THE EFFECT OF HURRICANE AGNES ON GROWTH AND SURVIVAL OF TERN CHICKS IN FLORIDA

By S. C. White, W. B. Robertson, Jr., and R. E. Ricklefs

INTRODUCTION

It has been commonly reported, but rarely described in detail, that storms may inflict heavy direct mortality on eggs and young of colonial birds nesting along shores in salt marshes, sand beaches, and low rocky coasts. High tides and strong winds have killed eggs and chicks of Least Terns, *Sterna albifrons* (Hagar, 1937), Black Guillemots, *Cepphus grylle* (Winn, 1950), Roseate Terns, *Sterna dougallii* (Robertson, 1964), Common Terns, *Sterna hirundo* (H. Hays, pers. comm.), and Laughing Gulls, *Larus atricilla* (J. Berger, pers. comm.). Storms may also indirectly increase mortality of chicks by adversely affecting feeding conditions for adults. This effect is little studied in seabirds, but has been documented for aerial feeders such as swifts, whose food supply is reduced by cold, rainy weather (e.g, Lack and Lack, 1951).

In June, 1972 Ricklefs and White were studying the energetics of nestling growth in Sooty Terns (*Sterna fuscata*) at the Dry Tortugas, located in the Gulf of Mexico 70 miles west of Key West, Florida, when hurricane Agnes passed west of the area. High winds, heavy rain, rough seas, and low temperatures prevailed for more than a week. Robertson worked in the colony from 28 June, about a week after the storm subsided, to 6 July. We report here the effects of hurricane Agnes on the growth and survival of young Sooty Terns and Brown Noddies (*Anous stolidus*).

WEATHER

National Weather Service records (Simpson and Hebert, 1973) show that a barometric pressure trough began to move from Yucatan to southern Florida and the western Bahamas on 11 June 1972. On 14 June, a strong localized depression developed near Cozumel Island, Yucatan, and it moved east on 15 June. Winds reached tropical storm strength overnight and Agnes was named on 16 June. By 18 June when the center of the storm was passing 175 miles W of Dry Tortugas, Agnes had reached hurricane status. Agnes was a relatively weak hurricane, but she had an exceptionally large circulation envelope, about 1,000 nautical miles in diameter. Disturbed weather patterns were seen in satellite photographs up to 2,000 miles from the center of the storm.

The Dry Tortugas had fair weather until 11 June, after which increasing rain, winds, and rough seas prevailed. The disturbance lasted about 10 days. We could not obtain weather records from the Dry Tortugas, but Key West records illustrate the degree of disturbance (Fig. 1). The mean temperature during June at Key West between 1832 and 1922 was 81.9° F (Clayton, 1944). Between 12 and 20 June 1972, temperatures at Key West were unseasonally low, with daily maxima at or below the mean temperature on 6 days. Winds recorded at Key West increased during the storm and

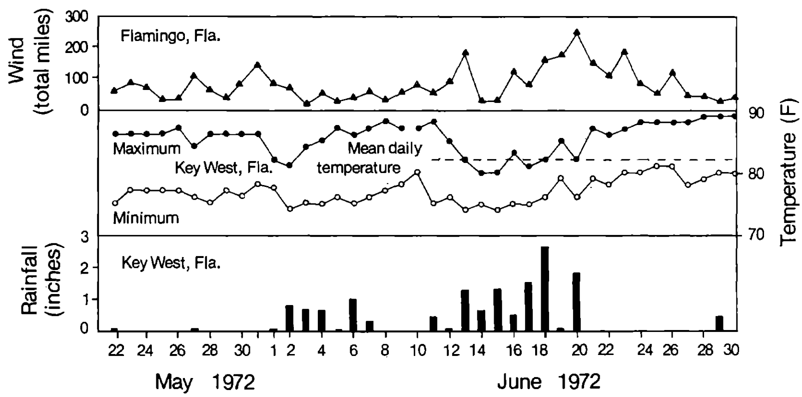

FIGURE 1. Meterological summary for Key West, Florida, from late May through June 1972; total daily wind from Flamingo, Florida (data from U.S., Weather Bureau summaries).

were strongest after 18 June. Precipitation was recorded every day from 11-20 June. Average June rainfall at Key West between 1832 and 1922 was 4.33 inches with extremes of 0.10 and 17.06 inches. The 14.52 inches recorded in June 1972 were exceeded in only two out of 100 years (1832–1922, 1931–1940) (Fig. 2).

METHODS

Working within a small area at the Southwest Point of Bush Key, we weighed, measured and released Sooty Tern chicks on 4-6 June (S.C.W. and R.E.R.), 14 June (S.C.W. and R.E.R.), and 29 June (W.B.R.). In the initial sample, 184 chicks, selected to cover the growth period as evenly as possible, were measured and banded with U.S. Fish and Wildlife Service bands. We recaptured 93 banded chicks on 14 June and 15 banded chicks on 29 June. White and Ricklefs obtained weights to the nearest gram with a triple-beam balance—shielded from high winds and rain on 14 June by placement within a deep box in the shelter of our upturned dinghy. Robertson used a 300 g capacity Pesola balance. Wing lengths, from wrists to tip of the longest primary, were measured with the folded wing flattened against a ruler. On 15 June, we recorded wing lengths of all the dead chicks found on the study area and estimated dates of death by body condition.

We recorded weights and wing lengths of Brown Noddy chicks on 5 and 6 June and marked some with colored leg bands. Thirty-three of the marked chicks were remeasured on 14 June, but they could not be weighed due to the wind. Twelve of the banded noddy chicks were weighed, but not measured, on 30 June.

Statistical procedures used here follow Sokal and Rohlf (1969).

RESULTS

The period between 4-6 June and 14 June included four days of increasingly stormy weather as Agnes approached the Dry Tortugas.

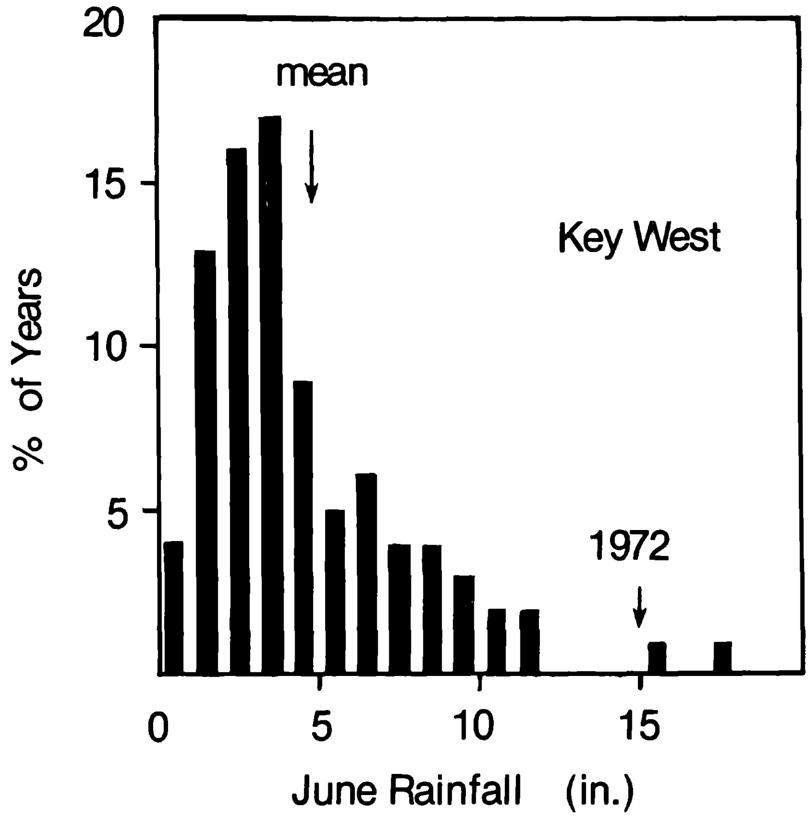

FIGURE 2. Frequency distribution of June rainfall for 100 years at Key West, Florida (Clayton, 1944; Clayton and Clayton, 1947). The mean value is 4.3 inches; 14.5 inches fell during June 1972.

The minimum surviorship was 0.505 (93 recaptures from 184 banded chicks). Of the 16 banded young caught in the banding area on 29-30 June, five were chicks we had not recaptured on 14 June. If we had failed to recapture this proportion of all banded chicks on 14 June, the 93 recaptures would have represented 135 live banded chicks, or a survivorship of 0.73. One can calculate the daily mortality (m), assuming constant probability of death, using the expression:

$$m = -(\log_e S)/t$$

where S is the proportion of chicks surviving t days (Ricklefs, 1969). For $S = 0.73$ and $t = 9$, the mortality rate is 0.035 (3.5%) per day.

Recaptures of banded chicks are tabulated by wing length in Table 1. Because we did not observe hatching, we used wing length as an index of age. We established a relationship between age and wing length from growth data for Sooty Terns on Manana Island, Oahu, Hawaii (Burckhalter, unpubl. data), and from our estimates of age determined from growth increments of the wings of terns on the Dry Tortugas (Ricklefs and White, 1975).

TABLE 1.

Recovery of Sooty Tern chicks banded on 4-6 June as a function of wing length.

Wing length 4-6 June (mm)	Estimated age (days)	Number banded 4-6 June	Number recovered 14 June	Percent recovered 14 June
<20	1-2	12	1	8.3
20-29	2-11	36	17	47.2
30-39	12-17	19	12	63.2
40-49	17-21	36	20	55.6
50-59	21-23	29	17	58.6
60-69	23-25	13	6	45.8
70-79	25-27	11	5	
80-89	27-28	7	1	
90-99	29-30	5	3	36.8
100-109	30-32	3	2	
110-119	32-34	4	1	
120-129	34-36	3	3	
130-139	36-37	2	1	88.9
140-149	38-39	2	2	
150-159	39-41	2	2	

Mortality rates varied among birds of different size (Table 1). Of birds with wing length less than 20 mm, only 1 of 12 (8.3%) was recaptured, The percent recaptured rose to a peak with the 30 to 59 mm wing length classes and decreased for larger birds, except that chicks with wing lengths exceeding 120 mm exhibited high survivorship (8 of 9). Sample sizes were too small to permit statistical tests of differences between all wing length groups. The following groups were found to differ significantly by arcsin transformation and using a probability of 0.95 as the acceptable lower limit for statistical significance: 20 vs 20-29; 80-119 vs 120-129; 20-29 vs 30-59. Differences between groups 30-59 and 60-119, and between groups 30-59 and 80-119 had probabilities of 0.90-0.95.

The 30 dead chicks (a few of them banded) collected on 15 June were mostly small chicks, (wing lengths < 40 mm) (Table 2). Many of them had been dead long enough to be completely dried and flattened. Judged by weight and plumage condition, 11 specimens had been dead almost certainly for less than two days, and seven of these had wings shorter than 30 mm. The fresh carcasses probably represent a random sample of the age distribution of

TABLE 2.

Wing lengths of Sooty Tern chicks found dead on 15 June within the chick banding area.

Wing length (mm)		Total dead	Freshly dead	Banded chicks recovered alive on 14 June
20-29		8 (27)[1]	7 (64)	12(17)
30-39		14 (47)	2 (18)	6 (8)
40-49		2 (7)		9 (13)
50-59		4 (13)	1 (9)	2 (3)
60-69				1 (1)
70-79		2 (7)	1 (9)	6 (8)
80-99				18 (25)
100-119				9 (13)
120-159				3 (4)
160-209				6 (8)
	Total	30	11	72

[1]Percentages of the samples enclosed in parentheses.

death caused by the storm. The remainder of the sample, however, indicates little about normal mortality because the smallest chicks are preyed upon preferentially by predators and the smallest carcasses are selectively removed by scavengers. Prior to the storm, we observed Cattle Egrets (*Bubulcus ibis*) eating small dead chicks; and Harrington (1975) reports that Cattle Egrets have learned to hunt recently hatched chicks. Also Magnificent Frigatebirds (*Fregata magnificens*) occasionally swooped down on the colony, but we observed no instances of predation.

WEIGHT

Weights of chicks during 4-6 June compared favorably with the weights of Sooty Tern chicks with similar wing lengths on Manana Island, except for chicks with wing lengths between 30 and 50 mm (Fig. 3 and 4). By 14 June there was a marked drop in weight for a given wing length in young of all ages (Fig. 5). Chicks were emaciated and weak, and many were inactive. In spite of fair weather during the week before 29-30 June, the weights of surviving chicks remained low for their wing lengths (Fig. 6).

DEVIATION FROM NORMAL WEIGHT AND SURVIVAL

Starvation was a possible cause of Sooty Tern chick mortality. This factor was compared between age groups by its effect on growth. Measurements of growth during normal conditions are not available for Sooty Terns of the Dry Tortugas. Comparable data were obtained for the Manana Island Sooty Terns, but since

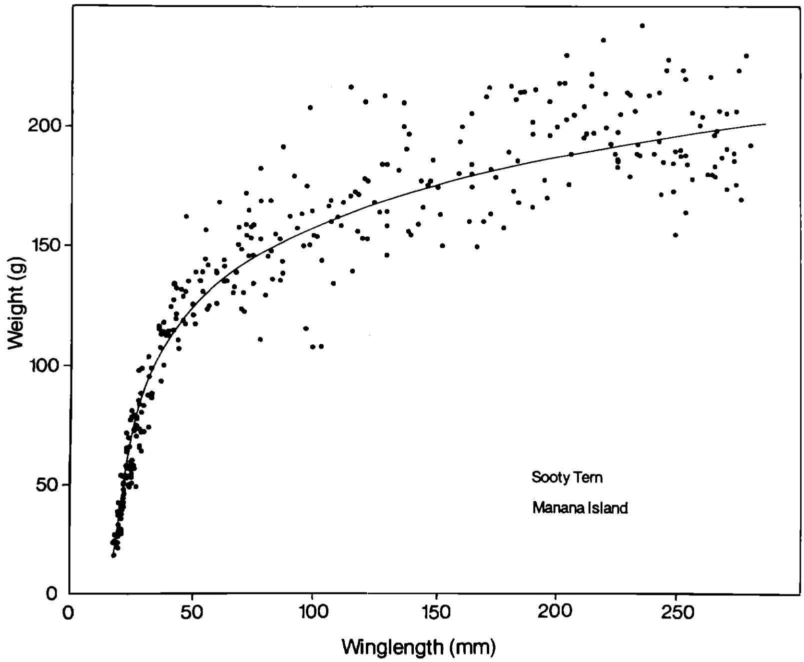

FIGURE 3. Relationship between wing length and weight for 12 Sooty Tern chicks on Manana Island between 5 June and 20 August 1968 (Burckhalter, unpubl data). The line represents an equation utilized to describe the relationship (see text).

Pacific Sooty Terns are larger as adults than Atlantic Sooty Terns, we must assume that the growth parameters are not identical. In the absence of an alternative, however, the Manana data were used as a standard of comparison for growth performance.

We selected a mathematical function to describe the relationship between average weight and wing length of Sooty Terns on Manana Island. Several equations were tried but the relationship:

$$\text{Weight (g)} = 24.1\,[\log_e(\text{wing length (mm)} - 18)]^{1.175} + 20$$

described the data most successfully (Fig. 3). Because weight initially increases nearly 10 g for every millimeter of increase in wing length we have based weight comparisons only on chicks with wings 40 mm or longer. Percentage deviation (D) from the weight-wing length relationship of Manana Island chicks was calculated by the equation:

$$D = \frac{(\text{observed weight} - \text{predicted weight})}{\text{predicted weight}} \times 100$$

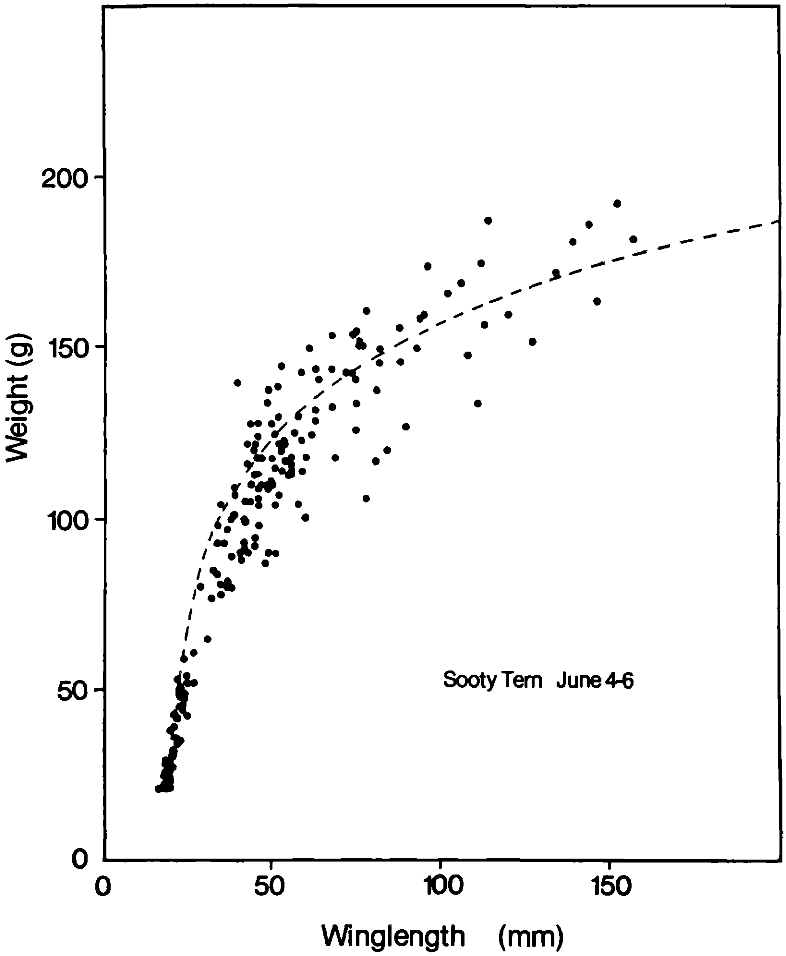

FIGURE 4. Relationship between wing length and weight for Sooty Tern chicks measured 4-6 June on Bush Key. The line represents the relationship between weight and wing length for the Hawaiian chicks in Fig. 3.

During the period 4-6 June, *D* averaged −3.7 (3.7% less than predicted weight) with a standard deviation of 11.1%. On 14 June, *D* averaged −14.4 ± 10.7%, a highly significant decrease (Fig. 7). By 29-30 June, *D* had increased slightly but not significantly to −11.2 ± 11.0.

To test whether survival was related to pre-storm weight, we compared initial weights of chicks that survived and were recaptured at the end of the study with those that were not recaptured. Recaptured chicks deviated less from predicted weight during 4-6 June (D = −3.7 ± 11.0, n = 69) than chicks not recaptured (D = −7.5 ± 9.5, n = 46). The means differed significantly

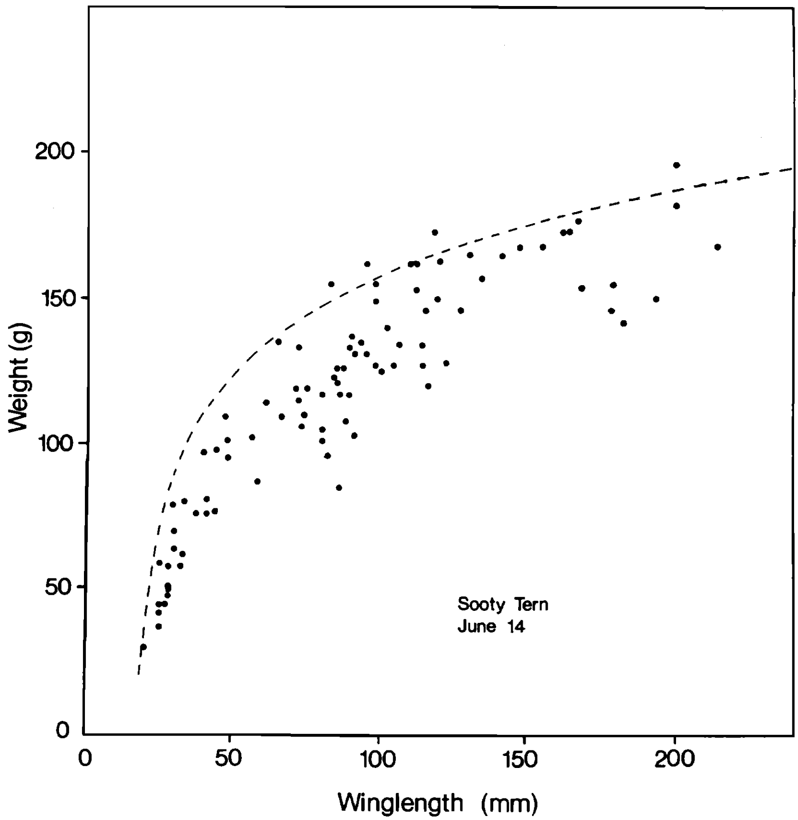

FIGURE 5. Relationship between wing length and weight for Sooty Tern chicks measured 14 June on Bush key. All the birds had been banded and measured during 4-6 June. The line represents the relationship between weight and wing length for the Hawaiian chicks in Fig. 3.

(one-tailed t-test; $t = 1.91$, $0.025 < P < 0.05$), but the weight distributions of the two groups greatly overlapped and only 5.6% of the total variation in D could be partitioned between the two groups by analysis of variance. Initial weight, therefore, contributed, but not substantially, to probability of recapture.

Values of D on 14 June for chicks whose wings were 40-59 mm during 4-6 June ($D = -17.1 \pm 10.0$) were lower ($P < 0.05$) than for chicks with wings 60-119 mm ($D = -10.6 \pm 11.0$), but the smaller chicks were also more underweight during 4-6 June. There was no significant difference between these size groups in the change in D (ΔD) between 4-6 June and 14 June, ($\Delta D = -12.5 \pm 11.7$ vs $\Delta D = -8.6 \pm 9.2$, $t = 1.13$, $0.2 < P < 0.4$, d.f. $= 48$).

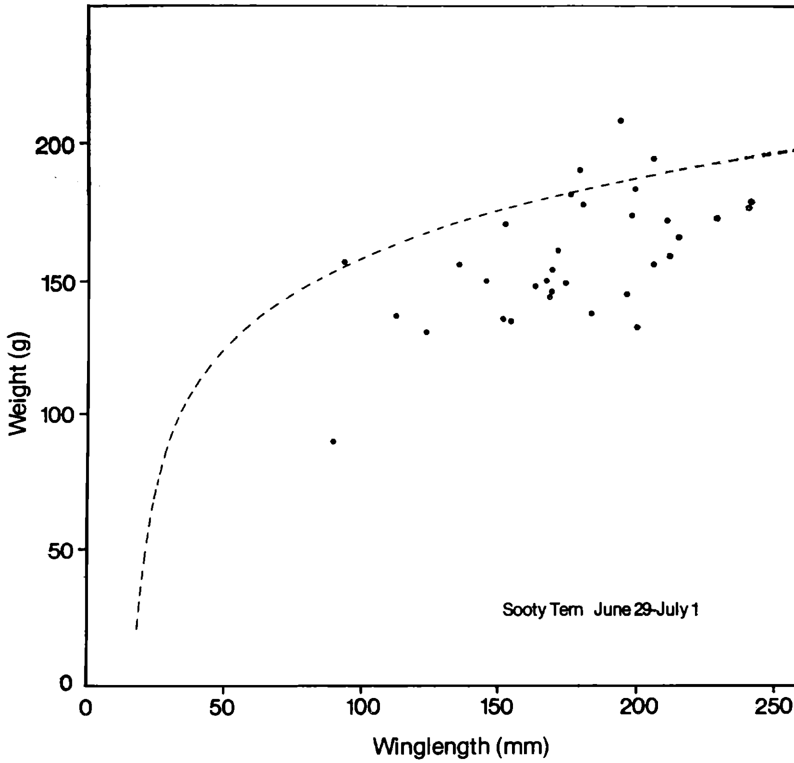

FIGURE 6. Relationship between wing length and weight for Sooty Tern chicks measured during 29 June and 1 July on Bush Key. Solid circles represent birds from the banding area on the southwest point of Bush Key, and also includes some birds banded 5 June in the southcentral area of the breeding colony. The line represents the relationship between weight and wing length for the Hawaiian chicks in Fig. 3.

RETARDATION OF GROWTH

Between 4-6 June and 14 June, banded chicks gained much less weight than normal and many lost weight (Fig. 8). Compared to data from Manana Island (Fig. 9) wing length growth over the 9-day period in chicks with initial wing lengths less than 50 mm (about 21 days of age) was retarded, but the wings of older birds grew at about the same rate as on Manana. All the birds captured both on 14 June and on 29-30 June gained weight, although many did not make up weight deficits incurred by 14 June (Table 3). Furthermore, wing growth increments were far below normal for the younger birds and were 20 to 30% below normal among older birds (Fig. 10).

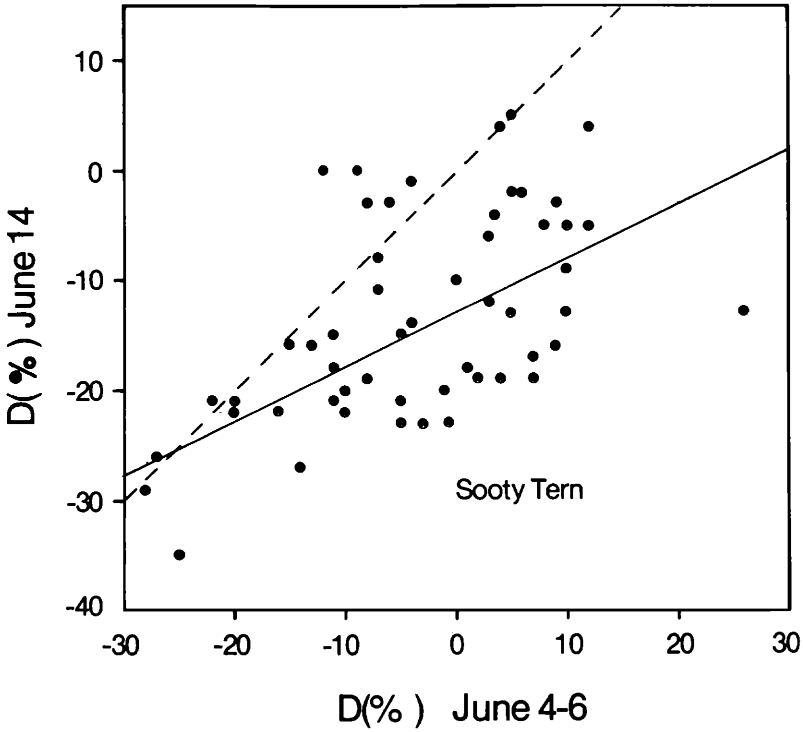

FIGURE 7. Relationship between deviations from normal weight (*D*) on 4-6 June and on 14 June for Sooty Tern chicks with wing lengths on 4-6 June equal to or greater than 40 mm. The dashed line represents no change in *D* between the two dates. The solid line represents the least squares regression between values of *D* on the two dates (correlation coefficient r = 0.05).

BROWN NODDY GROWTH

About 3,500 Brown Noddies nest on Bush Key where they build substantial nest platforms in low shrubs. Brown Noddy chicks did not suffer greatly during the passage of Agnes.

The weight-wing length relationship on 5-6 June (Fig. 12) showed that chicks were relatively light for their wing length compared to Noddy Terns measured on Kure Atoll by R. R. Fleet (unpubl. data). Nevertheless, Noddies on Bush Key appeared healthy and showed no signs of being undernourished. Differences between Brown Noddies of Kure Atoll and Bush Key may reflect inherent anatomical differences. The birds are assigned to different subspecies, and the Pacific Brown Noddy adults are somewhat larger. The Brown Noddies examined on 14 June were still in excellent condition and more than one half the young regurgitated large quantities of food when handled between 1600 and 1700. The wings of chicks did not show the retarded growth found in Sooty Terns.

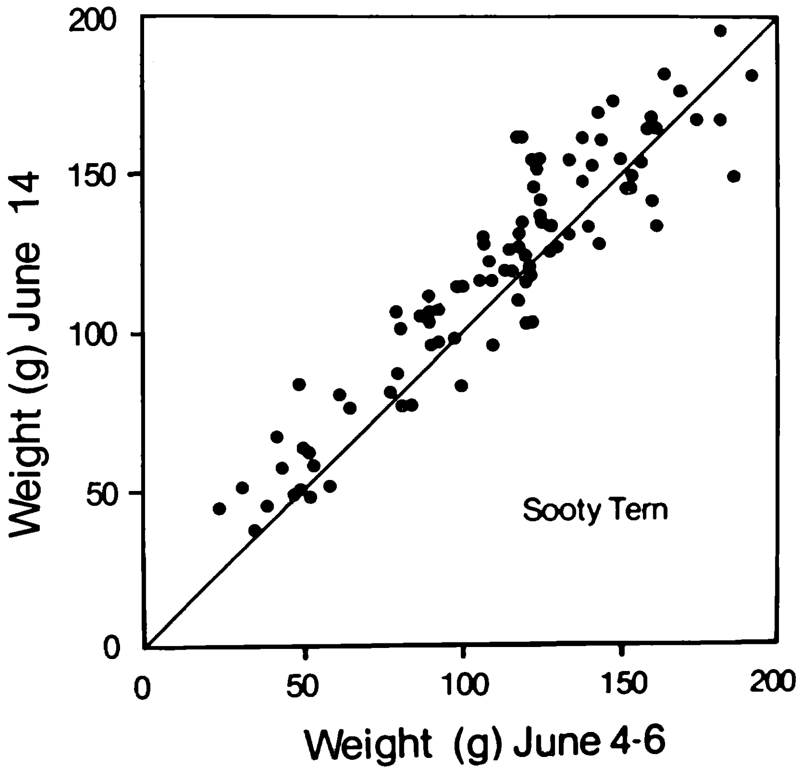

FIGURE 8. Relationship between weight on 4-6 June and on 14 June for all Sooty Tern chicks banded during 4-6 June. The line represents no change in weight between the two dates.

By 30 June, weights of all these banded young had increased substantially (Table 4) and the weight-wing length relationship was similar to that found on 5-6 June (Fig. 11). The excellent condition of the Brown Noddy chicks after the storm contrasted sharply with the poor condition of Sooty Tern chicks.

DISCUSSION

Our observations during a period of stormy weather in June 1972 suggest that growth of Sooty Tern chicks was slowed and their mortality rate increased. The storm probably impaired the ability of adults to provide food to their young, resulting in retarded body weight growth but it appears that starvation was not the major cause of mortality. First, the highest mortality occurred among the youngest chicks, which presumably have the lowest metabolic requirements (see Ricklefs, 1975). Between 4-6 June and 14 June more of the small birds gained some weight than the larger chicks. Second, we could not accurately weigh chicks found dead but few of the chicks captured alive were near starvation

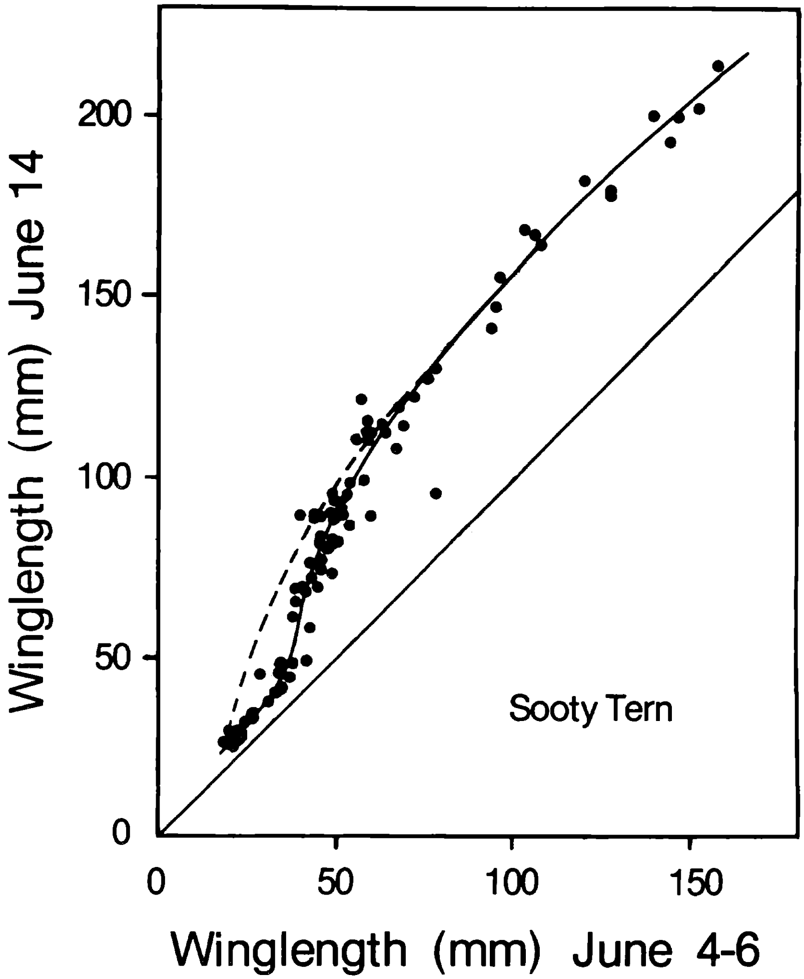

FIGURE 9. Relationship between wing length on 4-6 June and on 14 June for all Sooty Tern chicks banded during 4-6 June. The solid line represents no change in wing length between the two dates; the dashed line represents the relationship between wing lengths at the beginning and end of 9-day intervals chosen at random from Burckhalter's data on Hawaiian Sooty Terns (see Ricklefs and White, 1975).

levels of weight loss. Four chicks kept without food under a shelter in the field were still alive after five days and their weights had decreased to 45-58% of weights predicted from their wing lengths. On 14 June, only one out of 58 birds (with wing lengths $\geq$ 40 mm) was less than 60% of normal weight, 3 were 61-70% of normal and 17 were 71-80% of normal. Third, whether birds banded on 4-6 June were recaptured or not recaptured on 14 June was only weakly related to body weight.

TABLE 3.

Wing length, weight, and *D*-values of chicks recovered during 29-30 June 1972

		4-6 June			14 June			29-30 June		
	Band no.	Wing (mm)	Weight (g)	*D* %	Wing (mm)	Weight (g)	*D* %	Wing (mm)	Weight (g)	*D* %
1023-76	606	44	128	10	94	135	−13	164	147	−18
”	616	51	115	− 8	98	127	−19	169	143	−21
”	625	52	139	10	98	149	− 5	180	190	4
”	632	43	122	6	80	101	−31	153	170	− 3
”	636	58	130	− 1	104	127	−20	172	160	−12
”	640	68	153	10				212	171	−10
”	644	49	109	−11	84	123	−18	152	135	−23
”	659	23.5	44		28	58		43	113	
”	710	60	118	−12	112	162	0	181	177	− 3
”	721	63	132	− 3				195	208	12
”	727	84	120	−20				213	158	−17
”	737	38	80		58	87	−34	90	90	−41
”	752	20	24		25	42		35	95	
”	759	24	49		29.5	79		43	113	
”	777	46	104	−13				155	134	−20

Exposure to cold and wet, leading to reduced body temperature, inactivity, and inability to feed was probably the most important cause of death for Sooty Tern chicks. Adult Sooty Terns normally attend their nest scrapes persistently for the first two weeks after the young hatch. For the first few days the chicks are closely brooded (Dinsmore, 1972). During the rains and cold weather from 11-15 June most of the smallest chicks (wing lengths $\leq$ 20 mm) were huddled in scrapes with no parental protection and many that perished were probably abandoned.

The greater ability of Brown Noddies to withstand the storm must have been due in part to their nesting in more protected sites among vegetation and to the water repellent qualities of the plumage of the adults and older chicks. Sooty Tern plumage becomes soaked in a heavy rain. Whether the greater weight gain of Brown Noddy chicks was related primarily to ability to withstand exposure or to a feeding advantage could not be determined. The two species feed on similar prey (Ashmole and Ashmole, 1967; Dinsmore, 1972). Brown Noddies utilize the more protected waters inside the Tortugas lagoon, whereas Sooty Terns usually feed farther from Bush Key (Gould, 1974). Thus, feeding might have been less disrupted for Brown Noddies than for Sooty Terns, and this (plus the shorter travel distance) could have the side effect of allowing adult Noddy Terns to spend more time at the nest during the storm, thus reducing the exposure of chicks.

In spite of similar nutrition, Sooty Tern chicks with wing lengths

TABLE 4.

Wing lengths and weights of color banded Brown Noddy Terns measured 5-6 June, 14 June, and 30 June.

	5-6 June		14 June	30 June	
Band	Wing (mm)	Weight (g)	Wing (mm)	Wing (mm)	Weight (g)
Bb	28	44	53		132
Yg	43	82	95	188[1]	162[1]
YB1	54	98	107	194[1]	148[1]
Gb	64	105	120	220[2]	150
Gp	71	118	125		154[2]
WB	82	135	134		161
Pb	91	135	139		155
UP	93	132	153		156
YO	94	129	153		164
RO	96	127	152		147
YB	108	140	160		167
WR	109	144	152		158
gb	114	143	154		159
Gg	117	146	—		165
Yp	120	139	174		156

[1]Recovered 1 July.
[2]Recovered 5 July.

of 60 to 119 mm survived the storm less well than chicks with wing lengths of 30 to 59 mm and greater than 120 mm. During this middle phase of development, corresponding to ages 23 to 34 days, flight and contour feathers begin to grow rapidly. The feather sheaths are exposed by growing beyond the insulating layer of down before they are protected by feathers unfolding from the tips of the quills. The chicks may be particularly vulnerable to cold, wet weather during this period.

Severe retardation of body weight growth is well known for seabirds; Ashmole (1963) records several instances in Sooty Tern chicks on Ascension Island. Wing length growth can be slowed as well. Between 4-6 June and 14 June retardation was evident only in younger chicks, but during the second interval between measurements, which included the peak of the storm, all young were affected. The mechanisms leading to retardation of development in birds are not known.

Our data do not allow us to quantify the mortality of Sooty Tern chicks caused directly by Agnes. Mortality was disproportionately high in chicks less than 10 days old. Although we can estimate an average daily mortality rate of 3%, the 9-day period for which it was calculated included at least five days of fair weather and did not include the peak of the storm. It would not be surprising if the storm had killed virtually all the young less than one week of age and up to one half of all the chicks in the banding

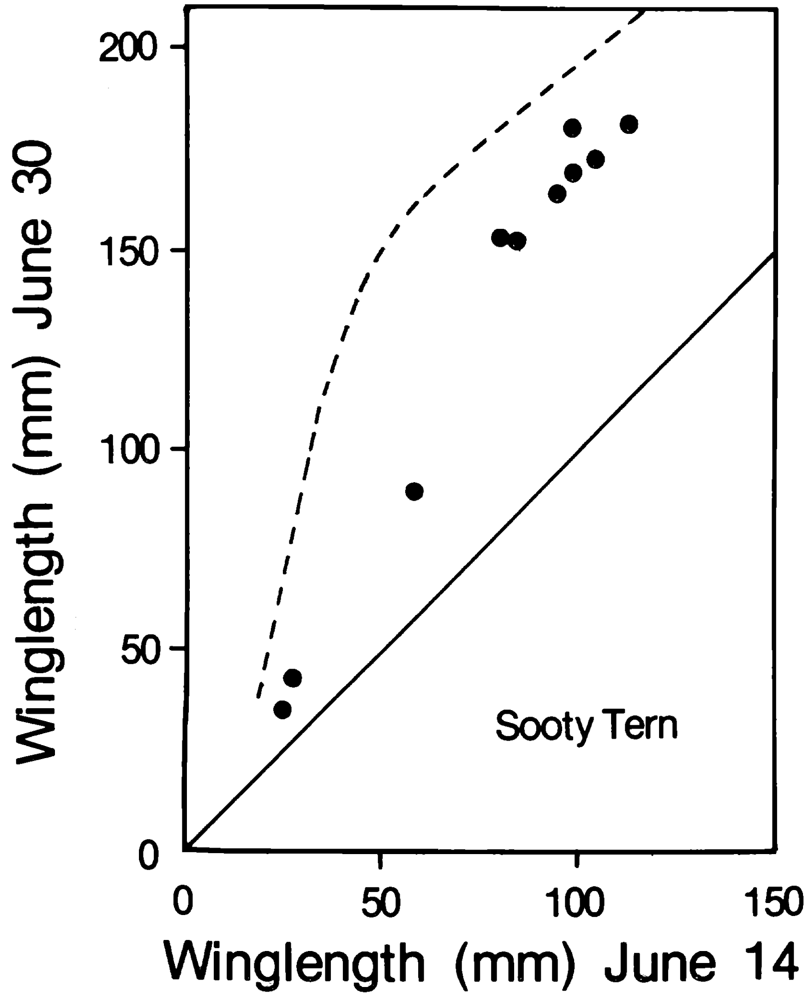

FIGURE 10. Relationship between wing length on 30 June and 14 June. The solid line represents no change in wing length between the two dates; the dashed line represents the relationship between wing lengths at the beginning and end of 16-day intervals chosen at random from Burckhalter's data on Hawaiian Sooty Terns.

area. The banding area suffered more than the colony as a whole because we worked in a section that is often colonized late in the season. Robertson found numerous thin, lethargic chicks there between 28 June and 6 July but did not observe unusual mortality or morbidity closer to the center of the colony. Also, the study area had less vegetation cover and was more exposed to the storm than other nesting areas.

Productivity of Sooty Terns in 1972 was low. Only 8,700 young were banded compared to 21,035 in 1970, 21,422 in 1971, 23,025

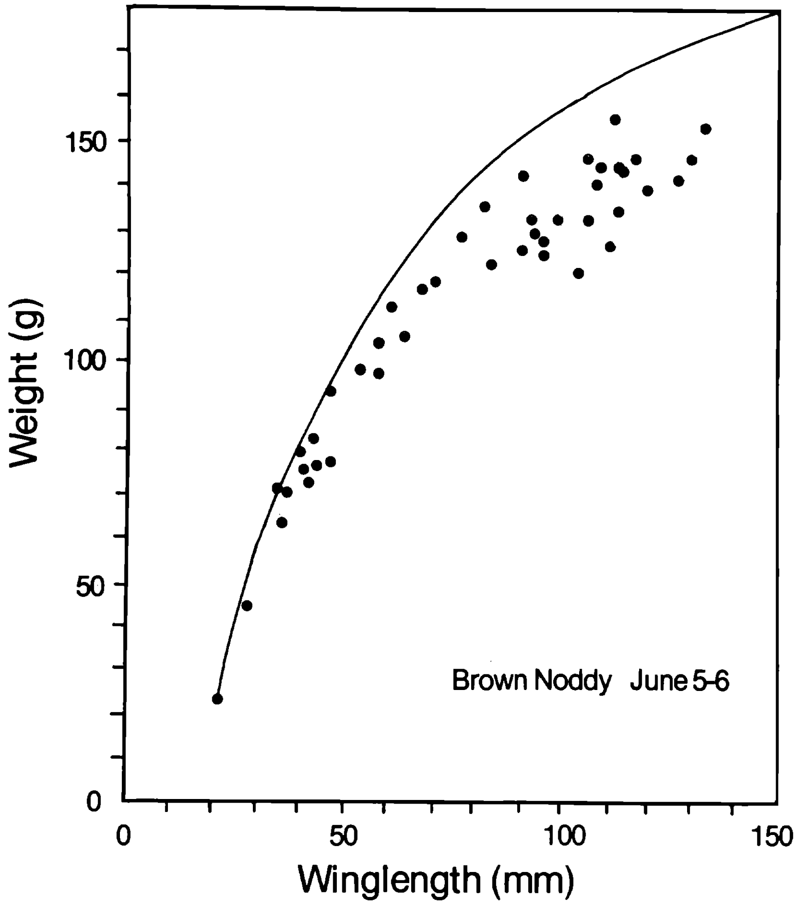

FIGURE 11. Relationship between wing length and weight of Brown Noddy chicks measured 5-6 June, on Bush Key. The solid curve represents the relationship for the Brown Noddy on Kure Atoll constructed from unpublished data of R. R. Fleet.

in 1973, 12,398 in 1974, and 21,200 in 1975. The totals in 1972 and, to some degree, in 1974, may have been depressed partly because the vegetation was unusually dense, thus limiting the space available to Sooty Terns for nesting. It is probable that the losses caused by Agnes decreased further a year-class of juveniles that was already destined to be weak.

An isolated storm can be an important cause of mortality in seabird colonies, and storms can exert selection on breeding adaptations if they occur frequently enough to be a persistent source of mortality, as in the tropical cyclone belt on either side of the central tropics. At the Dry Tortugas, records kept since 1903 (Robertson, 1964) indicate that 10 hurricanes passed near enough to cause some direct mortality of eggs, young, and adult birds.

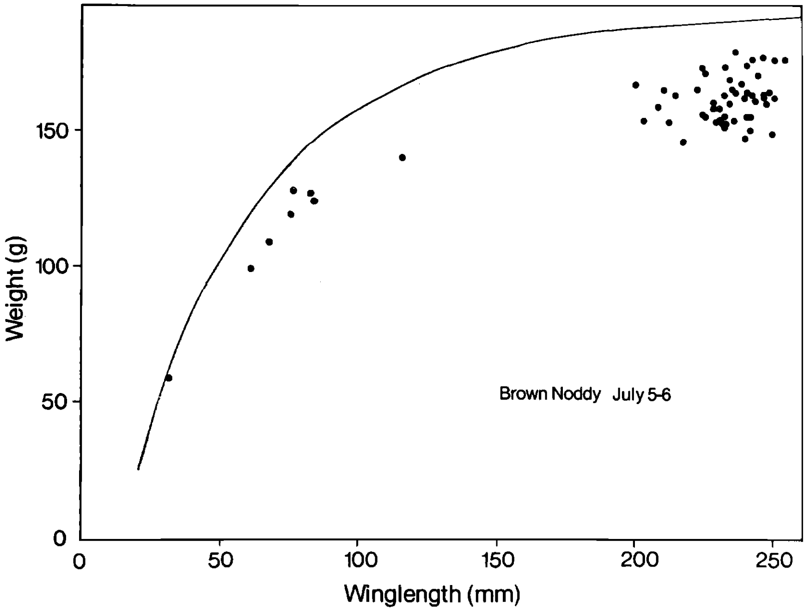

FIGURE 12. Relationship between wing length and weight of Brown Noddy chicks measured 5-6 July, on Bush Key. The solid curve represents the relationship for the Brown Noddy on Kure Atoll constructed from unpublished data of R. R. Fleet.

With a direct hit in 1966 by hurricane Alma, effects were dramatic (Owre, 1967). Most vegetation was wrecked and the north beach, which contained many nests, disappeared. About 1,500 chicks were found buried and in poor condition, and 1,412 were found dead. Inasmuch as both species of terns on the Dry Tortugas are essentially aerial feeders (Ashmole and Ashmole, 1967), disturbed sea conditions resulting from the more distant passage of hurricanes or from non-cyclonic tropical weather systems may indirectly affect breeding success, as they appear to have done during Agnes.

SUMMARY

Weights and wing lengths of banded Sooty Tern chicks were measured on Bush Key, Dry Tortugas Islands, Florida, before, during, and shortly after the passage of Hurricane Agnes in June 1972. Recoveries of banded birds during the storm indicated a mortality of 24% in the banding area even before the storm had reached its peak. Birds less than 10 days of age suffered the greatest losses. Many birds failed to gain weight during the storm and disappearance of young was weakly but significantly correlated with low body weight. Wing growth was retarded in young birds before the storm reached its peak, and in all birds before the storm had ended. Noddy Terns nesting on the island were apparently

unaffected by the storm. Mortality of Sooty Tern chicks resulting from Agnes was probably caused by exposure to cold and rain rather than by starvation. Adult terns did not brood very small chicks, perhaps because difficulty of foraging made long foraging periods necessary. Older chicks were badly soaked by the heavy rains.

ACKNOWLEDGMENTS

We appreciate the cooperation of the tern banding crew in recapturing banded chicks on 29 to 30 June. Mary LeCroy, James Dinsmore, and Brian Harrington provided helpful criticisms of the manuscript. The work was, in part, supported by N.S.F. grant GB 31554X to Ricklefs.

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Received 23 October 1975, accepted 31 December 1975.