COLONY VISITATION BEHAVIOR AND BREEDING AGES OF SOOTY TERNS (*STERNA FUSCATA*)[1]

By Brian A. Harrington

INTRODUCTION

The apparent regulation of population size in seabirds has been a topic of recent research by several ornithologists (e.g. Ashmole, 1963b; Harris, 1969a, b, c; Nelson, 1965, 1966, 1969a, b; Rowan 1965; and Lack, 1968). These authors theorize that major limiting factors are either availability of food or nest space and that consequently a direct or indirect extrinsic influence on population size exists through selected regulation of clutch-size, mortality, deferred maturity, long parental care, long breeding cycles, and social behavior. In contrast, Wynne-Edwards (1955) suggests that colonial seabirds have intrinsic responses to varying food supply and that by collective social mechanisms they maintain population sizes compatible with existing food supply. He further suggests one method of maintaining appropriate numbers is through regulation of colony size, and he implies that this regulation is often enforced by established breeders preventing young individuals from securing and utilizing space in a colony (1962: 557). Ashmole (1963b) argues that the Wynne-Edwards hypothesis requires limited nesting space or defense of unoccupied areas in colonies that are not filled to capacity. He believes (1963b) that it is more likely that a density-dependent variation of recruitment rates of young adults into the breeding population exists, and that the recruitment rate is likely to be mediated by competition for food round the colony.

Critical to any study of population regulation is knowledge of breeding ages, or specifically whether deferred maturity exists, and if so, whether it plays a role in population regulation. The major objectives of this report are to present such information for the Sooty Tern (*Sterna fuscata*) based primarily on observations of its breeding on a tropical Pacific island, and to discuss certain factors that may influence initial breeding ages. The Sooty Tern is especially suitable for several reasons: it is a tropical oceanic species, inhabiting an environment known to be of low productivity (Odum, 1971) where food is believed to be scarce or hard to catch (Lack, 1968), it usually breeds in large colonies, is long-lived (Clapp and Sibley, 1966; Austin, Ms), and, as will be shown in this study, has a long period of adolescence.

ISLAND DESCRIPTION AND COLONY BREEDING PHENOLOGY

Most of my observations were made on Johnston Atoll (16° 40′ N, 169° 30′ W) which lies about 720 nautical miles southwest of Honolulu, Hawaii, and is composed of four islands in a lagoon surrounded by live coral reef. Seabirds breed mostly on Sand Island, which in

---

[1]Contribution No. 94, Pacific Ocean Biological Survey Program, Smithsonian Institution, Washington, D. C.

this atoll is the only extant breeding site for Sooty Terns. The island has the shape of a dumbbell, the western end of which is man-made. The eastern end, which is connected to the west by a man-made causeway, is the original island. It consists of about 15 acres, and is the location of the tern colony. Sand Island is also the location of a United States Coast Guard LORAN station which is operated by about 25 men. Living quarters and maintenance areas are on the west end, a signal building is on the causeway, and a transmitter building with a 630-foot radio tower is in the middle of the bird colony on the east end. Vegetation on the east end is almost entirely herbaceous, the major genera being *Lepturus*, *Amaranthus*, *Boerhavia*, *Tribulus*, *Portulaca*, *Sesuvium* and *Ipomoea*. A more detailed description of the atoll and its vegetation will be given by Shelton (Ms).

The seabird colony at Sand Island includes 11 breeding species, the populations and cycles of which are to be described by Shelton (Ms). About 300,000 Sooty Terns comprise more than 90% of the breeding birds (personal observation).

Sooty Terns at Johnston Atoll breed on an annual cycle (Fig. 1) which contrasts with colonies on Ascension Island in the Atlantic

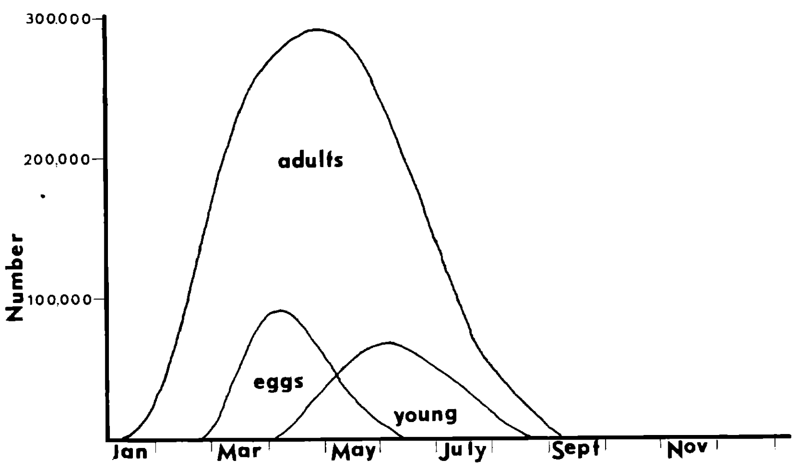

FIGURE 1. Breeding phenology of Sooty Terns at Johnston Atoll in 1967.

Ocean where breeding is on a 9.7-month cycle (Chapin and Wing, 1959) and on Christmas Island in the Pacific Ocean where many individuals attempt breeding at 6-month intervals (Ashmole, 1965). At Dry Tortugas, Gulf of Mexico, and all Hawaiian Island colonies, Sooty Terns also breed on annual cycles (Robertson, 1964; Richardson, 1957; Amerson, 1971; Ely and Clapp, Ms; Woodward, 1972). From 1964 to 1971 egg-laying at Johnston began within 15 days of mid-February. Laying normally continues into April and virtually ceases by mid-May. Incubation of the single egg requires about 30 days (Dinsmore, 1972); growth and development of the chick requires about 8 weeks (Burckhalter, 1969). Once able to fly, young remain in the vicinity of the colony for about three weeks after which they depart, apparently with at least one parent (Burckhalter, 1969; personal observations). Table 1 presents estimates for total numbers of adults, eggs, and young at Sand Island, Johnston Atoll in 1967, the year for which best estimates are available.

Other observations presented below come from my field work at Dry Tortugas, Florida from March-June 1970. This atoll and its tern colonies are described by Robertson (1964).

METHODS

In June 1963, personnel of the Pacific Ocean Biological Survey Program (POBSP), Smithsonian Institution, initiated studies of seabirds as part of a scheme to determine bird populations and movements in the central Pacific. The priorities of the program required mass banding which was employed on Sand Island at Johnston Atoll from 1963 through 1969 (Table 2). My analyses are based on repeated captures of these banded birds.

Incubating Sooty Terns were captured by hand or with small hand nets. Those standing on the ground or flying were caught with larger hand nets. Standing and incubating terns were best captured on especially dark nights whereas flying terns were caught most efficiently near sunrise or sunset. Chicks were caught by hand.

From 1966 to 1969, POBSP personnel, including myself during parts of 1966 to 1968, attempted to catch as many banded flying and incubating Sooty Terns as possible. I returned to gather similar data in March-June 1971 after termination of the POBSP. Condition of the brood patch, molt, time of day to the nearest hour, location on the island, and any unusual individual characteristics were recorded for most of the birds, and most were released within a minute of capture.

All statistical analyses included below are by Chi-square tests with one degree of freedom. Chi-square values less than 3.84 are not considered statistically significant ($P > .05$), values from 3.84 to 6.63 are considered significant ($P < .05$), and those values exceeding 6.63 are considered highly significant ($P < .01$).

RESULTS

Immigration and Population Maintenance

The maintenance of populations in seabird colonies requires recruitment either of natal birds or birds native to other islands. The POBSP banded slightly over 1,000,000 Sooty Terns at Johnston Atoll and all other major colonies within 2,000 miles of Johnston. This effort provided a unique opportunity to ascertain which method of recruitment is most important. Between 1963 and 1971 more than 10,000 banded Sooty Terns were captured at Johnston Atoll, and only 118 of these had been banded at other islands. Of these 118 immigrants, 10 were recorded as breeding on Sand Island (Table 3), but only three were known to have been breeders or chicks at other

TABLE 1.

Estimates of numbers of adults, eggs, and chicks of Sooty Terns at Johnston Atoll, Pacific Ocean, March-July 1967.[a]

Date of count	No. adults	Nests with eggs	No. chicks	Size of chicks (percent) small	medium	large
15 March	200,000 ±25%	64,000 ±10%	0	0	0	0
31 March	300,000 ±25%	128,000 ±10%	2,000 ±50%	100	0	0
15 April	300,000 ±25%	66,000 ±10%	16,000 ±25%	90	10	0
30 April	300,000 ±25%	23,000 ±10%	64,000 ±10%	70	30	0
15 May	400,000 ±25%	5,000 ±50%	90,000 ±50%	25	25	50
31 May	400,000 ±25%	1,500 ±25%	40,000 ±25%	10	20	70
15 June (day)	50,000 ±50%	500 ±25%	50,000 ±25%	5	10	85
(night)	200,000 ±50%					
9 July (08:00)	75,000 n.r.	5	30,000 ±25%	0	2	98
14 July (14:00)	50,000 n.r.	0	20,000 ±25%	0	0	100
30 July (08:00)	15,000 ±25%	0	5,000 ±10%	0	0	100
(14:00)	10,000 ±25%		3,000 ±10%	0	0	100
(23:00)	30,000 ±25%		10,000 ±25%	0	0	100

[a]March-April estimates by P. C. Shelton, others by author.
n.r.—estimate of error not recorded.

TABLE 2.

Numbers of Sooty Terns banded at Johnston Atoll, 1963-1969.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Total
1963 adults	0	0	0	0	0	0	3,700	8,400	3,100	15,200
chicks	0	0	0	0	0	0	1,500	0	100	1,600
1964 adults	3,806	8,900	4,000	0	500	900	4,500	200	400	23,206
chicks	0	0	0	0	6,700	13,300	1,000	0	0	21,000
1965 adults	0	200	2,053	2,457	2,200	3,400	12,900	9,500	0	32,710
chicks	0	0	0	500	10,800	7,600	2,500	0	0	21,400
1966 adults	5,100	10,100	16,800	30,000	6,000	7,913	10,085	5,850	0	91,848
chicks	0	0	0	0	4,000	16,000	5,500	0	0	25,500
1967 adults	0	400	100	300	100	0	0	0	0	900
chicks	0	0	0	0	5,000	6,500	1,500	0	0	13,000
1968 adults	0	0	0	0	0	0	0	0	0	0
chicks	0	0	0	500	13,000	1,500	0	0	0	15,000
1969 adults	0	0	0	0	0	0	0	0	0	0
chicks	0	0	0	36	464	21,200	0	700	0	22,400

TABLE 3.

Sooty Terns breeding at Johnston Atoll that were banded in other colonies.

Band number	Island and date of banding	Breeding status when banded	Date recaptured at Johnston Atoll
743–30121	Wake, June 1963	U	11 March 1968
793–99854	Midway, July 1964	U	07 March 1968
813–75129	Midway, July 1964	chick	25 May 1971
813–80536	Wake, May 1965	U	03 May 1969
903–08034	Kure, June 1966	breed. ad.	06 April 1971
903–17423	Kure, June 1967	U	16 April 1968
903–82859	Laysan, June 1966	U	23 May 1969
913–25783	Wake, June 1966	U	19 May 1969
913–27188	Wake, June 1966	breed. ad.	20 March 1971
913–27232	Wake, June 1966	U	11 April 1969

(U = breeding status unknown)

colonies. The circumstances of capture for the remaining 108 suggest they were not breeding at Johnston. Virtually all were known to be young birds and perhaps had yet to breed anywhere. From these observations I conclude that at Johnston Atoll immigration is a negligible source of breeding recruits and that the most important source of new breeding terns, by far, is natal birds.

Age of First Breeding

Although more than a million Sooty Terns have been banded in the Pacific and the Gulf of Mexico, and literature regarding their breeding is extensive, no one has established the ages at which the species first breeds. Part of the difficulty in establishing this aspect of behavior is that no external morphological feature identifies a breeding individual. Even the presence of a brood patch, which is considered proof of breeding in many bird species, is useless as non-breeding Sooty Terns often have bare brood patches (see below).

Starting in 1966, I captured banded Sooty Terns at Johnston in order to obtain a large sample of known-age birds. It soon became clear that my two methods of netting, on the ground and in the air, were sampling different age groups. Unknown-age, breeding adults were preponderant among the birds caught on the ground, while known-age birds, most of which subsequently proved to be non-breeding, were captured mostly from the air.

A few plumage characteristics suggest young age in Sooty Terns, the best of which is the presence of feathers with pale edges in the black dorsal plumage or feathers with dark edges in the white ventral plumage or on the forehead. Unfortunately this speckling is uncommon, at least at Johnston Atoll. In 1968, for example, only 30% of 227 three-year-olds, 11% of 830 four-year-olds, and 5% of 105 five-year-olds showed any speckling. Young birds also often have newer, less worn plumage than adults, but exceptions are frequent. Thus no known plumage feature distinguishes all young from older birds. I finally resolved that only the observation of a Sooty Tern incubating an egg was a good criterion for breeding.

Sooty Terns of ages four through eight years were captured on eggs at Sand Island in 1971. At this time known-age birds older than eight years of age did not exist. Of the 348 known-age birds captured on eggs, only five were four-year-olds. No other terns four years old or younger were ever found breeding even though circumstances allowed for this during three other seasons. The much larger number of five-year-old than four-year-old Sooty Terns incubating in 1971 (Table 4, column 1) suggests that many more Sooty Terns mature at age 5 than at age 4. The actual number of 6-year-olds captured on eggs was even larger, but the number of 7 and 8-year-olds declined (Table 4).

TABLE 4.

Numbers and age of banded Sooty Terns caught on eggs and in the air at Johnston Atoll, March-June 1971.

1971 age in years	Fraction caught on eggs in 1971[a]	Percent of original number banded that were on eggs in 1971	Percent caught in 1971 that were on eggs
over 8[b]	1333/2135	2.62	62
8	23/57	1.44	40
7	88/450	0.42	20
6	130/842	0.61	15
5	102/1366	0.40	7
4	5/562	0.04	0.9
3	0/421	0	0
2	0/7	0	0

[a]The numerator is the absolute number caught on eggs. The denominator is the combined number of those caught in the air and those caught on eggs.

[b]Virtually all were old, experienced breeders in 1971. See text for explanation.

Comparing the actual numbers of breeding terns of known-age, as done above, ignores two important factors: the number of chicks banded and mortality with time. The first of these variables is eliminated if the number caught incubating is expressed as a percentage of the number banded. By this method (Table 4, column 2) a more pronounced trend towards increasing numbers of older birds incubating exists. This percentage method continues to ignore mortality through time as well as differential mortality of different year classes. I have not devised any method using the total number of terns banded to compensate for mortality.

A method of measuring the integration of known-age birds into the breeding population suggested by William B. Robertson, Jr. (pers. comm.) uses combined numbers of known-age birds captured in the air and incubating as the total sample. The basis for using this measure is the fact that Sooty Terns return to their natal colony several years prior to their first breeding. I first suspected this to be true by comparing ages of banded birds netted from the air and on eggs and found that most of the younger, known-age Sooty Terns were captured in the air as opposed to on eggs. To verify that most birds captured in the air were not breeding, in 1968 I observed almost 1,800 known-age Sooty Terns caught from the air and marked with conspicuous plastic streamers. Not one of these birds was seen on an egg despite intensive search.

The method of using returnees of various year classes as the total sample minimized mortality as a factor in quantifying the fraction of different age classes that breed. By this method an ever increasing percentage of birds ages four through eight were caught incubating eggs (Table 4, column 3). For comparative purposes row 1 in Table 4 includes data for birds caught in 1971 and banded between January and March, 1964-1966. As virtually all birds banded during these months were on eggs I consider them experienced breeders. By comparing these experienced breeders with 8-year-olds I conclude that even by 8 years of age not all Sooty Terns breed. Comparative data collected in 1970 at Dry Tortugas, Florida, showed some Sooty Terns there were not breeding at age 9, but that virtually all 10-year-olds were breeding. Thus, as has been suspected for Sooty Terns (Robertson, 1969) and demonstrated for many other colonial seabirds such as Yellow-eyed Penguins, *Megadyptes antipodes* (Richdale, 1957),Adelie Penguins, *Pygoscelis adeliae* (Ainley, 1973a), Laysan Albatross, *Diomedea immutabalis* (Fisher and Fisher, 1969), Black-legged Kittiwakes, *Rissa tridactyla* (Coulson, 1966), and Gannets, *Morus bassanus* (Nelson, 1966), the Sooty Tern exhibits deferred maturity which in the case of the tern is longer than for any other member of its family (see Lack, 1968).

Time and Location of Breeding

Most studies of colonial seabirds show that young birds breed later in a season and at different locations in a colony than older birds (e.g. Fisher, 1969). Based on an analysis of records for 348 known-age birds captured on eggs at Johnston in 1971 I conclude that Sooty Terns also exhibit these phenomena. Table 5 shows that more known-age breeders were captured after than before 30 April, the date that separates earliest from latest periods of laying. This same table shows that older known-age individuals tend to breed earlier than the younger known-age individuals. For example, only 45% of the breeding 7 and 8-year-olds were caught after 30 April whereas 90% of breeding 4 and 5-year-olds were caught in the same period.

Most young Sooty Terns did not nest among older, earlier breeding birds. Figure 2 shows where laying occurred on Sand Island

TABLE 5.

Numbers of known-age Sooty Terns caught on eggs before and after 30 April 1971.

	4-year-olds	5-year-olds	6-year-olds	7-year-olds	8-year-olds
Before 30 April	0	10 (10%)	36 (28%)	50 (57%)	10 (43%)
After 30 April	5 (100%)	92 (90%)	94 (72%)	38 (43%)	13 (57%)

before and after 30 April. Those terns that began nesting after 30 April layed on portions of the island that had not been used, or had been totally deserted by 18 March, when I arrived, and not at the 40,000 $\pm 50\%$ deserted sites interspersed among the early breeders (Fig. 2, stippled areas). In the early nesting areas only 5% of banded birds were known-age, but in late nesting areas 41% were known-age.

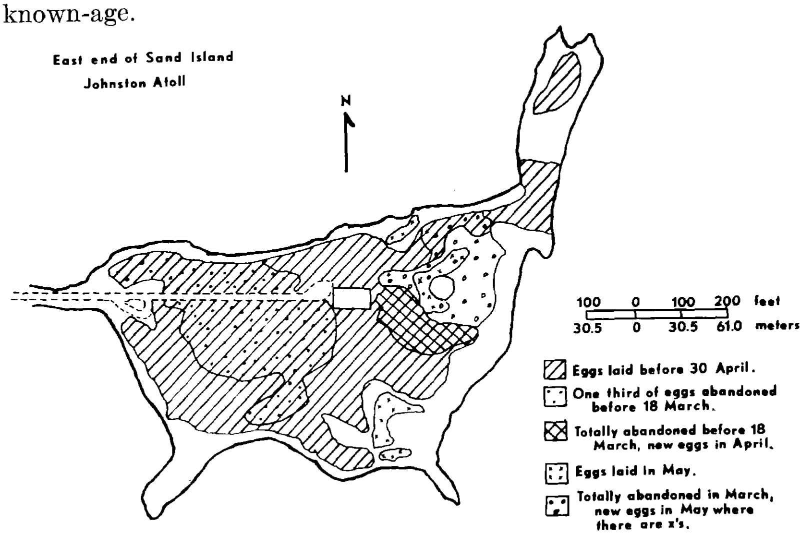

FIGURE 2. Locations where laying and abandonment of Sooty Tern eggs occurred at Sand Island, Johnston Atoll in 1971.

Age of Mates of Young Adults

Sooty Terns tend not only to nest with similarly aged neighbors, but also with similarly aged mates. After 30 April 1971, 39 banded pairs were captured while on eggs of which 14 were composed of known-age birds as follows:

both partners of unknown-age	19 pairs
one partner known-age, other unknown-age	6
both partners same age	4
one partner a year older than mate	7

one partner two years older than mate	2
one partner three years older than mate	1

Because the unknown-age birds in this sample were captured originally from the air in late summer, they were likely to have been adolescents when banded and therefore of similar age. Even disregarding this probability, pairing is clearly age-related. If pairing had been random among the 78 birds comprising the 39 pairs, then 12 pairs would have had both partners of unknown-age, 8 pairs would have had both members of known-age, and 19 pairs would have had mixed known and unknown-age mates. A Chi-square test shows highly significant differences ($P < .01$) between the expected random and the observed age composition of these mated pairs.

I have few data on ages of both individuals for Sooty Tern pairs incubating before 30 April. Between 13 and 21 April I caught twelve banded pairs from which only one individual was known-age. This 6-year-old was paired with an old bird known to have bred in April 1966.

Nesting Habitats and Nest Failure

Sooty Tern nesting habitats on Sand Island range from bare, open sand and coral rubble to sand that supports scattered vegetation. Observations in years prior to 1971 suggest that nest success is affected by nest habitat, and also that young adults often are relegated to nesting in the poorer, more open and featureless areas. Therefore, comparing breeding success between the seemingly poor, featureless, natural habitats, and the seemingly better featured, natural habitats may actually compare nest success of different aged birds, for as already mentioned, the age of birds breeding in different habitats apparently varies. Therefore I tested the effects of habitat quality on breeding success by manipulating surface features on three contiguous $9m^2$ plots, all of which were ultimately used by birds laying between 1-3 April and therefore presumably of similar breeding experience. The three plots were cleared of all major surface features prior to laying. One was left bare, in another 120 plastic stakes were aligned in rows, and in the third 100 rocks about the size of oranges were scattered approximately every $900cm^2$. The results of this experiment suggest a major source of nest failure is egg-abandonment (Table 6), and that abandonment is especially frequent on bare ground. The results further suggest that heterogeneity of features may increase nesting success (Table 6).

Seasonal Variation in Numbers and Arrival Times of Different Age Groups

Although many known-age Sooty Terns captured at Sand Island in 1971 were known to be breeding, most were caught flying over the colony and apparently were not breeding (Table 4). My observations also show that the dates when adolescents first visit the colony and the numbers of each age class that visit are age-related, and that in different years the times vary when groups of identical age return. In 1968, I caught about 1,700 known-age terns from the air, but

TABLE 6.

Sooty Tern nesting success on different manipulated habitats.

Plot type	No. of eggs on 6 April	Av. distance between eggs in cm.	No. of eggs on 15 April	Percent abandoned	No. of eggs on 28 April	Percent abandoned
Bare	44	47	65	34	63	71
Aligned stakes	?	40	63	25	71	62
Scattered rocks	53	41	70	19	67	24

despite intensive netting of incubating and standing birds, only 31 were captured on the ground, none of which was on eggs. Few of the known-age birds captured in 1968 were netted prior to 30 April even though intensive netting from the air was begun on 1 March. Numbers of known-age birds captured increased slowly in early May, and rapidly after 15 May (Fig. 3), a date that corresponds to the approximate date when chicks began to fly. Figure 3 also shows that older adolescents tended to visit the colony on earlier dates and in greater numbers than younger adolescents. For example, by 31 May I had netted 15% of all 1,194 four-year-olds captured, but only 5% of the 441 three-year-olds caught in all of 1968.

That young adolescent Sooty Terns return to the colony in lower numbers than older adolescents was shown earlier (Table 4); these same observations suggest that the age at which maximum numbers return as non-breeders is five or six years. For example, in all of 1968 I captured less than 0.1% of the chicks banded in 1966, but 2% of those banded in 1965, 6% of those banded in 1964, and 8% of those banded in 1963. This trend toward more birds returning with increased age has been shown for a few other colonial seabirds, and especially well documented for *Diomedea immutabilis* (Fisher and Fisher, 1969).

Brood Patch Condition of Adolescents

A pair of brood patches occurs in both sexes of Sooty Terns, with one patch on either side of the prominent breast keel. In external appearance Sooty Tern brood patches may be fully feathered (inactive), defeathering, wholly bare, or refeathering (all active categories). I have never found a bird with inactive brood patches incubating an egg. Most active patches have reddish skin, but in some young breeding birds and many non-breeding birds it is violet. I have insufficient data to determine whether patch color relates to age or to other factors such as amounts of subcutaneous fat, degree of vascularization, and/or edema.

Ornithologists frequently use the presence or absence of a brood patch for determining breeding status of birds, but in the case of Sooty Terns, certain other larids (e.g. *Larus ridibundus*, Lange,

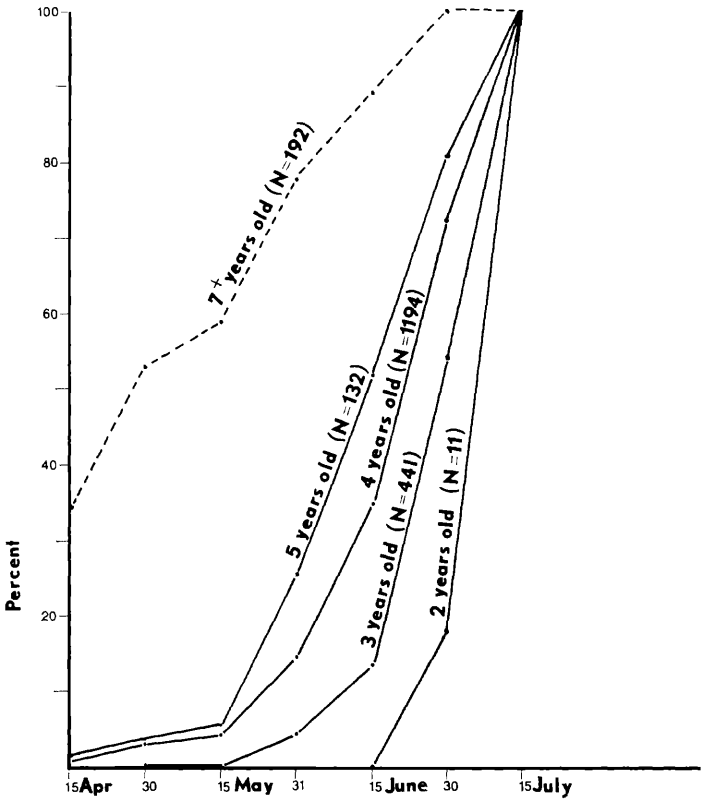

FIGURE 3. Cumulative percentages for numbers of known-age Sooty Terns caught in the air, Johnston Atoll, April-July 1968. Broken line indicates birds caught on eggs in 1964 when they were almost certainly more than five years old.

1928) and some colonial seabirds (e.g. Ainley, 1973a; Wilbur, 1969) this criterion can be misleading because adolescents frequently have bare brood patches. In 1967, when no known-age birds were breeding at Johnston Atoll, 83% of 124 four-year-olds, 54% of 565 three-year-olds, and 19% of 47 two-year-olds had active patches when first captured. One aspect of these data that complicates interpretation is the fact that many individuals captured early in a given year have inactive brood patches, but when caught later in the same year have active patches. In 1971, 63 of 70 birds that had inactive patches when first captured had active patches when examined later. Thus, while the frequency of inactive brood patches is age-related the actual percentage of each age class that develops active patches could be more nearly alike than my data on captured birds indicate because of the seasonal factor. The brood patch data have some meaning, however, for they show year-to-year consistencies for individual birds. For example, Table 7 shows that individuals having active brood patches when first caught at age three had active

TABLE 7.

Brood patch condition for Sooty Terns caught when 3 years old and again when older.

	No. caught in 1967	No. recaptured in 1968	No. active in 1968[a]	Expected no. active in 1968[b]	No. active in 1969 or 1971
3-year-olds with inactive brood patches in 1967	114	84	51 (61%)	70	31 (100%)
3-year-olds with active brood patches in 1967	135	115	103 (90%)	83	21 (100%)

[a]Considers brood patch condition only upon first capture in 1968.
[b]Expected numbers are calculated as in the Chi-square Test.

patches more frequently when first caught at age four than those which had inactive patches at age three. Other information suggests that all adolescents have active brood patches when visiting the colony two years after their first visit regardless of absolute age. For example, all birds that were first captured at age three had active patches when first caught at age five (n = 31), but 7 of 44 birds first captured at age four did not have active patches when first caught at age five.

TABLE 8.

Brood patch frequencies for known-age Sooty Terns with speckled and unspeckled plumage, Johnston Atoll, May-June 1968.

	Unspeckled birds			Speckled birds		
Age in years	No. with active patches	Percent	No. with inactive patches	No. with active patches	Percent	No. with inactive patches
5	86	90	11	3	—	2
4	559	76	176	44	46	51
3	75	47	85	11	16	56

The frequencies of active brood patches seem to vary not only between age classes, but also among certain groups within identical age classes. For example, adolescents with traces of immature speckled feathering in the plumage have lower frequencies of active brood patches than unspeckled birds (Table 8). Similarly, adolescents having arrested primary molt (i.e. having all primaries full-grown, but proximal feathers distinctly newer than distal feathers) have lower frequencies of active brood patches (Table 9).

TABLE 9.

Brood patch frequencies for known-age Sooty Terns with and without arrested molt, May-June 1968.

	No arrested molt			With arrested molt		
Age in years	No. with active patches	Percent	No. with inactive patches	No. with active patches	Percent	No. with inactive patches
5	78	90	9	11	73	4
4	468	75	152	135	64	75
3	47	39	74	39	25	67

The Relationship of Age During Colony Visits to Subsequent Breeding Age

In preceding sections I have shown that the frequencies of active brood patches, speckled plumages, arrested molt, and ages at which adolescents first return to Johnston Atoll are all age-related. This suggests that these traits probably are related to different degrees of physiological maturity, and that the variation exhibited within specific age classes reflects variable rates of maturation. One of these traits, the development of active brood patches, is known to be influenced by reproductive hormones in at least one larid (e.g. *Larus atricilla*, Segrè, 1965) and reproductive hormones have well known influences on brood patches in many other bird species (Jones, 1971). Because of the variable degrees of physiological maturity that apparently exist within adolescent age classes (e.g. Tables 8 and 9), it is difficult to verify statistically a direct relationship between ages when adolescents first visit Sand Island and age of first breeding. The data in Table 10, though suggestive, are not statistically significant ($P > 0.05$). As noted, I believe the lack of statistical significance is caused by the large variation in degree of maturity that exists within identical adolescent age classes. To minimize this variation I tested for differences in numbers of breeding birds of equal age that when caught at 3 or 4 years of age in 1967 or 1968 had either active or inactive brood patches. A significantly larger number ($P < 0.05$) of those that had active patches when caught as adolescents were found breeding in 1969 or 1971 (Table 11). Similarly, a significantly greater number of birds ($P < 0.05$) that were caught standing on the ground when adolescents were found breeding in 1969 or 1971 than birds that were caught only in the air when adolescents (Table 12).

In summary, my data suggest that a correlation exists between ages of first breeding and ages of first colony visits, for I have shown a relationship between age and active brood patch frequencies, and between adolescent brood patch activity and breeding age.

TABLE 10.

Numbers of 6- and 7-year-old Sooty Terns breeding at Johnston Atoll in 1971, that were known to visit the colony first at age three, four, or five.

Age when first captured[a]	Known breeding in 1971[b] Number	Known breeding in 1971[b] Percent	Not known breeding in 1971[b] Number	Not known breeding in 1971[b] Percent
3 years	20	16	103	84
4 years	14	13	96	87
5 years	1	8	12	92

[a]None were known breeding when first captured.

[b]No statistically significant difference between numbers known and not known breeding.

TABLE 11.

Relationship between adolescent brood patch activity and numbers breeding for Sooty Terns banded as chicks at Johnston Atoll, Pacific Ocean in 1964.

	Brood patch condition in 1967 or 1968[a]	No. known breeding in 1969 or 1971	Expected number breeding
Active	240	29	22.73
Inactive	161	9	15.25

[a]All were almost certainly adolescents when captured.

TABLE 12.

A comparison between breeding numbers of 7-8 year old Sooty Terns at Johnston Atoll which as adolescents were captured either on the ground or in the air.

	No. of 7-8 year olds caught in 1971	No. that had been caught on the ground in 1967-1969	Expected number[a]
Breeding in 1971	52	6	2.97
Not known to breed in 1971	158	6	9.02

[a]Expected numbers are calculated as in the Chi-square Test.

Annual Variation of Initial Breeding Ages

In the previous section I presented information showing that either genetic and/or environmental events occurring during adolescence probably influence ages at which Sooty Terns first breed. This evidence does not exclude the possibility that other factors, occurring at or near the colony island, also influence ages of first breeding. In fact, information collected in 1969 and 1971 indicates that considerable variation exists in numbers of young birds breeding in the two years. In 1971, 108 four- or five-year-old Sooty Terns were found incubating eggs, but in 1969 no 4-year-olds and only 16 5-year-olds were found incubating. Highly significant differences ($P <$ .001) exist for numbers of 5-year-olds breeding in these two years (Table 13). This difference could be the result of higher mortality of year-1964 chicks than year-1966 chicks; therefore I compared the number of each age class captured at age three. Four-year-olds could not be compared because no field work was done in 1970. In 1969 virtually all netting of Sooty Terns from the air was in June; therefore the comparison between 1967 and 1969 is restricted to this month. No significant difference in numbers between either class existed ($P > 0.90$); hence mortality at least through age three appears to have been similar. The same analysis, but with smaller samples, was performed for six-year-olds in 1969 and 1971, and again no evidence of significantly different mortality between the two classes was found ($P > 0.50$). Therefore it seems reasonable to conclude that a greater number of young Sooty Terns were breeding on Sand Island in 1971 than in 1969.

TABLE 13.

A comparison between numbers of 5-year-old Sooty Terns breeding at Johnston Atoll in 1969 and 1971.

	No. of banded birds caught on eggs	No. of 5-year-olds per 10,000 originally banded	Expected number per 10,000 banded
1969	4,359	7.62	28.26
1971	3,046	40.39	19.75

Selected Aspects of Adolescent Behavior

The daily cycles of arrival for adolescent Sooty Terns at Sand Island cannot be documented by direct observation as most individuals are constantly flying and cannot be followed in the milieu of other birds. Capture rates suggest highest numbers are at the colony in early morning and evening, but these data do not indicate when adolescents arrive at the colony. Furthermore, these data do not give a comparison of arrival times for adults and adolescents because adults tend to avoid stations where I netted from the air. In order to document the times of day when adolescents arrive I counted streamer-marked adults and adolescents flying by a selected point enroute to Sand Island on two days in June 1968. These daylight counts (Fig. 4) show that numbers of birds approaching the colony were highest before 10:00 and after 18:00, and that the proportion of marked adolescents to marked adults was highest at these same times ($P < .001$). From these observations I conclude that most adolescents visit the colony during the evening, but that many also visit during early morning.

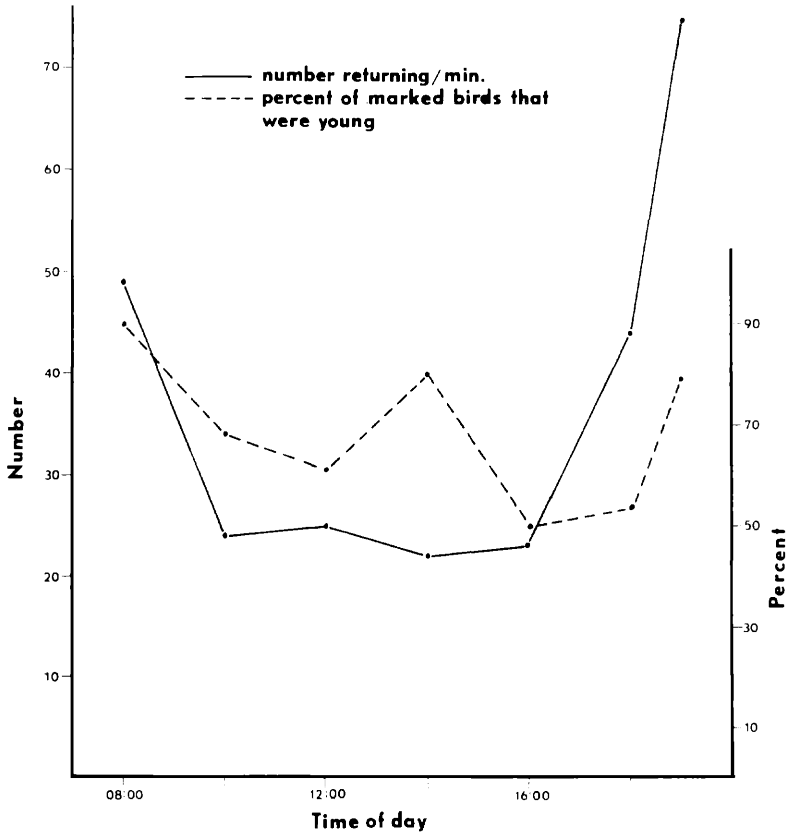

FIGURE 4. Summary of counts that show times of day when maximum numbers of Sooty Terns return to Sand Island and the relative proportion of streamer-marked adults to streamer-marked adolescents at different times of day. Sample sizes for marked birds at each point, left to right, are: 71, 23, 13, 10, 24, 57, and 62.

In 1968, I also counted flock size for birds returning between 18:00 and 19:00 on 23 May in order to ascertain whether most of the returning birds were in twosomes. Twosomes occurred with greater frequency than any other flock size (Table 14). Based on observations of streamer-marked birds I suspect most of the twosomes were adolescents whereas single birds were adults.

TABLE 14.

Frequencies and size of Sooty Tern flocks at Johnston Atoll with Chi-square values.[a]

No. of birds per group	No. of 5 second intervals in which flock size occurred.	Expected frequency	Deviation from expected	Chi-square value
0	339	311.1	27.9	2.4
1	16	62.2	−46.2	34.3
2	18	6.2	11.8	22.3
3	4	0.4	3.6	29.1
4	3	0.02	3.0	403.1

[a]The frequencies do not fit a Poisson Distribution, most likely due to disproportionately high frequencies of flocks of two.

The time of day when adolescent Sooty Terns visit Sand Island varies with age, season, and apparently with brood patch condition. During May younger adolescents tend to visit in the evening whereas older adolescents tend to visit in the morning (Table 15). As the season progresses, younger birds are caught more often in the morning. For example, in May significantly greater numbers of 4-year-olds visit Sand Island in evenings as compared to mornings ($P < 0.05$), but in August significantly fewer are caught in evenings ($P < 0.05$). Similarly, in May significantly more 3-year-olds visit in the evening ($P < 0.01$), but in August roughly equivalent numbers are caught both morning and evening ($P < 0.50$). Birds visiting in the morning also tend to have active brood patches more frequently than birds of equivalent age visiting in the evening (Table 16).

TABLE 15.

A comparison between age and the time of day that adolescent Sooty Terns were captured from the air at Johnston Atoll in May, 1971.

	Total no. of known age	Percent of total that were:			
		ages 6-8	age 5	age 4	age 3
Morning (dawn-10:00)	634	27	40	18	15
Evening (16:00-dusk)	1,530	19[b]	37 ns	23[a]	21[b]

ns Not significantly different frequencies between morning and evening ($P > .05$).

[a]Significantly different frequencies between morning and evening ($P < .05$).

[b]Highly significant difference of frequencies between morning and evening ($P < .01$).

TABLE 16.

The frequency of active brood patches in known-age Sooty Terns caught from the air at different times of day at Johnston Atoll, August 1967 and 1969.

	No. of 4-year-olds	Percent with active brood patches	No. of 3-year-olds	Percent with active brood patches	No. of 2-year-olds	Percent with active brood patches
Morning (before 10:00)	34	86	117	61	13	36
Evening (after 16:00 but before 20:00)	17	76	147	49	19	21
Night (after 20:00)	19	63	41	36	2	—

Most adolescents at the colony spend their visiting time flying five to fifteen feet over individually chosen sectors of the island. Many also try to land among breeding birds, but in most cases they are successfully opposed by low intensity threat postures of standing or incubating adults or standing adolescents. Even when successful, landings are often of short duration, for with slight aggression from the adults young intruders leave. Despite such aggression, adolescents persist in trying to land in breeding areas even though several large and unoccupied areas usually are available nearby. A few of these unoccupied areas, and especially a road running through the middle of the colony (Fig. 2), are used for standing by some adolescents, but only by a small percentage of those visiting the island. These observations are supported by data collected from banded birds. For example, Table 17 compares numbers of known-age birds standing in breeding and nonbreeding areas from May through August 1968 and 1969. Significantly ($P < .001$) more known-age birds were caught in standing areas (1969 columns, Table 17) than in breeding areas (1968 columns, Table 17). The lower numbers of adolescents standing in breeding areas probably results from the tendency of young birds to avoid aggression from adults in breeding areas. This is further supported by other information in Table 17, specifically the significantly increased frequencies ($P < .001$) of adolescents on the ground in breeding areas in July 1968 compared to May or June, 1968. Whether this increase is caused by declines in numbers of adults is not apparent in the table. However, counts of standing birds on study plots in breeding areas show that the late season increase probably is attributable to both a decline in numbers of adults at the colony and an increase of adolescents on the ground. This conclusion is verified by sporadic counts of marked standing

TABLE 17.

Relative numbers of banded known and unknown-age Sooty Terns standing in breeding (1968) and non-breeding (1969) areas at Johnston Atoll.

Age in years	May 1968	May 1969	June 1968	June 1969	July 1968	July 1969	August 1968	August 1969
5-6	1/440[a]	14/104	5/626	10/98	2/188	16/70	—	35/120
4	2/440	17/104	4/626	15/98	18/188	12/70	—	45/120
3	0/440	2/104	0/626	1/98	3/188	2/70	—	6/120
2	0	0	0	0	0	0	—	0
Total	3/440	33/104	9/626	26/98	23/188	29/70	—	86/120

[a]Numbers of young, known-age (numerator) and total numbers of banded birds (denominator) caught on the ground. See text for additional details.

adults and adolescents in 1968. Therefore, it appears that some adolescents do land in breeding areas, but not until the areas are partly or temporarily vacated by nesting adults. While in the breeding and standing areas during the day, adolescents often court with other standing birds. I have not made sufficient observations of their behavior to make precise comparison with adults, but certain aspects are conspicuously different. Most prominent is the frequent incidence of attempted rape, which often appears to be performed without sexual discrimination. Also conspicuous are adolescents apparently courting chicks.

The numbers of different-aged adolescents that land on Sand Island apparently are age related. For example, after making adjustments for numbers of each age class originally banded, 4-year-olds were caught on the ground about 10 times more frequently than 3-year-olds in 1968-1969. In the air, however, 4-year-olds were only about three times more abundant than 3-year-olds. Most of the adolescents caught on the ground had active brood patches. For example, from late June to late August of 1967-1969, 237 Sooty Terns 3-6 years old were caught roosting. Only nine (3%) had inactive brood patches whereas about one-third of the birds the same age caught from the air in the same period had inactive brood patches.

My behavioral observations show that young birds judged males by behavior often stand on the ground during the day and maintain display sites. Unmated females apparently are attracted to these males, thereby allowing adolescent pair bonds to form. I have no information on whether these pairs remain intact for more than a week or two, or whether such pairing facilitates initial breeding in later years.

In order to determine whether visiting the colony one year affects the time when adolescents visit in subsequent years, I compared

1967 and 1968 capture data from birds banded when chicks in 1964. Figure 5 compares capture dates for 3-year-olds caught in the air in 1967 to 4-year-olds caught in the air in 1968 that had not been captured at age three, and to 4-year-olds that were captured in the air when age three. The 1968 capture dates for these two groups are not significantly different ($P > 0.05$). All but one of a small sample of year-1964 birds that were caught in both 1967 and 1968, and on the ground in at least one of these two years ($n = 8$), returned before 10 June 1968 when age four (Fig. 5). The difference of capture dates between these and birds caught only in the air is highly significant ($P < .001$).

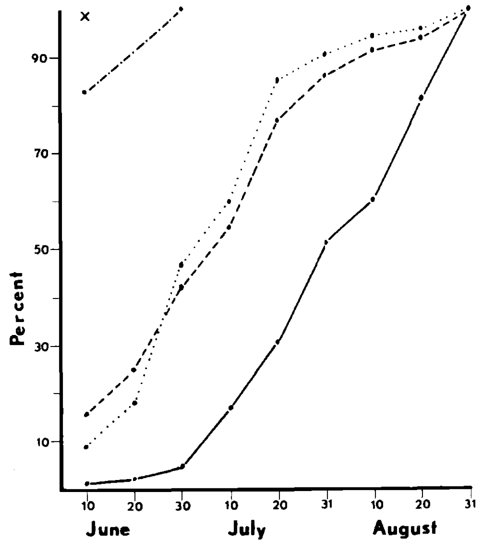

FIGURE 5. A comparison of capture dates by cumulative percentages for 3- and 4-year-old Sooty Terns that were banded as chicks in 1964 and caught in the air and/or on the ground in 1967 or 1968. The solid line indicates birds first captured in the air in 1967 when age three. The dashed line indicates birds first captured in the air when age four in 1968. The dotted line indicates birds captured in the air in 1968 which had also been caught in the air in 1967. The dotted and dashed line indicates 6 birds captured on the ground in 1967 when age three and again when age four in 1968. The X stands for 2 birds caught in the air in 1967, caught in the air before 10 June 1968, and caught on the ground between 3 and 10 July 1968. All samples are of 111 birds except where smaller samples are noted. The 111 birds caught for the first time in 1968 are randomly selected from a much larger sample. These cumulative percentages are not comparable to those in Fig. 3 due to differences of months in which data were collected.

Pre-laying Behavior of Adults

The pre-laying behavior of early laying Sooty Terns at Johnston is similar to that reported for Dry Tortugas (Robertson, 1964; Dinsmore, 1972) and other islands (e.g. Ashmole, 1963a). However, certain observations collected from notes of POBSP personnel, and especially Kenneth Amerman, Ralph W. Schreiber, and Philip C. Shelton, and my own personal observations at Johnston and Dry Tortugas, give additional details of pre-laying behavior relevant to topics discussed below.

In Sooty Tern colonies researchers have commonly found protracted periods of group aerial behavior two to three months prior to egg-laying (e.g. Ashmole, 1963a). Discreet flocks, which are small during early phases but may number many thousands later, swarm near the shore of nesting islands in the evening or at night. After dark these swarms may move over the island, but no birds land until about a month after first swarming. As the season progresses swarms begin appearing near shore in late afternoon, and move over the island at night, and many birds land. Usually most birds depart between 02:00 and 04:00 except for a short period before the beginning of egg-laying when birds remain on the island until dawn or shortly after. While on the ground at night during this and later phases of breeding, aggressive behavior between neighboring birds is infrequent (Ashmole, 1963a; personal observations).

The first day on which more than a few Sooty Terns remain on the island much after dawn is also the first day on which appreciable numbers of eggs are laid (pers. obs.). But still, most birds leave at dawn. The behavior of birds that remain contrasts with that seen at night in that fervent aggression among neighbors establishing nest sites is conspicuous. During this early laying stage virtually all of the Sooty Terns on the ground during the day have active brood patches. For example, in February through March 1967 Philip Shelton caught 51 Sooty Terns standing, but not incubating, and 50 had active brood patches. At night, however, only 66 of 101 standing birds had active brood patches. The frequencies of active brood patches on birds caught from the air in the same period were quite different: 81% of those caught in the day (n = 279), but only 5% of those caught at night (n = 756) had active patches. These data suggest that older breeding birds that have inactive brood patches, and therefore have not yet laid eggs, visit the colony mostly at night, or if they visit during the day they usually do not land.

Soon after initial seasonal egg-laying, swarming behavior stops. At Dry Tortugas I saw no swarming after the first day on which more than a few eggs were laid, and Dinsmore (pers. comm.) also recalls that swarming stopped soon after laying began. Yet at all colonies I have observed, laying continues long after swarming stops.

My observations show that many birds that have not laid eggs visit the colony island at night (Table 18). Many of these arrive at the island in late afternoon, but instead of forming swarms offshore, fly directly to the island and either land near or fly over birds that have already laid eggs. Thus, it appears that after laying begins, birds that have not laid eggs do not form aerial swarms, but rather are attracted to groups of birds that already are on the ground at the island.

Since Sooty Tern swarming behavior usually stops soon after first appreciable numbers of eggs are laid, it is possible that late breeders never participate in this activity. That this is correct is substanti-

TABLE 18.

Sooty Tern egg densities (no. per square foot), diurnal and nocturnal adult densities (no. per square foot) on the ground, areas occupied (square feet), and total numbers on the island calculated from nine 100-square foot plots, March, 1967, Johnston Atoll. Data from Shelton (unpublished POBSP report, March, 1967).

	Eggs			No. of adults (daytime)			No. of adults (night)		
	area	density	total	area	density	total	area	density	total
7 March	104,000	.23	24,000	104,000	.45	47,000	149,000	—	—
15 March	198,000	.32	64,000	198,000	.40	79,000	263,000	.47	124,000
23 March	283,000	.38	107,000	283,000	.43	120,000	311,000	.48	149,000
31 March	303,000	.42	128,000	303,000	.46	140,000	331,000	.52	172,000

ated by the fact that I have never found adolescents or suspected young birds among over 450 banded, experienced breeders that died from striking guywires at Sand Island during swarming phases of colony formation. Furthermore, I have not seen swarming activity at colonies during the period when late-breeders arrive. Instead, much pre-laying behavior by young adults, i.e. young birds probably pairing for the first time, occurred in standing areas, the location of which bore no apparent relationship to definitive nest sites. Other Sooty Terns using the same standing areas included a few established breeders, adolescents, and other pairs of young adults. In general, the behavior of each group was different. Both partners of young adult pairs were noticeably territorial and usually were successful in defending large areas, sometimes more than 30 ft^2, against other adults or adolescents. Often, when no intruders were present, males walked as far as six feet to challenge neighbors, especially if their mates were momentarily absent. Still, aggressive behavior was typically of lower intensity than that seen during nest-site establishment, there being few "Crouch" postures (Cullen, 1956; also called "Face-offs" by Dinsmore, 1972) and little physical fighting.

Most adolescents using the same roosting area were less aggressive than the young adults. While they frequently "Paraded" (see Palmer, 1941) with other adolescents, and often attempted copulation, they rarely defended an area and were easily supplanted, even by other, and usually older, adolescents.

After the roost phase of courtship most pairs of young adult Sooty Terns move to areas where other young pairs are establishing nest sites. Here they engage in intense aggression with neighbors which is typified by frequent "Crouch" posturing, physical fighting, and nest-scraping. Fighting continues until the egg is laid one to three days later. During nest establishment, pairs fight for small territories at many sites over a large area, make many nest-scrapes, but apparently do not establish a permanent nest site until the single egg is laid.

The above behavioral observations together with information gained from banding, suggest that young Sooty Terns must pass at least four stages before first breeding: (1) returning to the colony, (2) landing, (3) obtaining and defending a territory within a standing area, and (4) successfully obtaining a nest site. Through stages two through four young Sooty Terns must withstand increasingly intense aggression. Data presented earlier suggest transition between stages one and two probably is influenced by hormones associated with brood patch development. Still, birds in stage two are easily driven from standing sites by neighbors or other birds landing, but in stage three they successfully defend these standing sites. Data presented earlier also suggest the passing of each stage generally correlates with increased age, and hence probably with physiological maturity.

I witnessed only a few cases of young birds passing through all four stages in one breeding season. In 1971, I caught 17 young

Sooty Terns from the air that I later found breeding. Five of these had inactive brood patches when first caught, and for these the average time until capture on an egg was 44 days (range 34-50). Two of these five birds were among the five youngest Sooty Terns ever known to breed at Johnston (4 years old) and both were captured from the air at unusually early dates (late March) for their age. The remaining 12 birds had active brood patches when first caught and were found breeding an average of only 16 days later (range 3-34).

DISCUSSION

The mechanisms regulating breeding ages in colonial seabirds are topics frequently debated in recent years (e.g. Lack, 1954; Wynne-Edwards, 1962; Ashmole, 1963b). Delayed breeding age is known to occur in a wide variety of taxa, including albatrosses (Fisher and Fisher, 1969), shearwaters (Serventy, 1956; Harris, 1966), storm petrels (Wilbur, 1969; Harris 1969c), boobies (Nelson, 1966), penguins (Richdale, 1957; LeResche and Sladen, 1970; Ainley, 1973a, b), gulls (especially Coulson and White, 1958), terns (Austin and Austin, 1956), and probably skimmers (Modha and Coe, 1969) and alcids (Tuck, 1960). This study proves that Sooty Terns also have deferred maturity. However, the mechanisms that cause deferred maturity still are not completely known. Ainley (1973a) shows that gonads of male and female Adelie Penguins are physically mature by age 4, but that breeding may not occur until age 6 (females) or 8 (males). He suspects that delayed breeding may be caused by young individuals having immature or poorly executed social behavior. Other studies have shown that certain bird species with deferred breeding ages may breed at younger than normal ages if old males are removed from a local poplation (Orians, *in* Lack, 1968), that females may breed at younger ages than males (Ainley, 1973a; also see references in Cody, 1971), and that deferred breeding often occurs in species having complex social breeding patterns (Lofts and Murton, 1968). Robertson (1969) suggests that Sooty Terns have severe intraspecific competition for nest sites, and that young birds may ultimately leave more offspring by delaying return to the colony until better able to compete for suitable nest sites. In short, several indications suggest that birds having deferred maturity may be physiologically capable of breeding at younger ages than they normally breed, but that social behavior delays breeding. For reasons described below, I believe a combination of social and physical factors contribute to the delayed breeding ages found in Sooty Terns.

A major conclusion from this study is that many young Sooty Terns return to natal colonies for one or more years before breeding. Ainley (1973a) suggests young penguins return to natal colonies as a consequence of partial reproductive development of the hypothalamic-hypophyseal endocrine mechanism. Like penguins, the age-related development of brood patches in Sooty Terns probably indicates endocrine activity, and although not discussed in this report, the enlargement of gonads and accessory ducts (personal observations) also indicates endocrine activity. Other adolescent traits are seemingly affected by the same physiological mechanism. For example, the numbers of adolescents that return to Sand Island are age-related, and the frequencies of active brood patches also are age-related. Regardless of the precision involved, some physiological mechanism, which apparently becomes more refined with age, causes adolescents to return to the natal colony, but at variable ages and with variable brood patch conditions; this suggests that for genetic or environmental reasons different individuals of the same age mature at different rates. I have little information on the cause of this variation as it develops between the time immature Sooty Terns first leave the colony and the time they first return as adolescents.

Another source of variation of maturation rates appears to result from the response of adolescents to social events that occur while they are visiting the colony. For example, the birds known to land at young ages apparently bred at younger ages than those birds not known to land at young ages. However, what causes adolescents to land remains unknown. When breeders are present they usually prevent adolescents from landing in breeding areas, and older adolescents usually prevent younger adolescents from landing in standing areas. Therefore, it appears that the behavior of birds on the ground is sufficiently aggressive to intimidate young birds and older birds with inactive brood patches. The fact that older adolescents, and usually those with active brood patches, are the birds that appear best able to enact and tolerate aggression in standing areas suggests that landing and remaining in standing areas may be influenced by physiological processes associated with seasonal and/or age-related maturation. In adult and immature Herring Gulls, *Larus argentatus* (Boss, 1943) and Laughing Gulls (Segrè, 1965) aggressive and submissive behavior is known to change with experimental injection of certain reproductive hormones, which in the case of the Laughing Gull also are known to cause brood patch activity. But still, these observations do not explain why the youngest adolescent Sooties do not land on vacant portions of the island. My behavioral observations suggest that birds trying to land are attracted to other birds on the ground, but I have not obtained observations explaining why. Regardless, the sum of the above observations suggests that Sooty Terns that land are somehow more mature than those that do not land.

In the above discussion I have shown that landing by young Sooty Terns probably is affected by the presence and behavior of breeders and older adolescents on the ground. The information presented below suggests that the number of young adults that breed may be influenced by experienced breeders in a similar manner. It has already been shown that the number of young adults that breed at Sand Island may vary in different years (Table 13). I suspect the cause of this variation is that the size of the experienced-breeder population was larger in 1969 than in 1971, and that the availability of suitable nesting area in late 1971 allowed younger birds to breed. I noted earlier that Sooty Terns breeding at Sand Island early in 1971 had an unusually poor nesting season, and that when I arrived on 18 March an estimated 40,000 eggs had been abandoned. As other species were breeding normally, I do not believe that this abandonment was caused by any unusual fluctuation of food supply, but rather by one or both of two other causes. First, during late summer 1970 and late February-early March 1971, flagrant human behavior caused extensive disruption of nests and mortality of an estimated 10,000 $\pm$ 50% terns. Second, in 1971 Sand Island had unusually sparse vegetation, and as shown earlier, the resulting poor nesting habitat could have caused increased nest abandonment. Regardless of the cause, about a third of traditional nesting areas were unoccupied in mid-March, and about a third of the sites within the occupied areas had been abandoned (Fig. 2).

The 1969 breeding season was dramatically different from 1971 according to Philip Shelton (pers. comm.) who noted that by late April more Sooty Terns were nesting at Sand Island than he had seen since 1966, his first year of observation. As already shown, few young birds were included among the 1969 breeders.

On the basis of contrast between the numbers of 4 and 5-year-olds breeding in 1969 and 1971, as well as the different amounts of suitable area available for late nesters in both years, I suspect sufficient cause exists for postulating that the size of the experienced-breeder population may affect the number of inexperienced adults that attempt breeding in a particular year. Other observations from 1971 suggest this hypothesis is correct. During the first two-thirds of April some of the unoccupied areas on Sand Island were used for nesting, but by few of the younger, known-age birds. During May additional groups nested that had the following features in common: (1) they used areas that had been wholly unoccupied since mid-March, (2) almost half of the birds were known to be young, (3) nesting was in distinct groups, and (4) they chose areas where some new vegetation was sprouting. I suspect it is especially significant that virtually none of the late-layers nested where older birds were nesting even though these areas contained large numbers of individual sites that had been abandoned during March (Fig. 2). These observations also suggest that if sufficient suitable areas are not available for late groups, young birds may not breed.

In conclusion, available evidence from this study at Johnston Atoll suggests that both adolescent landing behavior and the number of young adult Sooty Terns that breed in a given year are influenced by aggressive behavior and probably numbers of experienced breeders. A variety of observations hint that the responses of young birds to the aggression could vary in a density-dependent manner.

SUMMARY

Two major conclusions come from the observations of known-age, banded Sooty Terns at Johnston Atoll, Pacific Ocean. First, youngest age of breeding is four years, but most individuals do not breed until ages six to eight, and a few probably do not breed until age ten. Second, during years prior to breeding, adolescents often visit

their natal colony, but not until they are at least two years old, and usually not until four or five years old. The number of adolescents that visit is age-related, and the time of visits within a breeding season also is age-related. Most two-year-olds return after adults have finished breeding whereas non-breeding five or six-year-olds return earlier, or about one to two months after most eggs have been laid. While visiting natal colonies, adolescents often attempt to land among breeding adults, but they appear to be prevented from doing this by aggression from the adults. Thus, the majority remain flying over the colony, but some, and especially older birds, land in non-breeding areas. The majority of adolescents that land, as well as many of those in the air, appear to be in breeding condition.

As regards breeding, young adults nest later than experienced breeders, tend to group with neighbors of similar breeding experience, usually have similarly inexperienced mates, and often nest in less desirable habitat than experienced breeders. Maturation rates as measured by initial breeding ages, are highly variable, differ between years, and are not rigidly age-related. Available evidence further suggests that even though unidentified environmental and/or genetic events occurring years before initial breeding may affect age of first breeding, other events, possibly relating to availability of suitable nesting space, also affect the number of young birds that breed in any given year.

ACKNOWLEDGMENTS

The major portion of field work was conducted while I was employed by the Pacific Ocean Biological Survey Program, Smithsonian Institution. The principal coordinator was Philip S. Humphrey, and he as well as Robert L. Pyle and Philip C. Shelton were especially helpful. I also thank the many POBSP personnel who worked at Johnston Atoll, especially Paul Woodward, Kenneth Amerman, A. Binion Amerson, the late Lawrence Huber, and Jeffery P. Tordoff.

Field work done at Johnston in 1971 would not have been possible without the logistic support of the United States Air Force and the United States Coast Guard, nor without the financial support of the Frank M. Chapman Memorial Fund, American Museum of Natural History. Mrs. Herbert M. Church and George E. Watson were also especially helpful in making arrangements enabling me to return to Sand Island in 1971. To all these persons and organizations I am deeply grateful.

Field work at Dry Tortugas, Florida was made possible through the kind assistance of William B. Robertson, Jr. and the U. S. National Park Service.

I also have benefited greatly from discussions with William B. Robertson, Jr., Glen E. Woolfenden, Ralph W. Schreiber, Philip C. Shelton, Ian C. T. Nisbet, James J. Dinsmore, and Bertram G. Murray, Jr. I also thank Glen E. Wooflenden, William B. Robertson, Jr., James N. Layne, and John M. Lawrence, all of whom read earlier versions of the manuscript and made many helpful suggestions.

This paper includes portions of a thesis submitted in partial fulfillment of the requirements for the Master of Arts degree at the University of South Florida.

LITERATURE CITED

AINLEY, D. G. 1973a. Development of reproductive maturity in Adelie Penguins. In press. B. Stonehouse (ed.). The biology of the penguin. London, MacMillan Co.

——— 1973b. Displays of Adelie Penguins: a re-interpretation. In press. B. Stonehouse (ed.). The biology of the penguin. London, MacMillan Co.

AMERSON, A. B., JR. 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. *Atoll Res. Bull.*, **150**: 1-383.

ASHMOLE, N. P. 1963a. The biology of the Wideawake or Sooty Tern (*Sterna fuscata*) on Ascension Island. *Ibis,* **103b**: 297-364.

——— 1963b. The regulation of numbers of tropical oceanic birds. *Ibis,* **103b**: 458-473.

——— 1965. Adaptive variation in the breeding regime of a tropical seabird. *Proc. Nat. Acad. Sci.*, **53**: 311-318.

AUSTIN, O. L., and O. L. AUSTIN, JR. 1956. Some demographic aspects of the Cape Cod population of Common Terns. *Bird-Banding,* **27**: 55-66.

BOSS, W. R. 1943. Hormonal determination of adult characters in Herring Gulls (*Larus argentatus*). *J. Exp. Zool.*, **94**: 181-206.

BURCKHALTER, D. L. 1969. Orientation and communication of Sooty Tern chicks. M.S. Thesis, Univ. of Arizona, Tucson.

CHAPIN, J. P., and L. W. WING. 1959. The Wideawake calendar, 1953-1958. *Auk,* **76**: 153-158.

CLAPP, R. B., and F. C. SIBLEY. 1966. Longevity records of some Central Pacific seabirds. *Bird-Banding,* **37**: 193-197.

CODY, M. L. 1971. Ecological aspects of reproduction. *In* (D. S. Farner and J. R. King, eds.) Avian Biology. Vol. I, New York, Academic Press. p. 461-512.

COULSON, J. C. 1966. The influence of the pair bond and age on the breeding biology of the kittiwake gull (*Rissa tridactyla*). *J. Anim. Ecol.*, **35**: 269-279.

COULSON, J. C., and E. WHITE. 1958. The effect of age on the breeding biology of the kittiwake. *Ibis,* **100**: 40-51.

CULLEN, J. M. 1956. A study of the behaviour of the Arctic Tern *Sterna macrura.* D. Phil. Thesis, Oxford Univ.

DINSMORE, J. J. 1972. Sooty Tern behavior. *Bull. Florida State Mus.*, **16**: 129-179.

FISHER, H. I. 1969. Eggs and egg-laying in the Laysan Albatross *Diomedea immutablis. Condor,* **71**: 102-112.

FISHER, H. I., and M. L. FISHER. 1969. The visits of Laysan Albatross to the breeding colony. *Micronesica,* **5**: 173-221.

HARRIS, M. P. 1966. Age of return to the colony, age of breeding, and adult survival of Manx Shearwaters. *Bird Study,* **13**: 84-95.

——— 1969a. Food as a factor controlling the breeding of *Puffinus lherminieri. Ibis,* **111**: 139-156.

——— 1969b. Breeding seasons of sea-birds in the Galapagos Islands. *J. Zool., London,* **159**: 145-165.

——— 1969c. The biology of storm petrels in the Galapagos Islands. *Proc. Calif. Acad. Sci.*, **37**: 95-165.

JONES, R. E. 1971. The incubation patch of birds. *Biol. Rev.*, **46**: 315-339.

LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

——— 1968. Ecological adaptations for breeding in birds. London, Methuen and Co., Ltd.

LANGE, B. 1928. Die Brutflecke der Vogel und die für sie wichtigen Hauteigentumlichkeiten. *Gegenbaur Morph. Jahrb.*, **59**: 601-712.

LERESCHE, R. E., AND W. J. L. SLADEN. 1970. Establishment of pair and breeding site bonds in young known-age Adelie Penguins (*Pygoscelis adeliae*). *Anim. Behav.*, **18**: 517-526.

LOFTS, B., AND R. K. MURTON. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *J. Zool.*, London (1968) **155**: 327-394.

MODHA, M. L., AND M. J. COE. 1969. Notes on the breeding of the African Skimmer (*Rynchops flavirostris*) on Central Island, Lake Rudolf. *Ibis*, **111**: 593-598

NELSON, J B. 1965. The behaviour of the Gannet. *Brit. Birds*, **58**: 233-288, 313-336.

——— 1966. Population dynamics of the Gannet at Bass Rock, with comparative information for other Sulidae. *J. Anim. Ecol.*, **35**: 443-470.

——— 1969a. The breeding behaviour of the Red-footed Booby *Sula sula*. *Ibis*, **111**: 357-385.

——— 1969b. The breeding ecology of the Red-footed Booby (*Sula sula*) in the Galapagos. *J. Anim. Ecol.*, **38**: 181-198.

ODUM, E. P. 1971. Fundamentals of ecology. Philadelphia, W. B. Saunders Co.

PALMER, R. S. 1941. A behavior study of the Common Tern. *Proc. Boston Nat. Hist. Soc.*, **42**: 1-119.

RICHARDSON, F. 1957. The breeding cycles of Hawaiian seabirds. *Bernice P. Bishop Mus. Bull.*, **218**: 1-41.

RICHDALE, L. E. 1957. A population study of penguins. Oxford, Oxford Univ. Press.

ROBERTSON, W. B., JR. 1964. The terns of the Dry Tortugas. *Bull. Florida State Mus.*, **8**: 1-95.

——— 1969. Transatlantic migration of juvenile Sooty Terns. *Nature*, **222**: 632-634.

ROWAN, M. K. 1965. Regulation of seabird numbers. *Ibis*, **107**: 54-59.

SEGRÈ, A. 1965. The hormonal control of incubation patch development in the Laughing Gull (*Larus atricilla*). M.A. thesis, Duke Univ., Durham, N. C.

SERVENTY, D. L. 1956. Age at first breeding of the Short-tailed Shearwater *Puffinus tenuirostris*. *Ibis.*, **98**: 532-533.

TUCK, L. M. 1960. The murres. Ottawa, Canad. Wildl. Serv.

WILBUR, H. M. 1969. The breeding biology of Leach's Petrel. *Auk*, **86**: 433-442.

WOODWARD, P. W. 1972. The natural history of Kure Atoll, Northwestern Hawaiian Islands. *Atoll Res. Bull.*, **164**: 1-313.

WYNNE-EDWARDS, V. C. 1955. Low reproductive rate in birds. *Acta XI Congr. Intern. Ornithol.*, Basel.

——— 1962. Animal dispersion in relation to social behaviour. London, Edinburgh.

Manomet Bird Observatory, Box 0, Manomet, Mass. 02345.

Received 25 July 1973, accepted 10 October 1973.