# BROWN NODDIES ON CAYO NOROESTE, CULEBRA, PUERTO RICO: WHAT HAPPENED IN 1990?

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ABSTRACT.—In the first seven years of our Brown Noddy (*Anous stolidus*) study (1985–1991), 1990 was atypical in several respects. Only 68% of adults alive in 1989 returned to breed in 1990, compared to about 90% in other years. In addition, adults were delayed in their diurnal occupation of the colony and in egg laying in 1990. Eggs laid in 1990 were the smallest of any year. However, head-bill length, body mass, and condition index of breeding birds that returned in 1990 were within the normal annual variation established for earlier years. None of the noddies that failed to return in 1990 has been seen through June 1993, and we suggest that they died, most likely as a result of Hurricane Hugo as it passed through the area in mid-September 1989. Despite the loss of a significant proportion of adults from the colony in 1990, the number of breeding pairs did not dramatically decline in that year, which suggests that a pool of young or inexperienced birds was available to recruit into the breeding population. The loss of regular breeders thus had the effect of reducing the average age or breeding experience in the colony, and also increasing the number of new pair bonds. These changes were the likely cause of late breeding and small egg size observed in 1990, and indicate the importance of a stochastic event such as Hugo on the population biology of a tropical seabird. *Received 29 July 1993, accepted 21 November 1993.*

SEABIRDS exhibit life-history characteristics typified by a relatively long breeding lifetime with many repeated annual breeding efforts, deferred maturity, low fecundity, and elaborate and potentially costly biparental care behavior (Lack 1968, Nelson 1983, Nisbet 1989). This suite of adaptations is thought to be a result of uneven, unpredictable, and sparse food resources available to seabirds, and constraints imposed by central-place foraging (Ricklefs 1983).

Within this overall pattern, seabird life-history characteristics vary with feeding habits and latitude. Where comparison within a taxonomic group is possible (e.g. within the terns, Laridae), tropical nesting species are more "K-selected" (Pianka 1970); they tend to lay smaller clutches of larger eggs relative to adult body size, and commit longer time periods to incubation and chick rearing than do more "r-selected", temperate counterparts (Langham 1983, Nelson 1983, Shea and Ricklefs 1985). The life-history characteristics of tropical seabirds are usually explained in terms of low productivity and food availability in tropical marine waters compared to marine regions at higher latitudes (Be et al. 1971). An alternate, but not exclusive, view was proposed by Dobzhansky (1950) and

reiterated by Pianka (1970). These authors suggested that density-dependent factors are important in regulating populations in tropical environments, which are relatively stable. This leads to selection for life-history traits that enhance competitive abilities at carrying capacity ($K$), such as high adult survival and low fecundity. In contrast, population regulation in temperate environments is more density independent due to greater environmental instability. Therefore, life-history traits such as high fecundity and rapid development enhance abilities to disperse and colonize in populations below $K$.

The Brown Noddy (*Anous stolidus*) is a tropical tern, which breeds mainly on small islands in the Indian, Atlantic, and Pacific oceans (Cramp 1985). Adult survival rates are high, and first breeding occurs at three to six or more years of age (Chardine and Morris unpubl. data); the single, relatively large egg is incubated for about 35 days, and chicks take 45 days or more to fledge (Brown 1976, Morris and Chardine 1992). We have studied a colony of over 100 pairs of Brown Noddies on Cayo Noroeste, Puerto Rico since 1985 and reported breeding-biology patterns that showed a high degree of stability

across years (Morris and Chardine 1992). In five successive breeding seasons (1985 through 1989), Brown Noddies at this location exhibited a synchronous arrival phenology, consistently high breeding success, narrow range of food items, and high adult survival rates (Morris and Chardine 1992, Chardine and Morris in prep.). We now report data from 1990, a year of departure from patterns seen in the previous five years, and from 1991, when patterns returned to those seen in 1985 through 1989. We consider a variety of explanations for the dramatic shift in patterns seen in 1990 and conclude that the likely cause was Hurricane Hugo as it passed by the study site in September 1989.

## STUDY AREA AND METHODS

Cayo Noroeste (18°21'N, 65°21'W) is one of about two dozen rocky islands and islets that form the Culebra archipelago about 35 km east of Puerto Rico. Referred to as Cayo Flamenco by Kepler and Kepler (1978), the island is within the Culebra National Wildlife Refuge, and lies immediately off the northwest tip of Culebra, the largest island in the group. Cayo Noroeste is about 1.5 ha in area, rises some 10 to 12 m above sea level, and is sparsely vegetated with a variety of scattered shrubs and small trees.

We visited the island in late May and June each year; it is during this period when the maximum amount of data can be collected on both eggs and chicks. In 1986, 1987, and 1990, we were present in late April to record details of arrival chronology and the dates when first eggs were laid. In 1986 and 1987 we remained through most of the chick-rearing period. Nest locations were permanently marked with numbered, stainless-steel tags fastened to the rock face above each nest site with silicone sealant. For eggs whose date of laying was unknown, we backdated from known dates of first pipping (30 days) or hatching (35 days). Eggs were marked when first found, they were measured (length and breadth) to the nearest 0.1 mm with calipers, and a volume index ([length × breadth$^2$]/1,000) was calculated. Chicks were banded with a stainless-steel band and a year-class PVC color band. We captured unbanded breeding adults each year, recorded various morphometric measurements, and gave each bird a unique combination of three PVC color bands and a stainless-steel band (Chardine and Morris 1987, 1989). From 1986 through 1991, 11 noddies were recaptured and similarly measured. Adult sex was determined by observation of courtship feeding, by deduction from known sex of a partner, or by discriminant-function analysis (Chardine and Morris 1989). Further details of the study site and methods used each year are in Morris and Chardine (1992).

In addition to the annual collection of demographic

TABLE 1. Chronology of diurnal adult arrival and egg laying for Brown Noddies, Cayo Noroeste, 1985–1991.

| Year | First diurnal arrival | First egg | Laying peak |
|------|------------------------|-----------|-------------|
| 1985 | No data | 4 May[a] | 13–14 May[a] |
| 1986 | 25 April | 29 April | 9–10 May |
| 1987 | 27 April | 29 April | 5–6 May |
| 1988 | No data | 2 May[a] | 7–8 May[a] |
| 1989 | No data | 1 May[a] | 7–8 May[a] |
| 1990 | 2 May | 3 May | 18–19 May[a] |
| 1991 | No data | 2 May[a] | 10–13 May[a] |

[a] Estimated by back-dating from known dates of first pipping (30 days) or hatching (35 days).

data from pairs nesting on Cayo Noroeste, we also monitored changes in numbers of breeding pairs on the island and interisland movement of banded birds. Census of breeding pairs of Brown Noddies on Cayo Noroeste was performed most years by us or U.S. Fish and Wildlife Service (USFWS) personnel. All nests containing an egg or chick were counted sometime during the first two weeks of June. We surveyed for color-banded Brown Noddies on two other islands and the adjacent peninsula on Culebra, all within 3 km of Cayo Noroeste; these support breeding populations of Brown Noddies. Other islands in the archipelago were opportunistically checked for banded birds during seabird surveys conducted by USFWS personnel.

## RESULTS

*Timing of diurnal adult arrival and egg laying.*—Culebran Brown Noddies initially occupy their breeding sites only at night and are not seen for the first time during the day at the colony for several days thereafter (J. Saliva pers. comm.). In the two previous years when we were there to record the event (1986, 1987), large numbers of Brown Noddies arrived synchronously at the island during the daytime on 25 and 27 April, respectively. In 1990, we were at the island on 24 April with the intention of adding further details to the arrival chronology and first-egg data recorded previously. It was then that we obtained the first suggestion that 1990 was an unusual year. In contrast to 1986 and 1987, the first Brown Noddies were not seen during the day at Cayo Noroeste until 2 May 1990, about one week late (Table 1). First eggs were laid the next day (3 May), which is within the range of first-egg dates seen in previous years. However, the peak of laying in 1990 occurred on 18–19 May, about 10 days later than usual. Further-

TABLE 2. Proportion of banded adult Brown Noddies returning each year to Cayo Noroeste, 1986–1991.

| Alive in | Returning in | Total banded | Total returning | Percent returning[a] |
|---|---|---|---|---|
| 1985 | 1986 | 51 | 46 | 90.2 |
| 1986 | 1987 | 76 | 70 | 92.1 |
| 1987 | 1988 | 85 | 78 | 91.8 |
| 1988 | 1989 | 121 | 107 | 88.4 |
| 1989 | 1990 | 126 | 86 | 68.3 |
| 1990 | 1991 | 142 | 132 | 93.0 |

[a] Tests for differences between periods: all periods, $X^2 = 45.6$, df = 5, $P < 0.001$; returning in 1990 vs. 1986–1989 plus 1991, $X^2 = 44.6$, df = 1, $P < 0.001$.

more, only about three dozen adults arrived at the colony on 2 May 1990, unlike in 1987, when birds arrived overnight in numbers that approximated the number of pairs that nested on the island in that year. In 1991, we were not present to record arrival data, but determined (from backdating) that the first egg was laid on 2 May, and that the laying peak occurred about 10 days later, during a similar time period of peak laying during the years 1985 through 1989 (Table 1).

*Return rates of color-banded adults.*—In all years except 1990, from 88 to 93% of all banded birds alive the previous year returned to the colony the following year (Table 2). In 1990, of 126 color banded birds at risk in 1989, only 86 (68%) returned to the colony in 1990. This represents a significant reduction from the combined return rate in the other years (1986 through 1989 plus 1991 vs. 1990, $X^2 = 42.4$, df = 1, $P < 0.001$). None of the noddies that failed to return in 1990 ($n = 40$) has been seen alive as of July 1995.

Did the set of noddies that failed to return in 1990 ($n = 40$) differ from the set that returned ($n = 86$)? We found no significant differences between the two sets of noddies in sex ratio ($X^2 = 0.04$, df = 1), year of banding ($X^2 = 7.60$, df = 4), morphometric measurements taken between 1985 and 1989 (head + bill length, $F_{1,121} = 0.93$; body mass, $F_{1,120} = 1.63$; condition index, $F_{1,119} = 3.63$), or general location of breeding site on Cayo Noroeste in 1989 ($X^2 = 3.62$, df = 2).

*Egg and adult morphometrics.*—Figure 1 shows the yearly trend in length, breadth, and volume index of Brown Noddy eggs laid on Cayo Noroeste. F-tests revealed significant interyear variation in all measures (length, $F_{6,510} = 2.36$, $P < 0.05$; breadth, $F_{6,510} = 2.25$, $P < 0.05$; volume index, $F_{6,510} = 2.87$, $P < 0.01$). Posthoc Sheffé
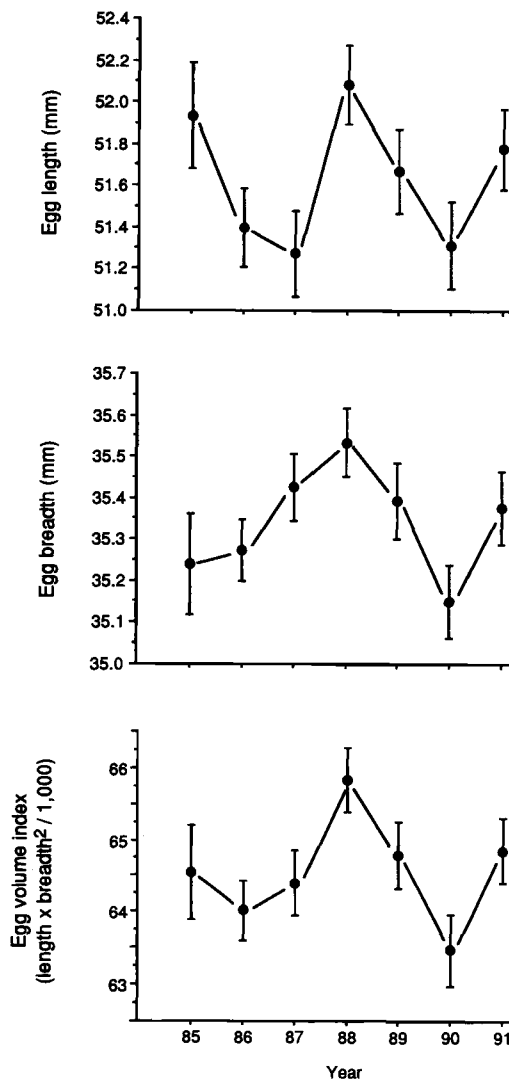


Fig. 1. Yearly trends ($\bar{x} \pm$ SE) in length, breadth, and volume index of eggs laid by Brown Noddies on Cayo Noroeste.

tests of length and breadth between pairwise combinations of years showed no significant differences (all $P > 0.05$). However, eggs laid in 1990 had the smallest mean volume index of any year studied and differed significantly from 1988 eggs, which were on average the largest (Sheffé test, $P < 0.05$). This trend was clear when the egg-volume index was compared between these two years within the same female. Of 27 females laying eggs in 1988 and 1990 for which we could calculate the volume index, 20 laid a smaller egg in 1990, and 1990 eggs were sig-
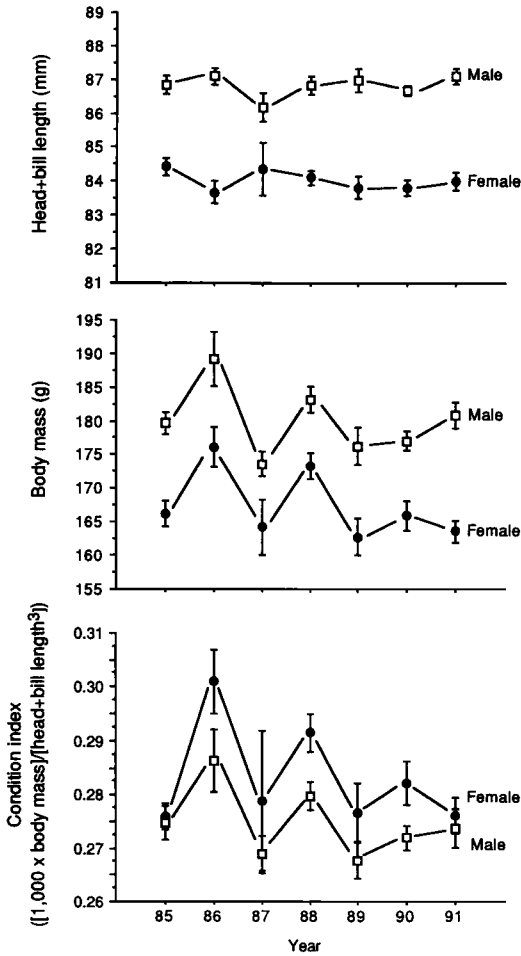
Fig. 2. Yearly trends ($\bar{x} \pm$ SE) in morphometric measurements of Brown Noddies breeding on Cayo Noroeste.
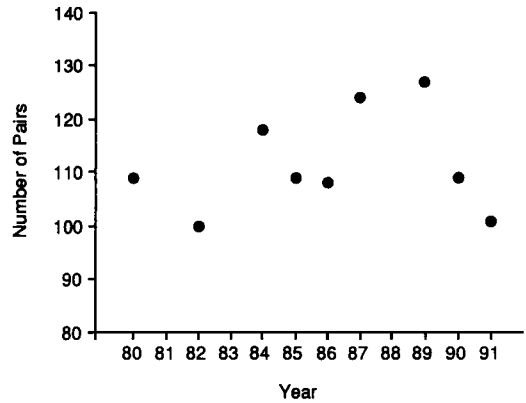


Fig. 3. Yearly trend in the number of pairs of Brown Noddies nesting on Cayo Noroeste.

Noddies on Cayo Noroeste for most years from 1980 to 1991 are in Figure 3. Overall, numbers have not varied substantially around the mean count of 112 $\pm$ SD of 9.4 pairs ($n = 9$). Numbers gradually increased from 1980 to 1989, and then declined in 1990 and further in 1991 to early-1980 levels.

## DISCUSSION

In the years 1986 through 1989 and 1991, Brown Noddies breeding on Cayo Noroeste, Culebra, were characterized by: a synchronous daytime arrival at the colony in late April; a period of peak egg laying some five to nine days thereafter; and high rates of return of adult birds between years (Morris and Chardine 1992, Chardine and Morris in prep.). In 1990, we recorded a marked shift in these consistent patterns; adults were delayed in their daytime arrival at the colony by about one week, and the egg-laying peak occurred about 10 days later than usual. Eggs laid in 1990 were the smallest of any year studied. Perhaps most significantly, there was a marked reduction in the proportion of banded adult birds that returned to the colony in 1990.

Our 1990 observations were consistent with a shift in environmental conditions in that year, which affected feeding conditions for noddies; however, did they reflect a shift in local conditions or were they the result of more widespread phenomena? We decided to assess this by surveying a number of investigators who had worked with colonial nesting seabirds at a single location for at least five years, and who

nificantly smaller than those laid in 1988 (paired $t = 4.10$, df $= 26$, $P < 0.001$).

Figure 2 shows the yearly trend in morphometric measurements of male and female Brown Noddies trapped in each year. Head + bill length did not vary significantly among years (males, $F_{6,137} = 0.80$; females, $F_{6,139} = 0.48$). In contrast, body mass and condition index ([1,000 $\times$ body mass]/[head + bill length]$^3$) did vary significantly among years for males and females (male body mass, $F_{6,135} = 3.95$, $P < 0.005$; females, $F_{6,139} = 4.50$, $P < 0.001$; male condition index, $F_{6,135} = 2.85$, $P < 0.05$; females, $F_{6,138} = 4.59$, $P < 0.001$), although 1990 was not an exceptional year in either regard.

*Size of Brown Noddy breeding population on Cayo Noroeste.*—Counts of breeding pairs of Brown

had a population of color-banded (or otherwise identifiable) study animals. We conducted a verbal survey at two professional meetings in 1990, and a written survey of authors noted by Nisbet (1989) in 1991. The surveys sought a qualitative assessment (early/late, increase/decrease, greater or less) of the 1990 breeding season relative to previous years. We asked for comments on: (1) timing of arrival, first egg and egg-laying peak; (2) number of breeding pairs and colony population size; (3) egg and adult morphometrics; and (4) hatching and fledging success. The results (Table 3) show that the 1990 breeding season was anomalous in mid- and low-latitude areas, but not in high-latitude or inland areas. The reports of two investigators working in the Virgin Islands, about 30 to 40 km to the west of Culebra, were of particular significance. They observed a decrease in numbers of breeding pairs of several species of seabirds in 1990 (Pierce), and a depression in several demographic and morphometric measures taken in 1990 compared to previous years (Southern). Their results show that the anomalies we observed in 1990 were not localized to the immediate area of Culebra or restricted just to Brown Noddies.

The most dramatic and biologically significant effect seen on Cayo Noroeste in 1990 was the marked reduction in the return rates of birds known to be alive in 1989. This effect could have been the direct result of: (1) a change in observational methods resulting in a larger proportion of birds being missed; (2) higher incidence of nonbreeding (see Wooller and Coulson 1977, Coulson 1984, Wooller et al. 1990); (3) movement of the missing adults to other breeding sites; or (4) the death of the missing birds. Since 1990, we have collected information that eliminates options 1 through 3 and suggests that, sometime between our last visit to Cayo Noroeste in 1989 (mid-June) and our first visit in 1990 (late April), a significant die-off of noddies occurred.

Options 1 and 2 imply that the missing birds in 1990 would be resighted in subsequent years at Cayo Noroeste. Since we have never resighted any of the missing noddies, we eliminate both options. Option 3 would be supported by the discovery of the missing noddies breeding at other locations. However, despite active searches up to June 1994 on other islands in the archipelago that support breeding populations of Brown Noddies, we have not found any of the missing birds. Indeed, we have evidence that breeding dispersal of Culebran Brown Noddies is very limited. Of 281 adults banded on Cayo Noroeste from 1985 through 1993, only two have been observed at another colony and presumably breeding. These two birds (not paired with each other) were last seen breeding on Cayo Noroeste in 1991 and, subsequently, observed by J.W.C. in June 1994 on Alcarraza, about 3 km to the northwest. An additional three adults banded on Cayo Noroeste (two of them members of the same pair) were found breeding on a point of land on the island of Culebra, about 100 m across a small water channel to the east in 1992. All three birds had previously bred on the side of Cayo Noroeste adjacent to the point, and we do not consider these observations as evidence of significant breeding dispersal. Adult noddies ($n = 43$) also were banded on Cayo Yerba about 3.5 km southwest of Cayo Noroeste between 1985 and 1993, none of which have been found breeding elsewhere. Our observations of limited movement of breeders between colonies are consistent with those of other seabird species (e.g. Coulson and Wooller 1976, MacDonald 1977, Greenwood 1980). Therefore, we are confident that the noddies missing in 1990 had not moved elsewhere to breed in that, or subsequent years.

Taken together the data strongly support option 4 that the noddies missing in 1990 had died. We have no tangible evidence as to why the birds died and can only speculate on possible causation. The lack of any significant differences between birds that survived in 1990 and those that did not suggests that mortality was random and not directed to birds that shared a particular set of attributes.

It is possible that the missing birds in 1990 died from predation, disease, or oil pollution. Potential or actual predators occur in the vicinity of Cayo Noroeste (e.g. Red-tailed Hawk [*Buteo jamaicensis*], Peregrine Falcon [*Falco peregrinus*]), but we have observed very few noddy carcasses showing evidence of predation during the course of our work. Diseases or toxins (e.g. Newcastle disease, botulism, paralytic shellfish poisoning, domoic acid) can cause mass mortalities in marine birds (e.g. Coulson et al. 1968, Wobeser et al. 1993, Work et al. 1993), but we have no evidence that these factors affected the population we studied. Although the effect of oil on waterbirds is usually more severe in cold-water environments (Bourne 1976), an oil pol-

TABLE 3. Results of informal survey of seabird investigators. Respondents asked to compare various demographic aspects of their 1990 data against patterns present in previous years, and to comment on whether 1990 data represented departure from "normal" trends.

| Investigator | Species | Years of study | Location | Comment on 1990 season |
|---|---|---|---|---|
| D. Ainley | Various | 1971–1990 | Farallon Islands, California | Multiple-egg species experienced reduced productivity and breeding failure in 1990. |
| J. Burger and M. Gochfeld | Common Tern (*Sterna hirundo*), Black Skimmer (*Rynchops niger*) | 1976–1990 | New Jersey | Late arrival/laying in 1990; otherwise normal. |
| J. C. Coulson | Black-legged Kittiwake (*Rissa tridactyla*) | 1953–1990 | North Shields, U.K. | "Normal." Nothing unusual in U.K. except seabirds on Shetland and kittiwakes on Isle of May. |
| G. J. Divoky | Black Guillemot (*Cepphus grylle*) | 1975–1990 | Cooper Island, Alaska | 1990 close to normal. |
| A. J. Gaston | Thick-billed Murre (*Uria lomvia*) | 1981–1990 | Coats Island, N.W.T., Canada | 1990 not regarded as an abnormal year. |
| B. W. Massey | California Least Tern (*S. antillarum*) | 1971–1990 | San Diego Co., California | Marked increase in breeding pairs and fledging success in 1990. |
| E. C. Murphy | Black-legged Kittiwake, Common Murre (*U. aalge*) | 1975–1990 | Bluff, Alaska | 1990 not an extreme year. |
| I. C. T. Nisbet | Roseate Tern (*S. dougallii*), Common Tern (*S. hirundo*) | 1970–1990 | Bird Island, Massachusetts | Roseate Tern: 1990 slightly worse than 1987–1989, slightly better than 1977–1979, but not back to best years of 1970s/1980s. Common Tern: 1990 not markedly different from 1988–1989. |
| J. Pierce | Various tropical species | 1976–1990 | U.S. Virgin Islands | Eight of 11 species decreased in numbers of breeding pairs in 1990 compared to "normal" years. |
| B. H. Pugesek | California Gull (*Larus californicus*) | 1958–1990 | Bamforth Lake, Wyoming | Nothing unusual in 1990 from previous years. |
| W. E. Southern | Brown Booby (*Sula leucogaster*) | 1984–1990 | St. Thomas, U.S. Virgin Islands | All measures lower in 1990 than previous years. |
| J. E. Spendelow | Roseate Tern, Common Tern | 1978–1990 | Falkner Island, Connecticut | Most notable aspect of 1990 was extreme lateness of laying, especially Roseate Terns. |

lution event could have resulted in the death of the missing birds. However, no oil-pollution event affecting seabirds was reported from the area between 1989 and 1990 (J. Wunderle pers. comm.).

Periodic El Niño events are known to cause a wide variety of environmental effects over sometimes large geographic areas. Effects on marine birds include short-term shifts in distribution, higher rates of nonbreeding, and adult mortality (Duffy et al. 1988, Schreiber and Schreiber 1989), and appear to be proximately driven by dramatic changes in food supply. Duffy et al. (1988) reported the effects of strong El Niño events in the 1980s on Caribbean seabirds and correlated Robertson's (1969) report of die-offs of Sooty Terns (*Sterna fuscata*) with an El Niño event.

Some of our observations (late laying, small eggs) suggest reduced food supply in 1990 within the foraging range of Brown Noddies breeding on Cayo Noroeste. Furthermore, adults and chicks handled in 1990 rarely regurgitated a food bolus, a regular occurrence in other years. However, if the overwintering food supply had been poor, we expected returning birds would indicate this by exhibiting lower body mass and condition index compared to typical years. In both regards, males and females measured in 1990 were not exceptional compared to other years. An El Niño event did not occur in 1989–1990 (sea-surface temperatures were about average in the eastern Pacific at that time; NOAA 1993), and we are not aware of any oceanographic anomalies in the Caribbean that occurred in these years.

The eye of Hurricane Hugo passed a few kilometers to the east of the Culebra archipelago on 18 September 1989. Based on the timing and ferocity of this event, we suggest that this storm may have been responsible for the death of Noroeste noddies. Damage to vegetation and physical structures in the path of this hurricane was extensive on both mainland and insular areas, and effects on other bird populations in its path have been noted (Shepherd et al. 1991, Wauer and Wunderle 1992). Culebra was devastated by the hurricane; most structures on the island were destroyed, most of the vegetation was defoliated or uprooted, and much of the coral growth in adjacent waters was broken or silted-up (pers. obs.).

Noddies are not normally seen in the vicinity of Cayo Noroeste during the day from some-

time in September to late April (T. Tallevast pers. comm., this study), and we can only speculate on their whereabouts when Hugo passed by. Noddies at other locations attend their colonies at night after the breeding season and feed in waters within tens of kilometers from breeding colony in the nonbreeding season (W. B. Robertson, R. van Halewyn pers. comm.). Therefore, we think that Noroeste noddies were in the vicinity of the colony when Hugo passed by, and likely would have suffered mortality through the physical effects of the storm.

Noddy eggs laid in 1990 on Cayo Noroeste were on average the smallest of any year studied, and differed significantly from those laid in 1988, when on average the largest eggs were laid. Although this could reflect poorer feeding conditions during the period of egg formation and before, we suggest that this could also result from changes in age structure, breeding experience, and pair status of breeders in 1990. Likewise, we think that the late arrival and egg laying observed in 1990 also was a result of these changes.

Even though 40 birds were removed from the pool of breeders on Cayo Noroeste in 1990, colony size did not decline appreciably. Since noddies show limited breeding dispersal (see above), the missing birds were most likely replaced by young or inexperienced birds newly recruiting into the population rather than from an influx of breeders from other locations. The loss of birds in 1990 also meant that many new pairs were formed (Chardine and Morris in prep.). Thus, the age structure, breeding experience, and pair status of breeders on Cayo Noroeste changed substantially in 1990, shifting toward younger, less experienced birds and newer pair bonds. From studies of known-age larids, it is well known that younger, less experienced birds lay smaller eggs (Coulson 1963, Thomas 1983), and arrive and lay later than older birds (Coulson 1966, Mills 1973). The age of the pair bond has an independent effect on timing of laying, with females in newly formed pairs laying later in the season than established pairs (Coulson 1966, Mills 1973).

The suggestion that young or inexperienced birds filled the openings left by birds dying between 1989 and 1990 implies that there is a substantial pool of birds available for recruitment. This would be expected in a seabird species such as the Brown Noddy, which does not breed on Cayo Noroeste until three to six or

more years of age (Chardine and Morris un-publ.). Such variation in age of first breeding is found in other seabirds (e.g. Wooller and Coulson 1977) and implies that some prebreeders are physiologically capable of reproduction but are prevented from doing so by other factors such as social competition. Porter and Coulson (1987) reported that, after years when mortality of adult Black-legged Kittiwakes was higher, or after the provision of more nest sites, recruitment rates in their study colony increased. They suggest that this indicated "a pool of potential recruits from which the new recruits needed could be drawn." In the case of Cayo Noroeste, we wondered why the colony was not increasing in size given this pool of potential breeders, especially since colony sites do not appear to be a limiting factor at this location? It is possible that the number of suitable sites for Brown Noddies may be limiting, and only in situations of reduced competition for these sites, such as what likely occurred in 1990, are young, inexperienced birds able to obtain suitable sites (see Coulson 1971, Porter and Coulson 1987).

Our long-term study of Brown Noddies thus far has shown that with the exception of one year, patterns of breeding and demography have been stable. This likely reflects overall environmental stability in our tropical study site. However, a stochastic perturbation in the form of a severe hurricane shifted these patterns in 1990, resulting in reduced survival of adults, increased recruitment, and concomitant changes in the structure of the breeding population of Brown Noddies on Cayo Noroeste. The question of whether tropical seabirds experience events such as Hugo frequently enough to shape the evolution of life-history strategies remains to be answered.

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