass *Eragrostis variabilis,* as a nest substrate, as has been noted by others (Crossin 1966, Ely and

Clapp 1973, Sincock and Kridler 1977). Otherwise, their nesting habits have been little studied.

The location, spacing, and composition of avian nests profoundly affect the microclimate in which the egg develops (Drent 1983), as well as the egg's subsequent success (Rendell and Robertson 1989). Numerous factors influence nest characteristics and site choice, e.g. prevailing winds (Ferguson and Siegfried 1989), the density of vegetation (Leonard and Picman 1987), the distribution of available nest sites (Hagan and Walters 1990, Kerpez and Smith 1990), and intra- and interspecific competition (Rendell and Robertson 1989). Many recent studies have attempted to summarize specific habitat attributes that are correlated with nest sites selected by various species (Burger and Gochfeld 1988, McAuliffe and Hendricks 1988, McCallum and Gehlbach 1988, Rendell and Robertson 1989). My objectives were to describe the nest characteristics, nest spacing, and relative reproductive success for Laysan Finch nests in the two major vegetation associations on Laysan Island, so that nest site selection could be better understood for this species.

Laysan was severely affected by humans in the

early part of this century (Ely and Clapp 1973). Although the vegetation has recovered substantially, non-native plants and invertebrates are present on this remote island and some are spreading (Newman 1988). These non-natives may exert long-term effects on the finches and their habitat. To assure that enough suitable nest sites remain available, the typical nest characteristics and distribution must be known. This knowledge is particularly important for an endangered species such as this, which has a restricted natural distribution on one small, remote island.

METHODS

Except for a few early-1986 nests that were in the northeastern area of the island, all nests in this 1986-to-1988 study were located in the primary study area (Fig. 1) on the northwestern side of the island. Most nests were located fortuitously during random walks while feeding observations were being recorded. Some nests were found while *en route* to check previously discovered nests. The behavior of the adult pair was the most common cue used to locate nests.

During each of the three field seasons, the plant substrate for each nest was recorded, as well as the vegetation association in which the nest occurred. The substrate was defined as the plant that the nest was resting upon. I recognized five vegetation associations, similar to Newman's (1988) and Lamoureux's (1963) systems. The two predominant vegetation associations are: (1) the *Eragrostis variabilis* bunchgrass association (Newman's *Eragrostis* Grassland and *Eragrostis* Mix, and Lamoureux's *Eragrostis* Association); and (2) the *Ipomoea-Boerhavia-Sicyos* viney association (Newman's *Ipomoea* Dominant and *Sicyos* associations, and Lamoureux's *Boerhavia-Ipomoea-Tribulus* Association). Individual *Eragrostis* plants also occur as a subdominant component in some areas of the *Ipomoea-Boerhavia-Sicyos* association. Based on regular feeding observations made concurrently in the same areas of all five vegetation associations in each year, I found that the vast majority of the nests occurred in the two main vegetation types, which I refer to as "bunchgrass" and "viney," respectively. The few nests outside these two associations, or on the border between two or more associations, were classified as "mixed." Because so few nests occurred outside the two primary associations, I concentrated my 1987 and 1988
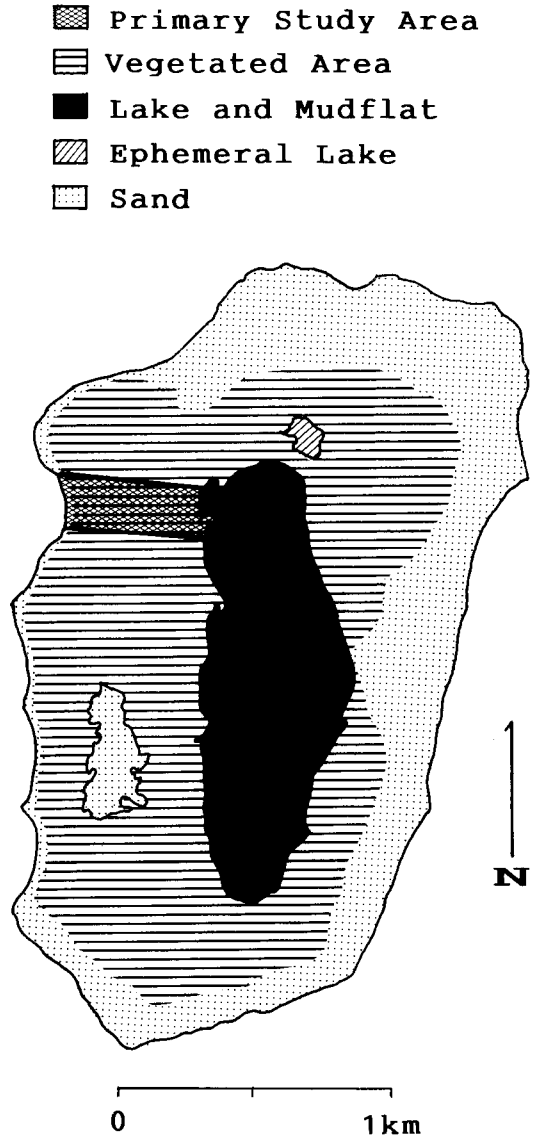

▨ **Primary Study Area**

▤ **Vegetated Area**

■ **Lake and Mudflat**

▨ **Ephemeral Lake**

▢ **Sand**

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

efforts in a study area containing only those two associations.

NEAREST-NEIGHBOR DISTANCES AND NEST DENSITY ESTIMATES

Accurate maps were drawn of all nests known to have had eggs during the 1987 and 1988 field seasons. The only concrete pillar on Laysan (a U.S. Geological Survey bench mark) was the origin point for each map. Laysan is relatively flat

(Ely and Clapp 1973), so elevational corrections were not made during map construction.

Graphs of simultaneously active nests were made for 1987 and 1988. A nest was considered active from the day that the first egg was laid until the last chick left the nest, or until the nest failed. If a nest was discovered with chicks, the nest's active period was calculated backward based on the apparent age of the chicks. For each year, the day with the most simultaneously active nests was selected as the peak day of breeding. The distances between nearest active nests on that day was used to calculate nearest-neighbor distances (Clark and Evans 1954) within the two main vegetation types, as well as average nearest-neighbor distance for both vegetation types combined. The few nests categorized as being from a mixed vegetation association were lumped into the same vegetation category as their nearest neighbor.

Using the scaled maps, a grid of 10 m × 10 m squares (0.01 ha per square) was superimposed over the study area, and the total area searched intensely during each year was estimated in hectares. The bunchgrass area intensely searched in 1987 was 7.16 ha, and in 1988 it was 8.16 ha. The viney area searched was a constant 1.28 ha in both years. For each year, the number of simultaneously active nests within each vegetation association in the intensely searched area was used to calculate the peak density within each association. Calculations of nest density were based on the assumption that all simultaneously active nests within the intensely searched area were located. This assumption was later shown not to be completely accurate, based on the ages of some nestlings that were later located in the searched area.

Using a Bryan Modified Acreage Grid (Mosby 1980) on Newman's (1988) 1984 vegetation composition map, I estimated the total hectares on Laysan for both the *Eragrostis* and the *Ipomoea-Boerhavia-Sicyos* vegetation associations, since such estimates were not otherwise available.

NEST CHARACTERISTICS

During the 1987 field season, especially detailed observations were made on the first 85 nests or nest-like formations located in the study area. This subset will be referred to as "intensely described nests." Only 68 of these 85 nests were

eventually finished and contained eggs; the other 17 nests are excluded from all the analyses. Data from these 68 active nests included: visual estimate of percent canopy of each plant species in the composite nest substrate, size (maximum height and width in cm) of the composite substrate, number of *E. variabilis* clumps in the substrate, inner depth and diameter (cm) of the nest cup, total height and diameter (cm) of the nest, and height of the nest bottom above the ground (cm). When a nest was suspended over the entrance of a seabird nest burrow, the height was measured from the bottom of the nest to the floor of the burrow.

The orientation of a nest in relation to the center of the plant substrate was recorded. For example, blades of *Eragrostis* almost always lean away from the prevailing winds from the northeast, and nests found beneath that overhang were given a southwest heading. Nests that occupied the interior of erect clumps were assigned the orientation category of "None."

The elevation of the nest within the plant substrate was assigned to one of four categories: on the ground, or lower, middle, or upper third of substrate.

The percent cover immediately over the nest cup was measured on the morning a nest was discovered, or on the following morning for nests found in the afternoon. A hand mirror marked with a metric grid was placed directly on the nest cup and the shaded area was estimated. Except for this measurement, the rest of the nest measurements were made either after the eggs hatched but before the chicks were banded (usually when they were 11–14 days old), or as soon as possible after a nest failed.

Nest characteristic variables were examined with multiple analysis of variance and were compared for significant differences between the bunchgrass and viney associations using t-tests or Mann-Whitney tests (SAS 1988).

CLUTCH SIZE AND FLEDGING SUCCESS

The number of eggs per nest and fledging success from known size clutches were compared between the two main vegetation types. Fledging success was defined as the mean number of chicks fledged per nest. A chick was considered fledged if it reached banding age (days 11–14) and was not found dead in or near the nest by fledging

TABLE 1.   Primary plant substrate (with secondary substrate and canopy plants listed in order of decreasing importance) for intensely described nests from 1987.

Substrate (secondary plants)	Frequency
Eragrostis variabilis (no secondary plants)	44
E. variabilis (unknown whether secondary plants included*)	2
E. variabilis (*Ipomoea pes-caprae*)	15
E. variabilis (*I. pes-caprae* and *Sicyos maximowiczii*)	2
E. variabilis (*S. maximowiczii*)	1
E. variabilis (*Cenchrus echinatus*)	1
I. pes-caprae (*E. variabilis*)	2
C. echinatus (*E. variabilis*)	1
Total	68

* Missing data.

age (22–26 days old). Nests which occurred in a mixed vegetation type were excluded from these analyses.

RESULTS

NEST CHARACTERISTICS

The nests were constructed mainly of stems, roots, and blades from the bunchgrass *Eragrostis variabilis,* although sometimes they contained stems of the non-native plant *Cenchrus echinatus.* The finches are open cup nesters, but on Laysan the nests are located within the densest part of the plant substrate and are functionally enclosed. Nests were hidden from view and were almost never (less than 5% of the time) visible without manually searching through the plant substrate.

Of the 68 intensely described nests from 1987, 65 (96%) had *Eragrostis,* one (1%) had *C. echinatus,* and two (3%) had *Ipomoea pes-caprae* as the nest-site substrate. The three nests with non-*Eragrostis* substrates had *Eragrostis* as a significant component on or mixed in the nest substrate. Twenty-two nests had two or more plant species making up part of the substrate or canopy (Table 1). When bunchgrass was the primary plant substrate, but other plants were mixed in or on it, the morning glory vine (*I. pes-caprae*) was the most common secondary plant. The introduced weed *C. echinatus,* and the native cucurbit vine, *Sicyos maximowiczii,* also occurred as primary or secondary substrate plants. In many instances the nest site was a composite of several species of plants and/or several individual plants of the same species.

TABLE 2.   Number of nests in 1986, 1987, and 1988 in each vegetation classification (and subset of nests with known size clutches).

Year	Bunchgrass	Viney	Mixed
1986*	26 (20)	56 (44)	12 (11)
1987	57 (27)	27 (18)	4 (4)
1988	64 (22)	27 (4)	5 (2)

* Includes nests from both the early and late breeding pulses.

In all three years, *Eragrostis* clumps were the preferred nest substrate (Morin and Conant 1990), and almost all nests occurred in the *Eragrostis* or the *Ipomoea-Boerhavia-Sicyos* vegetation associations where the bunchgrass primarily occurs (Table 2). While collecting feeding observations in the other three vegetation associations (*Pluchea, Scaevola,* and *Sesuvium-Heliotropium-Cyperus* associations) outside the primary study area, I also searched for nests with little or no success.

Of the 68 intensely described nests in 1987, 46 (67.6%) were in the bunchgrass association, 18 (26.5%) were in the viney association, and 4 (5.9%) were at the border of the bunchgrass and viney association and were classified as "mixed." These four mixed association nests had their nearest active neighbors in the bunchgrass type.

Nests tended to be beneath the bent, rather than erect, blades of *Eragrostis.* Of the 37 intensely described nests for which I recorded nest orientation, 15 (40.5%) had a southwest orientation (Table 3). Nest orientation was not random with respect to compass direction ($x^2 = 53.25$, df = 8, $P < 0.001$).

The elevation of a nest within its plant substrate was also not random ($x^2 = 25.6$, df = 3, P

TABLE 3.   Frequency of nest orientation. Orientation is significantly different from random ($x^2 = 53.25$, $P < 0.001$).

Compass orientation	Frequency
North	0
Northeast	0
East	2
Southeast	1
South	5
Southwest	15
West	10
Northwest	0
No orientation	4
Total	37 Nests

TABLE 4. Nest characteristic variables and definitions.

PERCENT CANOPY1	Percent of canopy composed of the nest's primary substrate plant.
PERCENT CANOPY2	Percent of the canopy made up of the most abundant plant other than the primary substrate.
TOTAL CLUMPS	Total number of bunchgrass clumps contiguous with the primary nest substrate, and considered part of the composite substrate.
MAJOR CLUMPS	Number of major (mature) bunchgrass clumps in a composite substrate.
MINOR CLUMPS	Number of immature bunchgrass clumps in a composite substrate.
MAXIMUM HEIGHT	Maximum height of the composite substrate (cm).
MAXIMUM WIDTH	Maximum diameter of the composite substrate (cm).
CANOPY OVER CUP	Percent of cover over the nest cup during the morning.
CUP DEPTH	Inner depth of the nest cup (cm).
CUP WIDTH	Inner diameter of the nest cup (cm).
NEST DEPTH	Total height of the nest (cm).
NEST WIDTH	Widest outer diameter of the nest (cm).
NEST HEIGHT	Height of nest's bottom above the ground (cm).

< 0.001). For the 44 nests where I remembered to record nest elevation, four were located in the upper third, 10 in the middle third, and 25 in the lower third of their substrate. Another five nests were on the ground within their nest substrate.

The 13 other nest characteristic variables are defined in Table 4 and summarized in Table 5. Values of these quantitative nest characteristics were compared between the bunchgrass and viney vegetation associations for the 68 intensely described nests from 1987. For this analysis, mixed nests were included with the bunchgrass nests, since they were the nearest active neighbors. A multiple analysis of variance test (MANOVA) indicated that the vegetation association had a significant effect on the character measures (Wilks' Lambda = 0.372, $P = 0.0004$). Only four variables: height of the composite substrate (MAXIMUM HEIGHT), percent of primary plant canopy (PERCENT CANOPY1), percent cover over the nest cup (CANOPY OVER CUP), and outside width of the nest (NEST WIDTH) were significantly different between nests occurring in the two vegetation types (Table 5).

NEAREST-NEIGHBOR DISTANCES AND NEST DENSITIES

In 1987, the peak of simultaneously active nests ($n = 66$ nests in 45 pairs) occurred on 15 June, and in 1988 the peak ($n = 51$ nests in 31 pairs) occurred on 26 May (Figs. 2 and 3, respectively). For both years, nearest-neighbor distances for simultaneously active nests were calculated for the bunchgrass and the viney vegetation types, as well as the two vegetation types combined.

Using the Dixon test for outliers (Sokal and Rohlf 1981), one 1988 active nest was excluded from the analyses as an outlier. In both years, the average nearest-neighbor distance between nests in the bunchgrass association was significantly greater than the average nearest-neighbor distance in the viney association (Table 6).

The average nearest-neighbor distance for combined habitats in 1987 tended to be smaller than in 1988, but this difference was not significant ($t = -1.1004$, df = 74, $P = 0.2747$).

An unbalanced two-way ANOVA with year and vegetation association as treatments revealed that the vegetation association, but not the year nor the interaction of year and vegetation association, had a significant effect on the nearest-neighbor distance (based on 76 observations, $F = 28.65$, $P = 0.0001$).

Figures 4 and 5 show every nest with eggs or chicks observed in the study area during the 1987 and 1988 field seasons, respectively. In each year, the greatest number of simultaneously active nests is fewer than the total nests shown on the map, partly due to non-overlapping renesting attempts. Table 7 summarizes the densities in the two main vegetation types for both years. In 1987 the nest density in the bunchgrass association was about one-half that in the viney association; in 1988, the ratio of bunchgrass to viney nests was even smaller. Thus, the viney association could be at least twice as productive per unit area as the bunchgrass association, (but see Fledging Success below).

I estimated from Newman's (1988) vegetation composition map of Laysan that the entire island had a total of 112.6 ha in the bunchgrass asso-

TABLE 5.   1987 nest variables for both vegetation associations, separately and combined, and results of t-tests or Mann-Whitney tests between the associations. Variables defined in Table 4.

Variable		Combined	Bunchgrass	Viney	Test parameter	P
PERCENT	Mean	90.38%	95.61%	75.29%	$Z = -5.726$	0.0001
CANOPY1	SD	19.24	14.99	22.46		
	n	66	49	17		
	Median		100%	85%		
PERCENT	Mean	28.41%	35.00%	25.94%	$Z = 0.890$	0.374
CANOPY2	SD	23.72	28.81	22.08		
	n	22	6	16		
	Median		0%	15%		
TOTAL	Mean	1.89	2.02	1.53	$Z = -1.604$	0.109
CLUMPS	SD	0.96	1.03	0.62		
	n	66	49	17		
MAJOR	Mean	1.35	1.41	1.18	$Z = -1.259$	0.208
CLUMPS	SD	0.59	0.64	0.39		
	n	66	49	17		
MINOR	Mean	0.55	0.61	0.35	$Z = -0.900$	0.368
CLUMPS	SD	0.83	0.89	0.61		
	n	66	49	17		
MAXIMUM	Mean	90.77 cm	93.69 cm	82.35 cm	$t = 2.292$	0.025
HEIGHT	SD	18.15	18.43	14.73		
	n	66	49	17		
MAXIMUM	Mean	149.83 cm	153.69 cm	138.71 cm	$t = 1.291$	0.201
WIDTH	SD	41.45	41.66	39.98		
	n	66	49	17		
CANOPY	Mean	82.75%	85.73%	74.35%	$Z = -2.137$	0.033
OVER CUP	SD	17.05	14.68	20.69		
	n	65	48	17		
	Median		92%	84%		
CUP	Mean	3.83 cm	3.80 cm	3.92 cm	$t = -0.410$	0.684
DEPTH	SD	0.85	0.87	0.85		
	n	44	32	12		
CUP	Mean	7.08 cm	7.13 cm	6.94 cm	$t = 0.733$	0.467
WIDTH	SD	0.76	0.73	0.85		
	n	44	32	12		
NEST	Mean	6.88 cm	6.91 cm	6.82 cm	$t = 0.169$	0.867
DEPTH	SD	1.60	1.71	1.35		
	n	44	32	12		
NEST	Mean	15.78 cm	16.40 cm	14.11 cm	$t = 2.786$	0.008
WIDTH	SD	3.39	3.65	1.77		
	n	44	32	12		
NEST	Mean	12.26 cm	11.64 cm	14.03 cm	$Z = 0.879$	0.379
HEIGHT	SD	9.24	9.12	9.78		
	n	46	34	12		

ciation and 50.8 ha in the viney association. Using my density estimates from both years, I calculated minimum estimated numbers of nests island-wide at the peak of the breeding season for each vegetation type and for both types combined for the whole island (Table 7). I consider these to be minima because I know from other observations that I did not detect every active nest.

Clark and Evans (1954) showed how the nearest-neighbor distances, r_a, could be used as a measure of spatial relationships. In this case, if r_e is the mean nearest-neighbor distance expected between nests in an infinitely large random distribution of nests with density rho, and given that $R = r_a/r_e$, then $R = 1$ in a random distribution, and $R = 0$ in a maximally aggregated distribution. In 1987, R was 0.85 for nests in the bunchgrass association, and 0.67 for nests in the viney association. In 1988, R was 0.83 for the

TABLE 6. Nearest-neighbor distances (meters) for simultaneously active nests in two vegetation associations, separately and combined. Mean distances compared (*t*-tests) between bunchgrass and viney associations within each year.

Year		Combined	Bunchgrass	Viney	*t*	*P*
1987	Mean	13.11 m	15.29 m	8.29 m	4.35	0.0001
	SD	6.88	6.86	3.88		
	n (pairs)	45	31	14		
1988	Mean	15.10 m	18.60 m	7.77 m	3.83	0.0006
	SD	8.87	8.25	4.77		
	n (pairs)	31	21	10		

bunchgrass nests and 0.57 for the viney association nests.

FLEDGING SUCCESS IN RELATION TO HABITAT TYPE

Mann-Whitney tests indicate no significant difference between average clutch size (using only known size clutches) in the bunchgrass versus the viney vegetation association during any year (Table 8). Nests categorized as mixed vegetation association were not used in these analyses.

There was no significant difference in the average number of fledglings per nest between the two vegetation associations for 1987 or 1988 (Table 9). Nests with clutches of unknown size and nests in the mixed vegetation category were excluded from these analyses. In 1986 there were significantly more fledglings per nest in the bunchgrass association when compared with the

FIGURE 2. Number of simultaneously active nests in the study area during the 1987 field season.

viney association (1.6 per nest versus 0.7 per nest; Mann-Whitney test, $Z = 2.108, p = 0.035$). However, these data were combined from two breeding peaks observed that year (Morin, unpubl. data); when the two peaks were examined separately (as "early" and "late"), there was no significant difference between the fledging success per nest in the two vegetation associations (Table 9). The only fledgling from an early 1986 nest of known clutch size occurred in the viney association. The few other fledglings seen immediately after the early peak of breeding in 1986 all occurred in, or next to, the viney plant association. There were few nests in the bunchgrass association in early 1986.

DISCUSSION

NEST CHARACTERISTICS

The inner nest cup and outer nest dimensions in this study (Table 5) are similar to measurements taken by Crossin (1966) on seven Laysan Finch nests (his averages: 5.3 cm inner cup death, 7.4 cm inner cup diameter, 6.9 cm outer nest height, and 13.7 cm outer nest diameter). Van Riper's (1980) measurements on 26 nests of a closely related Hawaiian honeycreeper, the Palila (*Loxioides bailleui*), also are similar to nests from this study (his averages: 3.9 cm inner cup depth, 7.4 cm inner cup diameter, 7.7 cm outer nest height, and 14.7 cm outer nest diameter). In the past, the Palila has been considered congeneric with the Laysan Finch (AOU 1983). Neither Crossin nor van Riper identified the ages of nests they measured. Age differences may account for Crossin's generally larger inner nest cup measurements, since the nest cup changes in size and shape as the nestlings age (pers. observ.). The Palila is a slightly larger bird than the Laysan Finch, and a larger nest cup is expected.

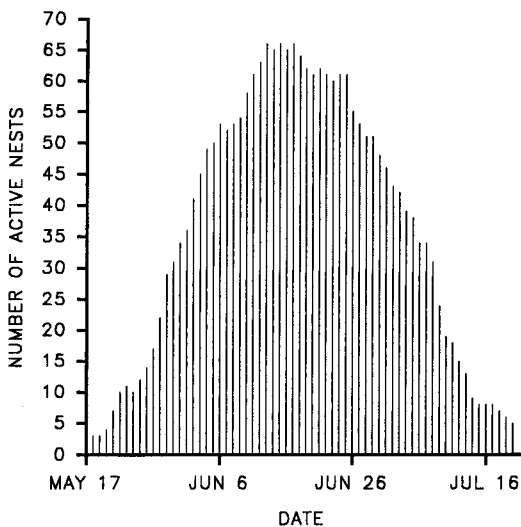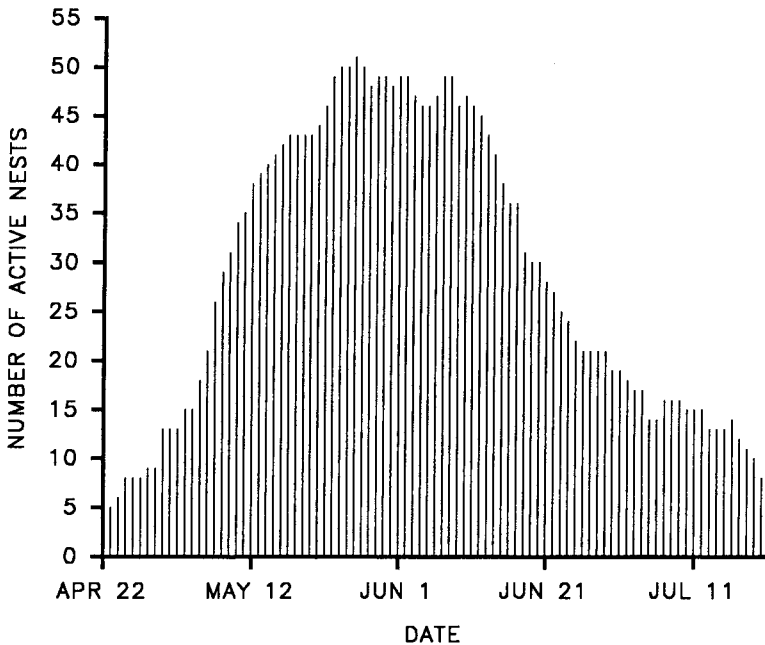Crossin's observations (1966), as well as those

FIGURE 3.   Number of simultaneously active nests in the study area during the 1988 field season.

of this study, confirm the Laysan Finch's proclivity for nesting in dense vegetation, presumably for thermal buffering (Weathers and van Riper 1982) and possibly for concealment from avian predation (Morin and Conant 1990). The high percent of cover over the nest cup (CANOPY OVER CUP) and the height of the nest above the ground (NEST HEIGHT) in proportion to the height of the nest substrate (MAXIMUM HEIGHT; Table 5) provide such protection and concealment. Others have recognized that nest orientation could influence thermal regulation: e.g., by facing into or away from the sun, or by facing into or away from prevailing winds, nests may be warmed or cooled (Burger and Gochfeld 1981, Drent 1983). Prevailing winds on Laysan blow from the east and northeast. The nests in this study (Table 3) tended to be built underneath the southwestern side of overhanging bunchgrass canopies. This orientation provided these nests with shade from morning and noon sun, as well as protection from direct exposure to prevailing winds. In addition, grass blades that bend (in any direction) provide better protection from heavy rainstorms than do erect blades.

Laysan Finches have a prolonged breeding season, so it is clearly advantageous to position nests where they will receive minimal environmental wear, as has been suggested for other species (Collias and Collias 1984, Ferguson and Siegfried 1989). They also roost in *Eragrostis* clumps, and although adult Laysan Finches have never been observed roosting in old nests, hatch-year birds have infrequently been seen resting in them.

In a recent study of Palila on Mauna Kea on Hawaii Island (Pletschet and Kelly 1990), nests in widely spaced, large trees were more successful than nests in closely spaced, smaller trees. The authors suggested that some extrinsic factor (such as cat and rat predation) made the larger trees better nest sites. They did not discuss the possibility that thermal or mechanical weather effects (e.g., high winds) could also heavily influence nest success in large versus small trees. Larger trees are generally more rigid than smaller trees and could provide more stability and less movement during high winds, which sometimes reach 120 km/hr or more near the summit of Mauna Kea.

High winds also occur on Laysan; in 1986, winds of at least 97 km/hr occurred during a February gale storm. Although a few non-native trees do occur on Laysan, none are used for nesting by Laysan Finches. By nesting and roosting close to the ground in the densest vegetation, the finches are less vulnerable to high winds.
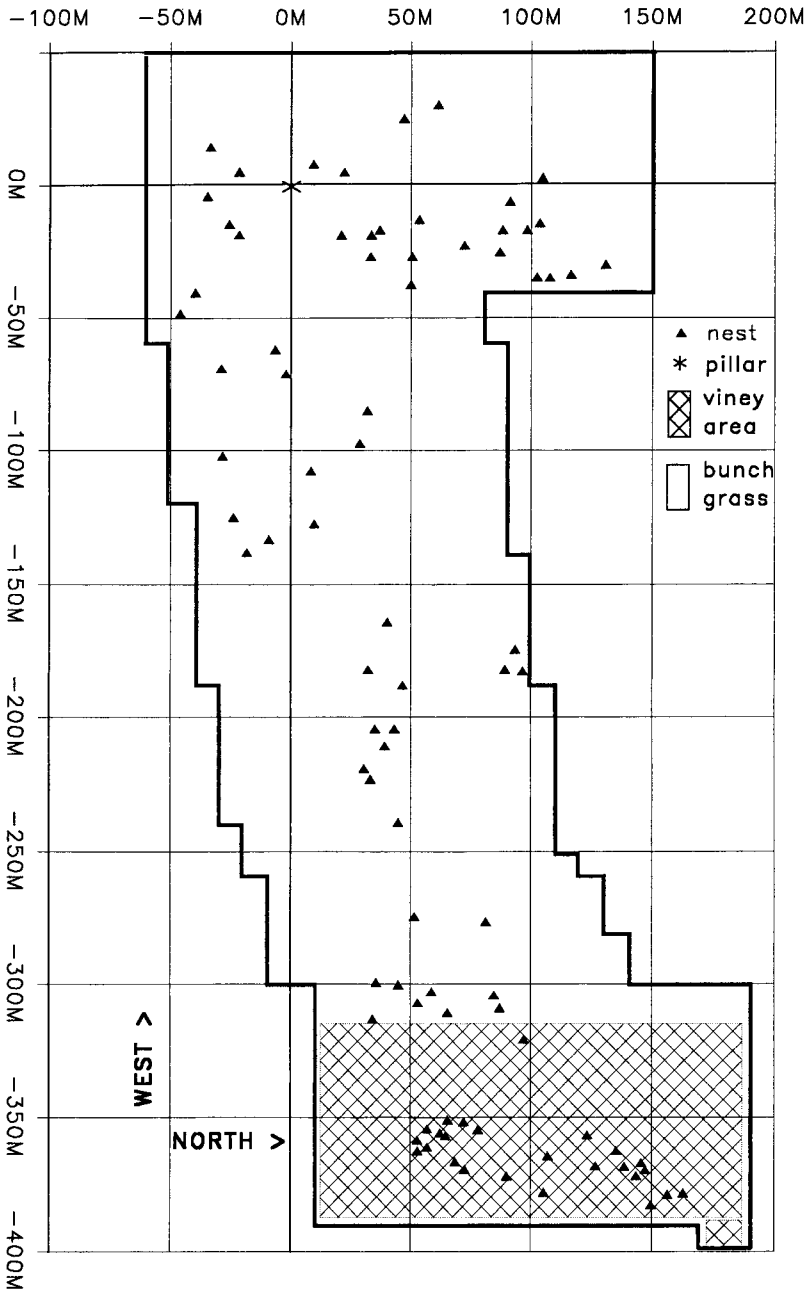
FIGURE 4.   1987 map from Laysan study area showing nest locations.

Laysan Finch nest characteristics appear to have minor differences between nests in the bunchgrass and in the viney associations. One might expect larger, seemingly better insulated substrates and nests to provide more thermal buffering and hence afford higher nest success. Counterintuitively, there was no difference in nest success between the two vegetation types, despite the taller substrate height, higher percent of cover over the nest cup, higher percent canopy of the
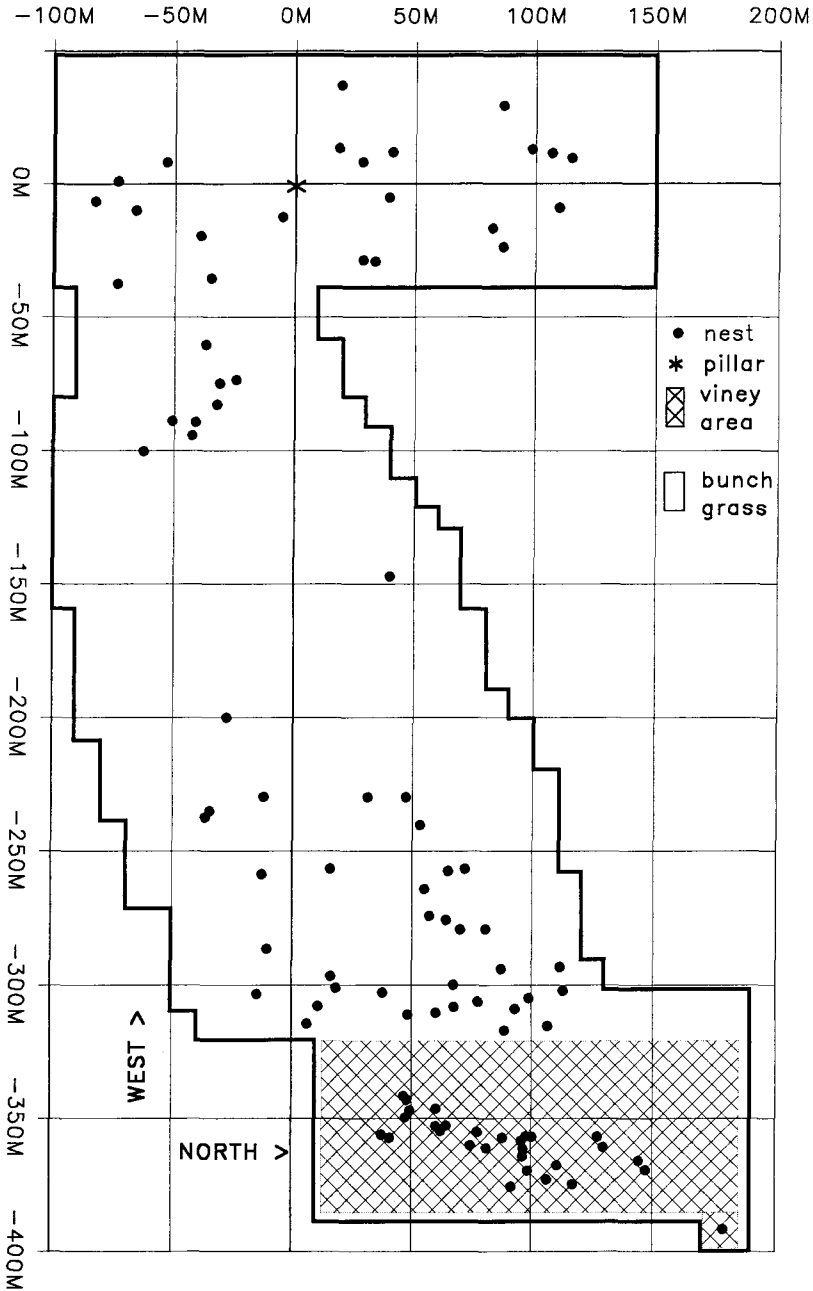
FIGURE 5.   1988 map from Laysan study area showing nest locations.

primary nest substrate, and wider outer nest diameter in the bunchgrass association (Table 5).

The greater substrate height (MAXIMUM HEIGHT) and cover over the nest cup (CANOPY OVER CUP) in nests from the bunchgrass association probably reflects an overall larger growth form of bunchgrass in that association, where vegetation in general tends to be spaced farther apart than it is in the viney association. The larger percent of primary plant canopy

TABLE 7. Density of simultaneously active nests in the study area for two vegetation types, and estimated total active nests island-wide on date of breeding peak.

Date	Combined	Bunchgrass	Viney
15 June 1987			
Simultaneously active nests	66	45	21
Hectares in study area	7.16	5.88	1.28
Nests/ha in study area	10.37*	7.65	16.41
Estimated ha island-wide	163.4	112.6	50.8
Estimated island-wide number of nests	1,695	862	833
26 May 1988			
Simultaneously active nests	51	34	17
Hectares in study area	8.16	6.88	1.28
Nests/ha in study area	7.53*	4.94	13.28
Estimated ha island-wide	163.4	112.6	50.8
Estimated island-wide number of nests	1,231	556	675

* Weighted mean number of nests/ha.

(PERCENT CANOPY1) in the bunchgrass association is an inevitable result of the fact that fewer nest substrates in the viney association were 100% *Eragrostis*. The larger outside nest width (NEST WIDTH) for nests in the bunchgrass association may simply occur because more nesting material is available there, especially since nest densities were lower in that association relative to the viney association. However, these divergent nest characteristics did not appear to be correlated with measurable differences in nest success during this study. If the microclimate of the bunchgrass association generally has a higher temperature due to its expanses of nonvegetated sand, or greater wind exposure due to its proximity to the ocean, then possibly the thicker nests and taller, denser-canopied nest substrates are needed in that association in order to successfully fledge chicks.

TABLE 8. Mean clutch size in both vegetation types for 1986 to 1988 and results of Mann-Whitney tests for differences.

Year		Bunch-grass	Viney	Z Value	P
1986	Mean	3.4	3.0	1.6278	0.1036
	SD	0.75	0.70		
	n	20	44		
1987	Mean	3.0	3.1	0.4217	0.6733
	SD	0.58	0.82		
	n	28	18		
1988	Mean	3.5	3.75	0.3817	0.7027
	SD	0.80	0.96		
	n	22	4		

NEAREST-NEIGHBOR DISTANCES, NEST DENSITY, AND FLEDGING SUCCESS

Warkentin and James (1988) felt that nest site selection, and hence spacing, could not be understood without knowing a species' territoriality. Similarly, Haila (1988) concluded that erroneous determinations of territory and home range in fragmented habitats could have serious consequences on estimates of density. Ripley (1985) considered that analysis of nest patterns was at or beyond the current limits of knowledge due to edge effects and the patchy nature of habitats. Notwithstanding such pessimism and because the vegetation associations are fairly discrete on Laysan, I have attempted to describe characteristic nest spacing for Laysan Finches using nearest-neighbor distances and densities, acknowledging that all habitats are patchy and heterogeneous at some level. For example, in the primary study area (Figs. 4, 5), nests in the viney association are clustered at the eastern side, probably due to an almost total lack of *Eragrostis* on the western side. However, the average number of bunchgrass clumps per unit area seems to be the same in both the viney and the bunchgrass associations (Morin and Conant 1990).

Laysan Finches do not defend a traditional territory, but forage away from the nest. Nests are often in close proximity to one other. In 1988, two simultaneously active nests were only 2.24 m apart. This is very similar to the typical "1–2 m between clumps" that Newman (1988) reported in her description of *Eragrostis* clump distribution. The R values (Clark and Evans 1954)

TABLE 9.   Average number of fledglings per nest (known-size clutches only) in each vegetation association in all three years and Mann-Whitney test results. Nests categorized as "mixed" association were not used.

Year		Bunchgrass	Viney	Z Value	P
Early 1986	Mean	0.00	0.05	−0.3814	0.7029
	SD	0.0	0.213		
	n	5	22		
Late 1986	Mean	2.13	1.41	1.5416	0.1232
	SD	1.506	1.297		
	n	15	22		
1987	Mean	1.04	0.44	−1.6149	0.1063
	SD	1.170	0.705		
	n	28	18		
1988	Mean	0.64	1.50	1.5078	0.1316
	SD	1.093	1.291		
	n	22	4		

of 0.67 and 0.57 for the viney association, and 0.85 and 0.83 for the bunchgrass association in 1987 and 1988, respectively, suggest that the nests are slightly more aggregated in the viney association. However, in both plant associations nests are more randomly spaced rather than aggregated. The tendency toward aggregation in the viney association may simply reflect the spatial distribution of appropriate nest substrates (i.e., bunchgrass clumps). Rendell and Robertson (1989) have suggested a similar explanation for the spacing of secondary hole-nesting birds because of the spatial dispersion of natural cavities.

Nearest-neighbor distances and density estimates from this study suggest that the viney association on Laysan usually has at least twice as many nests per unit area as the bunchgrass association (Tables 6 and 7). But why should the viney area have a higher nest density and appear to be a preferred vegetation type for nesting, even though the average clutch size per nest (Table 8) and the average number of fledglings per nest (Table 9) were not significantly different in the two vegetation associations? There are at least three possible explanations for the apparent preference for the viney association. First, the proximity of good foraging areas may influence nest site selection, allowing pairs to nest more densely and thus expend less time and energy foraging for food. The western side of the viney area at the primary study site was a popular finch foraging ground, partly because the native cucurbit vine (*S. maximowiczii*) and other heavily utilized food plants were usually abundant. The *Sicyos* fruit, as well as the numerous invertebrates on *Sicyos* and *Ipomoea* (morning glory) leaves,

seemed to be an important source of food for nestlings (Morin, pers. observ.).

Secondly, the viney association may be preferred because some characteristic of the habitat leads to increased fledging success there during breeding peaks very early or late in the season under marginal weather conditions. I was able to witness an early breeding peak only in 1986. After that peak, the viney area was the only vegetation association where a few fledglings were found. The few nests I found in the bunchgrass association during that early season produced no young. The topography of the island somewhat protects the innermost rings of vegetation around the lake (e.g., viney association) from the typical heavy wind and rain of winter storms; this may explain the differential nesting success (Table 9). Over time, selection would favor birds that nested in the more protected area.

A third possible explanation for the observed nest spacing is habitat constraint, such as availability of preferred nest sites (Rendell and Robertson 1989, Hagan and Walters 1990). However, the density of bunchgrass clumps is thought to be similar in the two associations, and few of the substrate measurements were significantly different. The absolute density of apparently suitable bunchgrass clumps seems high enough to be nonlimiting; on average there are approximately 35 bunchgrass clumps available to each Laysan Finch (Morin and Conant 1990). This suggests that other factors, such as the two mentioned above, may be more likely causes for the nest distribution. However, if the topography if the viney area is more protective, or foraging areas in or near the viney area are better, then nest

sites may in fact be limited in the viney area. In that case, at some threshold density, finches may be at a selective advantage if they nest in the less preferred bunchgrass association, especially if higher nest densities in the viney association facilitate predation on finch eggs.

From observations and assumptions elaborated upon elsewhere (Morin 1991), I have estimated that each year only about 60% of the nests that were active in the study area were found.

The apparent decline in nest densities between 1987 and 1988 (Table 7) coincides with a reduction in the finch population during that same time period (Morin and Conant, unpubl. data).

It is apparent that at the peak of breeding in both years, the much smaller area of viney habitat (an estimated 50.8 ha for the entire island) is as important for overall potential finch recruitment as the larger bunchgrass habitat (an estimated 112.6 ha; Table 7). The estimated number of total nests on the day of peak nest activity was almost the same in the two vegetation types, even though the total hectares of viney habitat is only half as large as the bunchgrass association.

Results of this study indicated few differences between nest sites in the viney and bunchgrass associations. It remains unclear why finch nest counts and nearest-neighbor distances from 1987 and 1988 indicated higher densities in the viney association, even though average clutch size and observed fledging success per nest in those two years were not significantly different between the two vegetation types.

MANAGEMENT IMPLICATIONS

The data illustrate the importance of the viney association to overall finch nesting and recruitment. The rapid spread of the non-native *Pluchea indica* shrub over the past 29 years along the lake shore (Newman 1988) is of concern; this shrub has invaded and is currently invading areas that were previously viney habitat. Despite many hours spent in the *Pluchea* association, I have never found a Laysan Finch nest in a live *Pluchea* shrub. The rapid spread of this plant into the important nesting habitat for the endangered Laysan Finch certainly deserves further study, and probably vegetation control.

Another accidentally introduced non-native plant, the sandbur *Cenchrus echinatus,* is currently being eradicated in the bunchgrass association. This aggressive weed is also competing

with native vegetation important to the finches for food and nest sites (Morin and Conant 1990).

Long-term protection of the nesting habitat from invading, non-native species should be a priority action for preserving this endangered species in situ.

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