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BREEDING BIOLOGY OF THE BROWN NODDY ON TERN ISLAND, HAWAII

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ABSTRACT.—We observed Brown Noddy (*Anous stolidus pileatus*) breeding phenology and population trends on Tern Island, French Frigate Shoals, Hawaii, from 1982 to 1992. Peaks of laying ranged from the first week in January to the first week in November; however, most laying occurred between March and September each year. Incubation length was 34.8 days (N = 19, SD = 0.6, range = 29–37 days). There were no differences in breeding pairs between the measurements of the first egg laid and successive eggs laid within a season. The proportion of light- and dark-colored chicks was 26% and 74%, respectively (N = 221) and differed from other Brown Noddy colonies studied in Atlantic and Pacific oceans. The length of time between clutches depended on whether the previous outcome was a failed clutch or a successfully fledged chick. Hatching, fledging, and reproductive success were significantly different between years. The subspecies (*A. s. pileatus*) differs in many aspects of its breeding biology from other colonies in the Atlantic and Pacific oceans, in regard to year-round occurrence at the colony, frequent renesting attempts, large egg size, proportion of light and dark colored chicks, and low reproductive success caused by inclement weather and predation by Great Frigatebirds (*Fregata minor*). *Received 31 Mar., 1995, accepted 5 Dec. 1995.*

The Brown Noddy (*Anous stolidus*) is the largest and most widely distributed of the tropical and subtropical tern species (Cramp 1985). The breeding biology of the nominate subspecies *A. s. stolidus* has been studied extensively in its Atlantic range (Dorward and Ashmole 1963, Robertson 1964, Morris and Chardine 1992); however, few studies exist for *A. s. pileatus* which ranges over most of the Pacific and Indian oceans (Cramp 1985). Brown (1973, 1977) published most of the information on Brown Noddies breeding in the Hawaiian Islands; however, his observations spanned only two breeding seasons. Here, we present observations of the breeding biology of this species in the Northwestern Hawaiian Islands, the northern-most part of its range, and compare it to previous reports from other Hawaiian Islands and with observations of the biology of the subspecies *A. s. stolidus* in the Atlantic Ocean.

STUDY AREA AND METHODS

French Frigate Shoals is a crescent-shaped atoll situated approximately midway in the Hawaiian Archipelago (23°45′N, 166°17′W) and is part of the Northwestern Hawaiian Islands National Wildlife Refuge administered by the U.S. Fish and Wildlife Service (USFWS). The atoll contains 10 well-established islands and as many as nine sandy islets that are seasonally awash (Fig. 1). Tern Island, located near the northwestern tip of the atoll,

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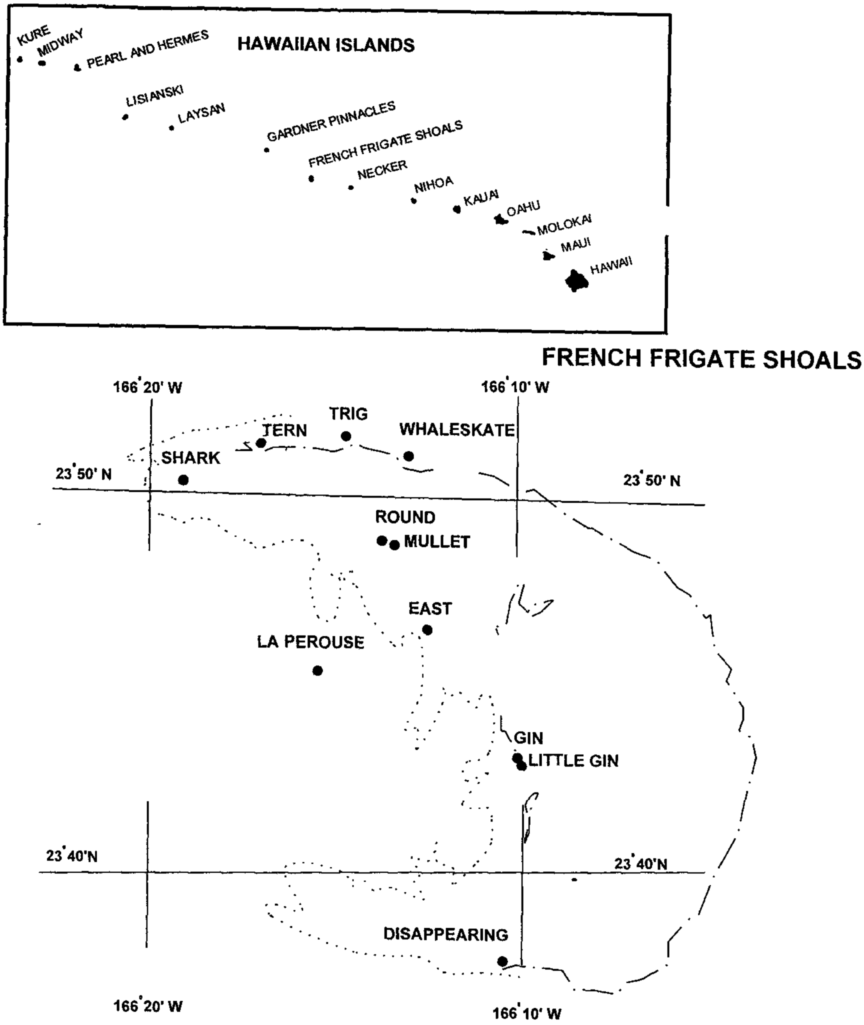

FIG. 1. French Frigate Shoals, with insert of the Hawaiian Islands.

is the largest island and the only human-made island at French Frigate Shoals. Originally 4.4 ha in size, the island is now approximately 15.0 ha, measuring 945 m in length and 99.1 m wide (Amerson 1971, USFWS unpubl. data). The island was expanded to accommodate military operations during the 1940s. An active, crushed-coral runway, approximately 76.2 m wide, extends the length of the island. Sixteen species of seabirds nest on Tern Island (Amerson 1971, USFWS). No mammalian land predators occur within the atoll. At French Frigate Shoals, Brown Noddies nest on Tern, La Perouse, Whaleskate, East and Little Gin islands. Tern Island has the largest nesting colony, with approximately 1700–

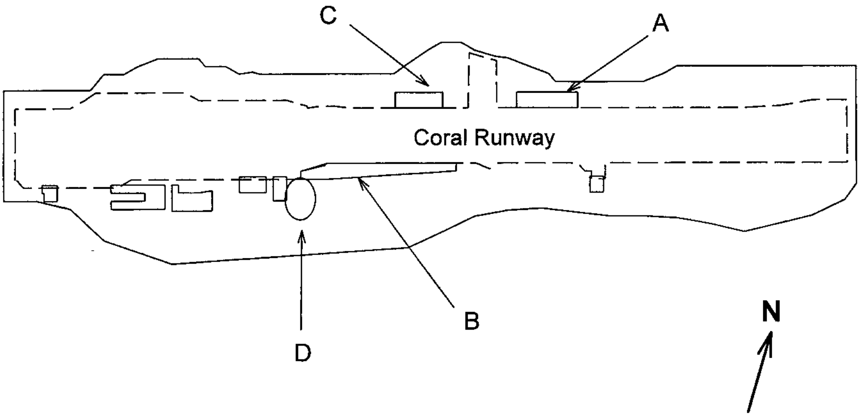

FIG. 2. Location of Brown Noddy study plots A, B, C, and D on Tern Island, French Frigate Shoals, Hawaii.

2500 nesting pairs. East Island, approximately 13 km southeast of Tern Island, is the next largest colony with approximately 500 breeding pairs.

Four study plots were chosen on Tern Island because of high numbers of accessible Brown Noddy nests (Fig. 2). Study plot A occurred on the north side of Tern Island. The plot measured 78 m in length and ranged from 10.3 to 7.8 m wide. The plot consisted of non-vegetated areas of coralline rubble, dense stands of the grass *Lepturus repens* on its northern edge and sparse patches of small *Chenopodium oahuense* shrubs on its southern edge; two small *Tournefortia argentea* bushes were in the middle of the plot. Study plot B was on the south side of the island, extending 120 m east to west and 3.5 m north to south from the edge of the runway. Small (<2 m in height) *Tournefortia argentea* bushes, *Lepturus repens, Boerhavia repens, Portulaca* spp., and *Eleusine indica* were the major vegetative cover in study plot B. A coralline berm extended along the plot's length, approximately 1.5 m from the north edge of the plot. Habitat and total area of study plot C were similar to that of study plot A. Study plot D was used to determine breeding success of Brown Noddy nests >1 m above the ground in *Tournefortia argentea* and *Pluchea* spp. bushes. Study plot A was used in all years of the study, while study plot B was used in 1989–1992; plots C and D were used in 1980, 1981, and 1982.

We made observations of Brown Noddy breeding phenology and population trends on Tern Island from 1982 to 1992. Data on other aspects of breeding biology, including incubation behaviors, egg measurements, chick polymorphism and growth, and parental care and breeding success were collected in 1980–1982 and 1989–1992 (Table 1). Observations in 1980 through 1987 were made by several U.S. Fish and Wildlife Service personnel; observations in 1988–1992 were made primarily by the senior author.

Beginning each breeding season, from 1982 to 1992, we conducted island-wide searches and recorded dates of first arrival for Brown Noddy adults, first eggs laid, and first chicks hatched and fledged. Because of protracted laying and numerous nesting attempts, only the minimum number of breeding pairs on the island was determined each breeding season by recording the highest number of nests containing either an egg or a chick on island-wide monthly counts of nests during 1982–1985 and by island-wide counts made every 36 days (the mean incubation length of Brown Noddies reported by Brown [1977]), during 1985–

TABLE 1
DATA COLLECTION ON TERN ISLAND, FRENCH FRIGATE SHOALS, HAWAII

Data collected	Year collected	Study plot[a]
Breeding phenology	1982–1992	Island-wide
Number of breeding pairs	1982–1992	Island-wide
Incubation behaviors	1980–1981, 1989–1992	A, B, C, D
Egg morphometrics	1980–1982, 1989–1992	A, B, C, D
Chick polymorphism	1980–1981, 1988	A, C, D
Chick growth	1980	A, C, D
Relay intervals	1989–1992	B
Parental care of nestling	1989–1992	B
Breeding success	1982, 1989–1992	A, B, C, D

[a] Study plots C and D were primarily used only in 1980 and 1981 and in 1982 for breeding success.

1992. Study plots were checked every other day while nests were active, and every five days when there were no active nests, except during inclement weather (winds exceeding 8.6 km/h in combination with rain). Because laying occurs throughout the year on Tern Island but is extremely synchronous for noddies, we defined breeding season as the period between the laying of the first egg to the laying of the last egg within the study plots, regardless of calendar year. In 1980 and 1981, breeding occurred from March to October. However, from November 20, 1988 to October 7, 1990, Brown Noddies nested continuously. We considered the beginning of the 1990 breeding season to be December 21, 1989, when there were no chicks less than four weeks of age left on the island and within the plots and when a new peak of laying occurred. From this peak, study plot A was monitored continuously for three successive breeding seasons, December 21, 1989 to October 7, 1990, March 15 to September 10, 1991, and February 2 to November 12, 1992. In 1980 and 1981, all nests within study plots A, C, and D were marked with individually numbered metal tags, and the fate of each nest was recorded. In 1989–1992, nesting success in study plot A was observed by marking each nest with a blue-painted piece of coral placed 5–12 cm north of the nest. For all of study plot A, the total number of new eggs, eggs lost, and newly hatched chicks were recorded at each check. All chicks that reached three weeks of age were banded with a size 3 incaloy USFWS band. All dead chicks found within the plot were recorded.

Beginning in October 1989, breeding adults were color-banded within study plot B to monitor individual breeding success and effort. Twenty-one pairs were banded during 1989. All breeding attempts for these color-banded pairs were recorded. Thereafter, pairs were captured at the beginning of each season so that the number of breeding attempts for each pair could be monitored for the entire breeding season. Thirteen pairs were banded in 1990, and 29 pairs were banded in 1991. All birds were captured by hand, or by using a long-handled minnow net during daytime hours. They were then banded with a unique color-band combination consisting of three plastic bands and a size 3 incaloy, USFWS band. A total of 114 birds, representing 62 pairs, were color-banded.

All nests within study plot B belonging to color-banded pairs were marked with a uniquely numbered rock. Dates of laying, hatching, fledging, and chick departure from the island for each nesting attempt were recorded. Eggs in marked nests were weighed with a 100-g Pesola scale to the nearest 1 g; eggs three days of age or older were not weighed. Measurements of egg length and breadth were taken with digital or manual vernier calipers to the nearest

0.1 mm. The fate of each marked nest was recorded (i.e., failed egg or dead chick). In addition to daily searches, observations of color-banded birds were conducted from May 1 to May 27, 1992 at 06:00–07:45, 12:00–13:45, and 20:00–21:45 h. All sightings of color-banded birds on any part of the island were recorded during 1989–1992. Incubation lengths were gathered periodically throughout 1989–1992 for nests with known dates for laying and hatching. Incubation shifts were followed for a total of 10 pairs in 1980 and 57 pairs in 1981; one bird from each pair was marked on the crown with picric acid. Incubation shifts were recorded every 2 h for a total of 72 h during each of five observation periods. The sex was not known for any of the 67 pairs of birds, and pairs were in various stages of incubation at the time of monitoring.

Proportions of chicks with light down versus dark down were determined in 1980, 1981, and 1989. Although there were intermediate plumages, chicks were considered light-colored if they did not contrast markedly with the coralline rubble and dark if they resembled the color of the adult plumage. In 1980, chick growth for an initial sample of 28 chicks in study plot A was measured every 3–4 days until chicks fledged. Chicks were weighed with a Pesola scale to the nearest 0.5 g; culmen, wing chord, and tarsus lengths were measured with vernier calipers to the nearest 0.1 mm. In 1989–1992, fledglings were weighed (≥one week post-fledging) using a 500-g Pesola scale to the nearest 2.0 g, and culmen and wing chord were measured with vernier calipers to the nearest 0.1 mm. In all years of study, chicks were considered fledged at the first sign of sustained flight when nests were being checked. Island-wide searches for fledglings were conducted, and their nests were checked periodically after dusk between 19:00 and 22:00 h. After 14 days of no sightings, a fledgling was considered absent from the island.

RESULTS

Breeding phenology and population estimates.—The minimum nesting population on Tern Island appeared to increase during the ten years of the study from at least 375 pairs in 1982 to at least 2410 pairs in 1992. Breeding phenology varied widely between years ($\chi^2 = 15824.28$; df = 88; $P < 0.001$); however, the largest peaks of laying occurred between March and September each year (Fig. 3). Peaks of laying varied widely during these months from 1982 through 1985 and in 1991; while in 1986 and 1987, peak laying occurred in late April, and in late June in 1992. From 1988 through 1989, Brown Noddies nested continuously.

Noddies usually nested on the ground in open, coralline rubble areas. Nests varied, ranging from inornate to elaborately lined with pieces of colored plastic, shells, crab carapaces, and vegetation. Brown Noddies nested as high as 1.0 m above the ground in *Pluchea* spp., *Chenopodium ohauense,* and *Lepturus repens,* in which nests consisted of dense platforms of vegetation as large as 0.5 m in diameter and 20 cm thick.

Egg measurements, incubation behaviors, and renesting.—Of 2,889 nests observed on Tern Island, all contained one egg that ranged in color from all white to heavily speckled brown. There was little variation in mean egg length and breadth between years (N = 304 and 303, respectively); however, egg mass differed in some years (N = 253;, one-way ANOVA, Table 2). Mean length, breadth, and mass of color-banded pairs'

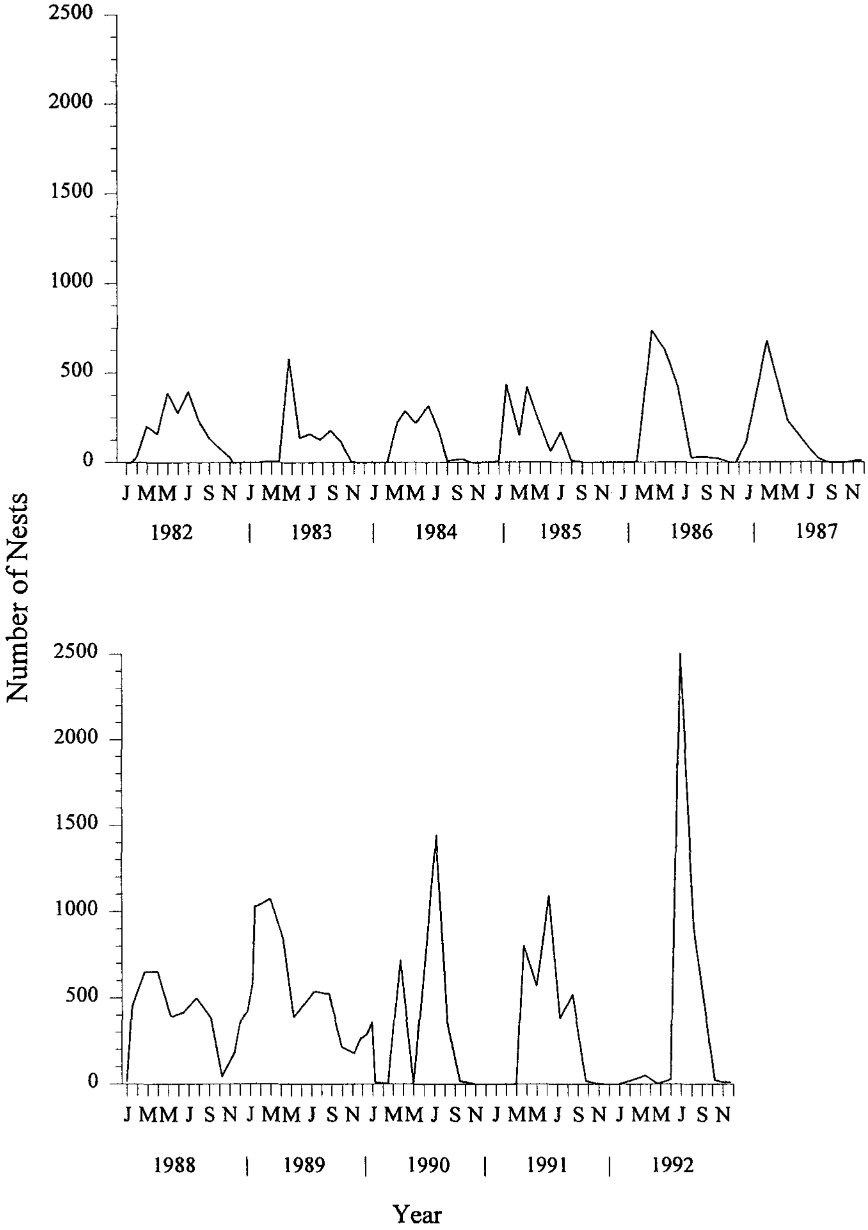

FIG. 3. Nesting phenology and numbers of nests containing eggs of Brown Noddies on Tern Island, French Frigate Shoals, Hawaii, 1982–1992.

TABLE 2

MEAN EGG MEASUREMENTS (±SD; N IN PARENTHESES) FOR TERN ISLAND BROWN NODDIES

Year	Length (mm)	Breadth (mm)	Mass (g)
1981	53.7 ± 2.0	36.9 ± 1.0	36.0 ± 2.4
	(30)	(30)	(30)
1982	53.4 ± 2.2	36.7 ± 1.2	37.2 ± 3.0
	(150)	(149)	(124)
1989	53.3 ± 1.5	36.6 ± 1.6	38.2 ± 2.5
	(20)	(20)	(2)
1990	53.2 ± 1.8	36.9 ± 0.9	39.0 ± 2.7
	(94)	(49)	(48)
1991	53.2 ± 2.1	36.8 ± 1.1	37.9 ± 3.0
	(55)	(55)	(49)
F^a	0.28	0.53	7.89
P	0.89	0.71	$<0.001^b$

[a] ANOVA tests for differences between years; df = 4, 299, for length; 4, 298, for breadth; and 3, 247, for mass.

[b] Egg mass in 1990 differed significantly from 1981 and 1982; in 1991 egg mass differed significantly from 1981; 1989 was not compared due to small sample size.

first eggs were not different from eggs laid later in the same season ($F_{2,102} = 0.29$, $P = 0.02$ and $F_{2,83} = 2.63$, respectively; $P > 0.05$ for all three measures).

Incubating noddies shifted more frequently in the morning (02:00–08:00 h) and night (20:00–02:00 h) than in the midday (08:00–14:00 h) and evening (14:00–20:00 h) (N = 67; $\chi^2 = 31.5$; df = 3; $P < 0.001$), with adults averaging as much as 2.0 shifts during the night period (Table 3). There was no difference in mean shift length between years, so data were pooled ($F_{4,61} = 0.02$; $P > 0.05$). Average shift length for 67 pairs during 360 hrs of observation was 11.3 h (SE = 0.9; range = 5.3–25.2 h). Average duration from laying to hatching was 34.8 d (N = 19, SD = 0.6, range = 29–37 d).

Of the total number of pairs, 47.0% (N = 34) and 34.3% (N = 35) renested after the first nest failed in 1990 and 1991, respectively. Thirteen of the renests occurred after the loss of an egg, and 24 occurred after losing a chick; one pair relaid twice after losing a chick on each of the two previous attempts (Table 4). There were no differences in the proportion of pairs that relaid in 1990 compared to 1991 ($\chi^2 = 1.17$; df = 1; $P > 0.05$), nor were pairs more likely to relay after losing an egg versus losing a chick ($\chi^2 = 1.56$; df = 1; $P > 0.05$). Average age of chicks lost among pairs that relaid was 7.1 d (N = 26; SD = 7.1; range = 1–20 d). Further, relay interval lengths (the time from laying the first

TABLE 3
INCUBATION BEHAVIORS FOR BROWN NODDIES ON TERN ISLAND DURING EACH OF FIVE 72-H PERIODS OF OBSERVATION

Year	Mean incubation shift length (hours)	Total number of shifts per pair	Number of shifts per time period[a]			
			Morning	Midday	Evening	Night
1980	10.4 ± 6.7[b]	6.0 ± 2.3[c]	1.6 ± 1.1	1.5 ± 1.3	1.6 ± 1.1	1.3 ± 0.9
	(50)	(10)	(10)	(10)	(10)	(10)
1981						
March	11.1 ± 9.5	7.7 ± 3.4	1.9 ± 1.6	0.4 ± 0.9	1.5 ± 1.0	2.3 ± 1.4
	(73)	(14)	(14)	(14)	(14)	(14)
May	12.6 ± 7.9	6.4 ± 1.9	1.5 ± 1.1	1.1 ± 1.2	1.5 ± 0.9	1.2 ± 1.1
	(57)	(15)	(15)	(15)	(15)	(15)
June	11.7 ± 7.7	6.9 ± 1.96	1.3 ± 1.0	1.0 ± 0.9	0.9 ± 1.0	1.7 ± 1.2
	(68)	(15)	(15)	(15)	(15)	(15)
August	10.5 ± 7.8	7.2 ± 2.6	1.3 ± 1.6	1.2 ± 1.1	1.4 ± 0.8	1.6 ± 1.3
	(67)	(13)	(13)	(13)	(13)	(13)
All years	11.3 ± 0.9[d]	6.8 ± 0.7	1.5 ± 1.3	0.96 ± 1.1	1.1 ± 1.0	2.0 ± 1.1

[a] Morning: 02:00–08:00 h; midday: 08:00–14:00 h; evening: 14:00–20:00 h; night: 20:00–02:00 h.
[b] Mean ± SD; number of shifts per observation period in parentheses.
[c] Mean ± SD; number of pairs in parentheses.
[d] Mean ± SE.

egg to laying the replacement egg) were not different whether the pair lost an egg, a chick <1 week of age, or a chick >1 week of age (Kruskal-Wallis, H = 4.11; df = 2, N = 7, 11 and 7, respectively; $P > 0.05$). However, pairs that successfully fledged a chick waited longer to nest again than did pairs that lost an egg or a chick (Kruskal-Wallis, H = 16.08; df = 2; N = 6; $P < 0.001$). These data should be interpreted with caution, however, as the sample sizes were small.

Chick polymorphism, growth and parental care.—There were no differences between years in the proportion of light- and dark-colored chicks in 1980, 1981, or 1989 (N = 221; $\chi^2 = 0.253$; df = 2; $P > 0.05$). Down color for chicks during these three years was 26% light- and 74% dark-colored. For 84 of 160 chicks, average age prior to disappearance from the nest did not differ with respect to color (N = 19 and 65, mean = 9.9 d and 7.5 d, SD = 6.9 and 4.6 for dark and light-colored chicks, respectively).

Average chick mass at one day of age was 28.8 g (N = 29, SD = 3.83); chicks attained average adult mass (200.4 g, N = 122) at 34 d of age. Chick mass increased until 38 d post-hatching and began decreasing on day 43 (Fig. 4). At the end of the measurement period (range = 47–51 d), the average chick mass was 195.8 g (N = 13, SD = 18.39). There

TABLE 4

NUMBER OF RELAYS AND CLUTCH INTERVALS FOR BROWN NODDIES DURING 1990 AND 1991

Number of relays (% of pairs)				Relay interval length according to prior attempt (days)[a]			
None	One	Two	Three	Unhatched	<1 week-old	>1 week-old	Fledgling
41 (59.4)	28 (40.1)	4 (14.3)	1 (3.5)	43.5 ± 26.2[b] (31) 12–87 days	22.7 ± 10.3 (11) 15–49 days	33.4 ± 19.5 (7) 17–65 days	212.3 ± 37.8 (6) 180–279 days

[a] Interval lengths not different except for those pairs fledging chicks ($F = 154.46$, df = 2, $P < 0.05$).
[b] Mean ± SD, (N), range in days.

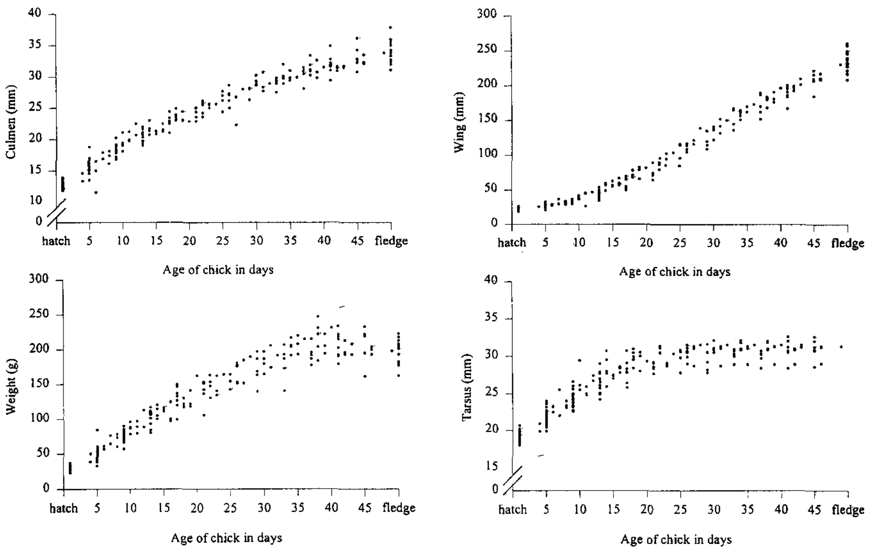

FIG. 4. Growth of Brown Noddy chicks on Tern Island.

was no difference in weight loss between newly fledged chicks and chicks that were weighed ≥ one week post-fledging (t = 1.01, df = 21, $P >$ 0.05). There was relatively little growth in wing length until 10 d of age, followed by steady growth up to 50 d post-hatching, when the measurement period ended (Fig. 4). Culmen length increased throughout the 50 d of measurement, while tarsus length increased until 20 d of age (Fig. 4). Mean duration from hatching to fledging was 47.8 d (N = 31, SD = 4.3, range = 39–61 d); however, chicks remained in the nest and were fed by their parents an average of 65.1 d after fledging (N = 14, SD = 13.4, range = 38–88 d). Three birds returned to within 10 m of their natal site 11, 21, and 24 months after leaving the island. The youngest bird observed breeding was two years and 11 months old.

Breeding success.—In 1990, a combination of severe storms during peak laying period and depredation of chicks by Great Frigatebirds (*Fregata minor*) resulted in poor reproductive success in comparison with 1991 and 1992 (Table 5). Similarly, breeding success was poor from February 1 to June 23, 1992; only three of 79 eggs laid hatched, and no chicks survived to fledging. However, after this date, nearly all eggs laid hatched and resulted in fledged chicks (Table 5). There was a difference in hatching and fledging success between study plots; both plots B and D had greater hatching success than A and C, while fledging success was lower in plot B and greater in plot D when compared to plots A and C

TABLE 5

BROWN NODDY HATCHING, FLEDGING, AND REPRODUCTIVE SUCCESS

	1982	1990	1991	1992
Total # eggs laid	222	1239	702	726
Total # eggs lost	51	644	128	161
Total # eggs hatched	171	595	574	565
Total # chicks found dead in nests	0	42	12	3
Total # fledged	62	15	263	324
Hatching success (%)[a]	77	48[b]	82[c]	78[c]
Fledging success (%)[a]	36	3[b]	46[c]	57[c]
Reproductive success (%)[a]	28	1.2	38	45

[a] Hatching success is the number of chicks hatched from the total number of eggs laid; fledging success is the number of chicks fledged from the total number of chicks hatched, and reproductive success is the number of chicks fledged from the total number of eggs laid.

[b] Lower than in other years; $\chi^2 = 313.2$ for hatching success and 430.4 for fledging success; df = 3; $P < 0.001$.

[c] Higher than in other years; $P < 0.001$.

($\chi^2 = 22.3$ and 60.4 for hatching and fledging, respectively; df = 3; $P < 0.001$).

DISCUSSION

Collectively, the Hawaiian Islands support between 89,500 and 150,000 breeding pairs of Brown Noddies. Nearly 32% of these occur in the northwestern Hawaiian Islands, with the largest population found on Nihoa Island (Harrison et al. 1983). Breeding Brown Noddies were documented by the Rothschild expedition at French Frigate Shoals as early as 1891, when thousands were observed nesting on Tern Island (Munro 1941). Wetmore observed 500 pairs nesting on Tern Island in 1923; however, they were not observed nesting on the island from 1953 to 1969 (in Amerson 1971). This period of non-nesting corresponds with its use by Coast Guard personnel as a LORAN station and the presence of cats and dogs on the island (Richardson 1954, Amerson 1971). In June 1967, an estimated 10,182 Brown Noddies were observed at French Frigate Shoals. However, the maximum number of nests recorded was 1675, occurring mainly on East and Whaleskate islands (Amerson 1971). Breeding noddies were observed again on Tern Island in 1977, shortly before the island was abandoned by the Coast Guard (M. Rauzon, pers. comm.). It is difficult to interpret whether an increase in the nesting population at French Frigate Shoals has occurred since 1891, but the population at Tern Island has expanded greatly since 1977 (Fig. 3; USFWS unpubl. data).

Time of arrival for breeding adult Brown Noddies and their occurrence at a breeding colony vary among Pacific, Indian, and Atlantic ocean colonies (Table 6). In the Hawaiian Islands, Brown (1973) observed adults year-round on Manana Island but noted their absence during the day from December to March in 1971 and 1972. Similarly, noddies are year-round residents on Nihoa, Necker, and Laysan islands, but fewer adults are present during the day from December to March (Ely and Clapp 1973, Clapp et al. 1977, Clapp and Kridler 1977). Woodward (1972) noted that Brown Noddies are entirely absent from January to March on Kure Atoll. We observed adults on Tern Island year-round except during an El Niño event which occurred from October 1990 to March 1991, when adults abandoned the island and left fledglings still dependent on parental care to starve (Fig. 3). In contrast, Murphy (1936) stated that noddies from all of the sub-tropical South Atlantic Islands migrate from their nesting grounds between May and December. Similarly, Morris and Chardine (1992) reported that noddies were absent annually from Cayo Noroeste, Culebra, Puerto Rico from September to March. In Florida, Robertson (1964) noted that Brown Noddies departed the Dry Tortugas as early as May, and Watson (1908) reported that all birds were absent annually from these colonies by the end of September. We suggest that the variation in occurrence of Brown Noddies at Pacific and Indian Ocean breeding colonies versus those in the Atlantic may be due to a variety of factors, including food availability, ocean currents, and water temperature. However, there are no data to confirm these relationships.

In the Hawaiian Islands, the Brown Noddy's breeding season is erratic. Laying occurs from May to August on Manana Island (Brown 1973), while on Nihoa, Necker, and Laysan islands egg-laying has been documented throughout the year (Ely and Clapp 1973, Clapp et al. 1977, Clapp and Kridler 1977). Woodward (1972) documented egg laying at Kure Atoll annually from April through August (Table 6). We observed that laying on Tern Island could occur throughout the year, although most eggs were laid between March and September during 1982 to 1992 (Fig. 3). Brown Noddy breeding phenology and synchrony has been explained as a response to food availability (Ashmole 1963). Morris and Chardine (1992) attributed variation in Brown Noddy breeding phenology to geographic differences in feeding regimes. ffrench (1990) stated that inclement weather on Soldado Rock, Trinidad, prolonged the breeding season so that two peaks of laying occurred in 1966, but during other years, only one peak of laying was recorded. High loss of eggs and chicks to high tides, inclement weather, and predation by Pied Crows (*Corvus albus*) on Aldabra Atoll in the Seychelles also caused variability in laying patterns (Diamond and Prys-Jones 1986). Likewise, Dorward and Ashmole (1963) attributed the double peaks of laying on Ascension Island to relaying or

TABLE 6

BREEDING PHENOLOGY OF BROWN NODDIES IN PACIFIC, ATLANTIC, AND INDIAN OCEAN COLONIES

Colony name	Latitude-longitude	Arrival of adults	Laying	Departure of adults	Source
Green Island, Kure Atoll, Hawaii	28°25′N, 178°10′W	March	Apr–Aug	January	Woodward 1972
Laysan Island, Hawaii	25°42′N, 171°44′W	Year-round	Variable	—	Ely and Clapp 1973
Tern Island, French Frigate Shoals, Hawaii	24°52′N, 166°17′W	Year-round	Variable	—[a]	This study
Dry Tortugas, Florida	24°40′N, 82°52′W	April	Apr–Jul	September	Sprunt 1948
Nihoa Island, Hawaii	23°35′N, 164°42′W	Year-round	Variable	—	Clapp et al. 1977
Necker Island, Hawaii	23°06′N, 161°58′W	Year-round	Variable	—	Clapp and Kridler 1977
Manana Island, Oahu	21°20′N, 157°40′W	Year-round	May–Aug	—	Brown 1973
Sand Island, Johnston Atoll, Pacific Ocean	16°45′N, 169°31′W	Year-round	Feb–Oct	—	Amerson and Shelton 1976
Cayo Noroeste, Culebra, Puerto Rico	18°21′N, 65°21′W	April	Apr–Jun	September	Morris and Chardine 1992
Little Tobago, Trinidad	11°18′N, 60°30′W	February	Mar–Jul	August	Morris 1984
Ascension Island, Atlantic Ocean	07°57′S, 14°22′W	November	Nov–Apr	May	Dorward and Ashmole 1963
Aldabra Atoll, Seychelles, Indian Ocean	09°24′S, 46°20′E	Year-round	Variable	—	Diamond and Prŷs-Jones 1986
Christmas Island, Indian Ocean	10°25′S, 105°42′E	Year-round	Apr–Sept	—	Gibson-Hill 1947

[a] In 1990, Brown Noddies deserted the island in October, leaving fledglings to starve, and did not return until May 1991.

to birds laying for the first time that had been prevented from nesting due to high seas. On Tern Island, Brown Noddy pairs attempted to renest as often as four times during a breeding season after losing an egg or chick. We know of no other study that has documented Brown Noddies relaying after losing their second and third clutches within the same breeding season. Ashmole (1963) observed that Sooty Terns will renest more frequently if loss of an egg occurs early rather than late in the incubation period. He also suggested that predation of Sooty Tern chicks by Ascension Frigatebirds (*Fregata aquila*) may have contributed to the breeding cycles observed on Ascension Island, where birds laying during the peak season are more likely to fledge young. The renesting efforts we observed on Tern Island could explain the multiple peaks in laying and, consequently, the variation in Brown Noddy breeding phenology. Predation on chicks by Great Frigatebirds, on eggs by Ruddy Turnstones (*Arenaria interpres*), and inclement weather resulting in nesting failure may all contribute to the multiple laying peaks we observed.

Brown Noddy eggs on Tern Island were significantly larger than those laid on Manana Island and at other Pacific and Atlantic ocean colonies (One-way ANOVA, $P < 0.05$; Table 7). Morris and Chardine (1992) stated that differences in egg sizes between Pacific and Atlantic ocean colonies were probably not due to a difference in body size. However, the body mass of 122 adults studied on Tern Island averaged larger than those on Cayo Noroeste, Culebra; Ascension Island (mistakenly reported as a Pacific Ocean colony by Morris and Chardine 1992); and Manana Island (SD = 16.7, range = 165–242 g, $F = 65.5$, df = 3, $P < 0.001$). Egg weight as a function of body weight has also been discussed by Rahn et al. (1975), Verbeek and Richardson (1982), and Pierotti and Bellrose (1986). Our data support the results of Morris and Chardine (1992) who found no differences in the measurements of a pair's first egg in comparison with subsequent eggs laid during the breeding season.

Mean incubation period did not differ for noddies nesting at Tern Island or Cayo Noroeste, Culebra, although both of these colonies had shorter incubation periods than did noddies on Manana Island (One-way ANOVA, $F = 118.6$, df = 2, $P < 0.001$; Brown 1973, Morris and Chardine 1992). Mean incubation shift lengths for noddies on Tern Island were also shorter than those observed on Manana Island (Brown 1973) and the Dry Tortugas, where Watson (1908) reported shifts occurring every two hours during the day. Finally, birds at both Tern and Manana islands switched most often during the morning and night.

Although the proportion of light- and dark-colored chicks was not different between years on Tern Island, it did differ among five colonies in the Pacific and Atlantic oceans (Table 7; $\chi^2 = 72.92$, df = 4; $P < 0.001$).

TABLE 7

ASPECTS OF BROWN NODDY BREEDING BIOLOGY COMPARED TO SOME PACIFIC, ATLANTIC, AND INDIAN OCEAN COLONIES

	Incubation length (days)			Egg dimensions[a]			Chick color[b]		
Colony name	N	Mean (range)	SD	Length (mm)	Width (mm)	Weight (g)	N	% Dark	% Light
Green Island, Kure Atoll (Woodward 1972)	76	36.1 (34–40)	?	—	—	—	265	67.0	33.0
Tern Island, FFS (this study)	70	34.8 (29–37)	2	53.4 ± 2.2 (304)	36.8 ± 1.3 (304)	37.5 ± 2.9 (253)	221	26.0	74.0
Dry Tortugas, Florida (Watson 1908)	49	35.0–36.0 ?	?	52.0 ± ? ?	35.0 ± ? ?	?	—	35.0	65.0
Manana, Oahu* (Brown 1973)	12	36.0 (35.5–37.5)	0.55	52.8 ± 2.2 (129)	36.0 ± 0.9 (129)	36.3 ± 2.5 (68)	392	51.0	27.0
Sand Island, Johnston Atoll (Amerson and Shelton 1976)	93	35.6 (30–41)	?	—	—	—	573	48.5	51.5
Cayo Noroeste,* Culebra (Morris and Chardine 1992)	37	34.5 ?	0.6	51.7 ± 1.8 (345)	35.4 ± 0.8 (345)	34.3 ± 2.2 (116)	215	44.0	56.0
Ascension Island* (Stonehouse and Stonehouse 1963)		—		52.7 ± 2.0 (113)	36.3 ± 0.8 (113)	33.5 ± 3.3 (32)	57	84.0	16.0
Christmas Island, Indian Ocean (Gibson-Hill 1951)	8	?	?	53.3 ± ? ?	36.0 ± ? ?	?	—	10.0	90.0

[a] Mean ± SD, N in parentheses.

[b] Brown (1973) placed 110 chicks in a gray category; these chicks were omitted from the analysis. N = number of chicks analyzed.

* Egg dimensions from these colonies compared to Tern Island, one-way ANOVA, $P < 0.05$ for all three measures.

While there were more light-colored chicks at Kure Atoll and Cayo Noroeste, Culebra, there were more dark-colored chicks on Ascension, Manana, and Tern islands. Because of the subjective methods used at all five colonies to classify chicks as either light or dark, some observer bias may explain the differences between colonies.

Brown Noddy chick growth rates on Tern Island were similar to those reported by Dorward and Ashmole (1963), Brown (1973), and Morris and Chardine (1992) at other Pacific and Atlantic ocean colonies. However, chicks on Tern Island fledged at a later age than those observed on Cayo Noroeste, Culebra (mean = 45.7 d, cf Morris and Chardine 1992) and Manana Island, although this difference may be the result of observer bias in determining when a chick has fledged. Gibson-Hill (1951) remarked that chicks are fed by their parents some weeks after learning to fly, and Brown (1973) observed a chick being fed more than 100 days after fledging. It seems likely that Brown Noddy chicks are attended at the colony and learn to forage during this time rather than leaving the colony with adults as is the case for Sooty Terns and Red-tailed Tropicbirds (*Phaethon rubricauda*) (Ainley et al. 1986). This is further supported by our observation of both members of a pair back at the breeding colony within 12 d after the departure of their fledglings from the island. Finally, although our data support Burger's (1980) conclusion that terns defer breeding until their third year, our study documents that birds can return to their natal site as early as 11 months after independence.

Ashmole (1963) attributed poor breeding success on Ascension Island to chick starvation. Likewise, Morris and Chardine (1992) concluded that higher breeding success at Cayo Noroeste, Puerto Rico, was the result of a reliable food source for adults. In contrast, Brown (1973) reported that on Manana Island all eggs hatched after June 11 were preyed upon by Black-Crowned Night-Herons (*Nycticorax nycticorax*), and although breeding seasonality was governed by food supply, the ultimate factor affecting fledging and success of the breeding season was predation on Brown Noddy chicks. Robertson (1964) also reported predation by Magnificent Frigatebirds (*Fregata magnificens*) on Brown Noddy chicks on the Dry Tortugas, although neither he nor Watson (1908) quantified the effect on reproductive success. In our study, Great Frigatebird predation was responsible for nearly all chick losses in 1990–1991 (Megyesi 1995). Anecdotal observations collected by USFWS personnel in previous years since 1979 confirm that Great Frigatebird predation occurs regularly on Tern Island. Although most Brown Noddy chick loss was attributed to frigatebird predation in this study, in 1992, Brown Noddies, Black Noddies (*Anous tenuirostris*), Sooty Terns, and White Terns (*Gygis alba*) experienced complete nesting failure, where incubating adults abandoned pipped and hatching eggs and newly hatched chicks up to June 23. Following this date, Brown Noddies renested, and reproductive success was higher than had been observed in previous years of study. We suggest that this series of events in 1992 may be related to El Niño Southern Oscillation (Schreiber and Schreiber 1984; unpubl. data, USFWS).

The differences in fledging success between plots B and D are probably a result of Great Frigatebird predation. Plot B lies parallel to the runway and is more readily accessible to hunting frigatebirds. In contrast, plot D contained nests built in low growing vegetation that might have provided more cover from hunting frigatebirds. We suggest that lower reproductive success for Brown Noddies on Tern Island in comparison with other colonies is the result of inclement weather and constant predation pressure by Great Frigatebirds.

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