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PART II. SEABIRDS, OTHER TERRESTRIAL ANIMALS, AND CONSERVATION

BY

CAMERON B. KEPLER, ANGELA K. KEPLER, AND DAVID H. ELLIS

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PART II. SEABIRDS, OTHER TERRESTRIAL ANIMALS, AND CONSERVATION

BY
CAMERON B. KEPLER1, ANGELA K. KEPLER2, AND DAVID H. ELLIS3

ABSTRACT

Approximately 1,000,000 seabirds of 11 species bred on Caroline Atoll between September 1988 and June 1990. The most abundant species, with over 900,000 birds, was the Sooty Tern. Two species (Red-tailed Tropicbird, Blue-gray Noddy) are reported breeding for the first time. The known seabird fauna now includes one tropicbird, 3 boobies, 2 frigatebirds, and 5 terns.

Seabird distribution on Caroline is determined by the distribution of plant communities and nonvegetated substrates, the prevailing trade winds, and to a lesser extent, rats and coconut crabs. Red-tailed Tropicbirds and ground-nesting Brown Noddies nested on small islets relatively free of rats and coconut crabs. Masked and Brown Boobies preferred exposed windward beaches, primarily on Long and Nake. The tree-nesting Red-footed Booby and frigatebirds attained their highest nest densities in areas with reduced wind speed. Black Noddies were found in dense colonies, generally high in pisonia trees, while the uncommon Blue-gray Noddies nested solitarily on open coral rubble. Sooty Terns nested in large colonies, generally near or under relatively open Tournefortia scrub, but also in open areas under Tournefortia and closed-canopy Pisonia forests. Not all sites were utilized annually. Tree-nesting Brown Noddies and White Terns, found throughout the native forests, were the only species utilizing anthropogenic forests. The lowest seabird population densities were found in the disturbed forests on South and southwest Nake, and no seabirds nested on inhabited Motu Ana-Ana.

About 300 Bristle-thighed Curlews overwinter on Caroline, foraging in all terrestrial habitats, including Pisonia and disintegrating Cocos-Ipomoea forests. We extended the known winter range of the Long-tailed Cuckoo by discovering a small population on the atoll, the first record for the Southern Line Islands.

The known lizard fauna was increased from 3 to 6 species. Approximately 2,200 coconut crabs inhabited 12 islets on Caroline. Although primarily associated with Cocos, we also found them in Pisonia and Tournefortia. Pacific green turtles breed in small numbers; we found the first known nests (old) in 1990. Polynesian rats are abundant, and Pacific bottlenose dolphins were seen close to the windward side in 1990.

1 National Biological Survey, School of Forest Resources, The University of Georgia, Athens, Georgia, 30602, USA
2 400 Snapfinger Drive, Athens, Georgia, 30605, USA
3 National Biological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, 20708, USA

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The populations of seabirds and coconut crabs on Caroline Atoll are of national and international importance. The Black Noddy (17,000 birds) and White Tern (8,000 birds) populations are the largest in the Republic of Kiribati, while the Red-footed Booby population (7,000 birds) is one of the largest in the world.

Caroline's conservation attributes are numerous: large, varied seabird populations, wintering grounds for several species of migratory shorebirds and the Long-tailed Cuckoo, plant ecosystems of national and international importance (lushly wooded motus with significant groves of Pisonia grandis, Cordia subcordata, Tournefortia argentea), virtually pristine coral reef ecosystems exceedingly rich in giant clams (Tridacna maxima), a coconut crab population of Pacific-wide importance, ancient Tuamotuan marae (religious sites), and a breeding site for green turtles. The marine ecosystems, terrestrial biota, and geology of its 39 motus of varied size, 22 of which are pristine or near-pristine, provide prime outdoor ecological laboratories for numerous areas of research. These qualities, plus its exceptionally clear, essentially unpolluted lagoon, and its relative lack of disturbance, render it worthy of permanent protection.

A. HISTORY OF ORNITHOLOGICAL STUDIES

"There were a great quantity of sea birds of several kinds, and so importunate that they seemed to want to attack the men" (Markham 1904). So wrote the Portuguese explorer de Quiros on 21 February 1601, the first European to see Caroline Atoll.

Precisely which seabirds were present remained a mystery until the island was surveyed 364 years later by the Pacific Ocean Biological Survey Program (POBSP) (Clapp & Sibley 1971a). Prior to that visit, accounts of the avifauna had been incomplete. Bennett (1840) described Red-footed Boobies, a frigatebird (species ?), White Terns, Bristle-thighed Curlews, tattlers, and "a great number of small pigeons" with white heads (certainly noddy terns, perhaps both A. minutus and A. stolidus). The "shoal birds" that greeted him were probably Sooty Terns. His most unusual contribution was mention of a possible flightless rail: "The other birds of the coast were a kind resembling a coot..." (p. 372).

The 1883 Solar Eclipse Party (Pt. I, Sect. B) published a few sketchy notes, adding Lesser Golden-Plover, Reef Heron, and Masked Booby ("gannet") to the bird list. Of dubious identity were 2 species of "seagull" and a "snipe" (Dixon 1884). Holden, one of the astronomers, heard "the notes of a singing bird," which prompted us to add mist nets to our equipment in the hopes of capturing an Acrocephalus warbler. This resulted in our discovery of the Long-tailed Cuckoo (Ellis et al. 1990) and piqued our curiosity about what Holden might really have heard.
The POBSP expedition spent 3 days on Caroline in June 1965. They found 10 species of seabirds (9 breeders), 4 migrant shorebirds, and a Reef Heron (Clapp & Sibley 1971a), providing rough population estimates for each species. This work laid the foundation for later expeditions. Brief visits to Caroline by the Kiribati government in 1974 (Gilbert & Ellice Islands Government 1974, Vickers 1974) and Roger Perry in 1977 (Perry 1974, Garnett 1983) added no further information.

The 1988 expedition to Caroline was longer and more extensive than all former visits. We found 3 new island records: a breeding seabird (Red-tailed Tropicbird), a shorebird (Sanderling), and a migratory land bird (Long-tailed Cuckoo), and mapped islet-by-islet distributions for each species. Our population estimates, calculated from numerous transect surveys, aerial photographs, and detailed vegetation analysis, indicate that Caroline's avifauna is far more important than had previously been suspected (King 1973, Garnett 1983). In March and May 1990, the ICBP 1990 Line and Phoenix Islands Expedition (Pt. I, Sect. C), of which AKK was co-leader, filled in minor gaps in our knowledge. Seven-year-old Alexandre Falconer, then living on Caroline, added another breeding seabird, the Blue-gray Noddy, in summer 1990.

B. METHODS

From 22-29 September 1988, C. B. Kepler, A. K. Kepler, D. H. Ellis, and K. Teeb'aki surveyed all of Caroline's 39 islets except North Arundel Islet, naming most of them (Fig. 1; see also Pt. I, Sect. C). We established 50 linear transects, extending 13,300 m x 30 m, laid out to ensure that at least 5% of each islet was sampled for birds and plants (see Pt. I, Sect. C and Fig. 9). Sampling was increased with 19,300 m of perimeter surveys along the windward and leeward coasts of 21 islets (Pt. I, Fig. 9). On Noddy Rock, Skull, Atibu, Bo'sun Bird, Coral, Reef-flat, and Fishball (Fig. 1) we made total counts of the breeding seabirds. All surveys were conducted during daylight hours. Some incidental data have been added from the 1990 ICBP expedition.

Distribution and habitat preference: We described 7 major plant communities on Caroline Atoll (Pt. I). With the use of aerial photos and the transect data, we mapped the communities found on each islet. Bird distribution was determined and plotted using these islet vegetation maps. If a species nested within a particular plant community, it was plotted on the distribution maps as occurring throughout that community unless determined otherwise.

Population sizes and breeding phenology: We measured transect distances for each islet using a hip-chain and biodegradable cotton thread. We recorded all birds seen within the 30-m-wide strips; transect width was estimated visually. We assigned birds to one of several mutually exclusive categories: adults present, adults on territory, adults on nests (contents unknown), eggs, naked chicks, downy chicks, chicks with remiges erupting, chicks with scapular feathers, or chicks in juvenile plumage. We created a range of possible laying dates for each egg and
Figure 1. Caroline Atoll, Republic of Kiribati, with newly-named islets.
chick using known growth parameters for each species (C. Kepler 1978, Kepler & Kepler 1978). This enabled us not only to estimate seabird populations, but also to determine and plot a rough breeding phenology for each species (Figs. 3, 5, 7, 9, 10, 12). In these figures, the height of the bar for each category ("downy," "scapulars," etc.) represents the number of nests found or estimated with that development stage in September 1988. The bar width represents the approximate time span over which eggs could have been laid to produce that stage, while the "no. days" is a count back from the survey dates to accommodate growth and development that had occurred. Thus, while each figure shows what breeding stages we found, we extend those nests back in time to show roughly when they would have begun. The number of clutches begun per day is determined by dividing the number of nests per stage by the time span in days over which those eggs were laid.

Sooty Terns nested in dense colonies. Each colony was mapped, and its total size (m²) was calculated. A minimum of 10 plots (3 m x 3 m or 3 m x 6 m), within which all eggs and chicks were counted, were randomly located along a compass line in each colony. The population size of each colony was estimated from these plot densities.

**Mist nets:** We operated 4 ATX 4-shelf 36 mm mesh mist nets (2.6 x 12 m) for 43.5 net hours, according to the following schedule: 14.5 net hours (daylight) beneath a 10-15 m Cocos canopy on South, 27.5 net hours (day and night) in Pisonia-Cocos interface (12 m tall) near Transect 10 on Long, and 1.5 net hours in Pisonia-Tournefortia within a 4-6 m canopy on Transect 4, Long. One cuckoo was collected (USNM 607191).

**Collecting other vertebrates:** Lizards that were active and conspicuous were collected at base camps on South and Long, either by hand or with a blowgun firing steel darts. No attempt was made to search for reptiles under coral, litter, or in other concealed locations. Rats were collected with a blowgun or snap traps baited with coconut, the former proving far more effective because most traps were sprung by hermit crabs. We preserved all specimens in formalin and sent them to the U.S. National Museum.

**C. SEABIRD SPECIES ACCOUNTS**

Eleven species of seabirds occur at Caroline, most of which breed in large numbers. They include one tropicbird, 3 boobies, 2 frigatebirds, and 5 terns.

**RED-TAILED TROPICBIRD (Phaethon rubricauda)** Figs. 2, 3; Pl. 1

Red-tailed Tropicbirds breed at widely scattered locations throughout the tropical Pacific and Indian Oceans. In the Line Group, they nest from Palmyra south to Starbuck (Perry 1980), with a large population (8,500 birds) on Christmas Island (Clapp 1967). Prior to our expedition it was unrecorded from Caroline, Vostok, or Flint.
Figure 2. Distribution map of breeding Red-tailed Tropicbirds and Brown Boobies on Caroline Atoll, September 1988. In this and the following distribution maps, arrows indicate concentrations of breeding birds.
Figure 3. Approximate laying dates for Red-tailed Tropicbird nests found on Caroline Atoll in September 1988. In this and the following similar figures the numbers of nests begun during a given time period (bars) were determined by tallying each nest into one of several age classes (bar labels): bar widths indicate length in days for each class. The dotted line connects mean number of surviving clutches begun per day for each class. For example, a juvenile found in September began its egg stage in the previous May or June. The number of days are counted backwards from field observations.
Distribution and habitat preference: Our first indication that Red-tailed Tropicbirds nested on Caroline was the discovery of a skull, tail feather, and broken egg (Pt. I, Pl. 46) under a small Tournefortia bush on a previously unnamed islet between Pig and North Brothers Islets. We named this sparsely vegetated collection of rubble "Skull Islet" (Pt. I, Pls. 46, 49). We later found 47 nests on another islet, naming it Bo’sun Bird (Fig. 1) after the species' common name.

All nests were located under relatively open Tournefortia scrub less than 3 m tall in open, windy locations, with the majority (91%) on small islets (0.24-0.86 ha). All nests were under shrubs with few stems within a 0.5 m² nest space, and most had peripheral cover on the sides of the shrubs, both important factors in nest-site selection (Clark, Ricklefs, & Schreiber 1983). All nests were in areas relatively free of Polynesian rats (Rattus exulans) and coconut crabs (Birgus latro): five nests on Long were within 50 m of the island’s south point.

There are large populations of Polynesian rats and coconut crabs on Caroline’s bigger, more wooded islets. This rat, though basically vegetarian, is an effective seabird predator (C. Kepler 1967, Norman 1975) that in some years has taken 65% of the Red-tailed Tropicbird eggs and 100% of the chicks on Kure Atoll (Fleet 1972). Coconut crabs are also known bird predators (Helfman 1979, Reese 1987): on Caroline in 1965 they preyed upon Sooty Terns (Clapp & Sibley 1971a), and in 1990 AKK photographed the aftermath of predation or scavenging on at least one species of tern on Brothers Islet. It may be no accident that tropicbirds on Caroline occur only on small, relatively open islets that harbor few, if any, rats and crabs, and the southern tip of Long Island, where predator densities are low. We saw no rats on Bo’sun Bird Islet. Although rats could swim the 165 m to the islet, the nearly continuous presence of black-tipped reef sharks (Pt. I, Pl. 10) in the channels surrounding the islet provides protection to its nesting tropicbirds.

Numbers: In September 1988, we found 56 active nests on 5 islets (Fig. 2, Table 1) and estimated a minimum population of 60 pairs. The May 1990 expedition found 130 nests on Bo’sun Bird; our revised estimate for Caroline is approximately 300 birds. Bo’sun Bird Islet was surveyed by POBSP in June 1965, and no tropicbirds were located on the ground or in the air (F. Sibley, pers. comm.). It is unlikely that Red-tailed Tropicbirds were present but overlooked at that time, suggesting that they have colonized the atoll only recently. The Caroline population is now the second largest colony known from the Line Group, and Caroline is only one of 5 islands in the archipelago where Red-tailed Tropicbirds are known to breed.

Phenology: Of the 56 nests found in 1988, 54 contained eggs or chicks (Table 2). The 33 chicks were divided into 4 age classes (Fleet 1974, Diamond 1975a), which, together with the 21 eggs, provided an indication of laying phenology for 140 days prior to our arrival (Fig. 3). Eggs in surviving nests had been laid at a fairly even rate from early May (possibly starting earlier) through September. The finding of only 2 additional pairs on territory, and only one courtship flight, indicated
Table 1. Estimated number of breeding seabird pairs on Caroline Atoll, September 1988.

<table>
<thead>
<tr>
<th>Location</th>
<th>Red-footed Booby</th>
<th>Black-footed Albatross</th>
<th>Brown Noddy</th>
<th>Frigatebird</th>
<th>Terns</th>
<th>Total Estimated Pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td>South</td>
<td>5</td>
<td>105</td>
<td>47</td>
<td>37</td>
<td>368</td>
<td>*</td>
</tr>
<tr>
<td>South West</td>
<td>5</td>
<td>105</td>
<td>47</td>
<td>37</td>
<td>368</td>
<td>*</td>
</tr>
<tr>
<td>West</td>
<td>5</td>
<td>105</td>
<td>47</td>
<td>37</td>
<td>368</td>
<td>*</td>
</tr>
<tr>
<td>East</td>
<td>5</td>
<td>105</td>
<td>47</td>
<td>37</td>
<td>368</td>
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<td>368</td>
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<td>North East</td>
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<td>105</td>
<td>47</td>
<td>37</td>
<td>368</td>
<td>*</td>
</tr>
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</table>

Breeding confirmed in 1989 or 1990.
Table 2. Stages in the breeding cycle of the Red-tailed Tropicbird, Caroline Atoll, 27-29 September 1988 (ages after Stonehouse 1962).

<table>
<thead>
<tr>
<th>Nest Stage:</th>
<th>Juv.</th>
<th>Remiges</th>
<th>Scapulars</th>
<th>Downy</th>
<th>Egg</th>
<th>Pairs on Territory</th>
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</thead>
<tbody>
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<td>Approximate Age in Days From Laying:</td>
<td>90-133</td>
<td>69-89</td>
<td>58-68</td>
<td>44-57</td>
<td>0-43</td>
<td>-</td>
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<tr>
<td>No. Nests:</td>
<td>18</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>21</td>
<td>2</td>
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that laying was ending. On 24 May 1990, many nests contained eggs and downy chicks (75% nests with chicks) and pairs were still courting.

On Christmas Island, peak laying generally occurs from June to October (Schreiber & Ashmole 1970), later than those parts of the 1988 and 1990 breeding seasons we observed on Caroline.

MASKED BOOBY (*Sula dactylatra*)

The Masked Booby is widely distributed in the Atlantic, Indian, and Pacific Oceans. Clapp (1967) estimated that 19,100 Masked Boobies bred in the Line and Phoenix Islands, with about 13,000 of them in the Line Islands, mostly (ca. 9,000) on Jarvis.

Distribution and habitat preference: Eighty-four percent of Masked Booby nests (159) were on the windward, rubbly shores of Long and Nake Islands, extending to the north end of the atoll. Fifteen additional nests were scattered along the lagoon edges of 5 South Nake Islets (Table 1). Nests consisted of bare scrapes with exposed sand, usually within a sparse ground cover of *Portulaca* and *Heliotropium* (Pl. 2). Over half the nests were amassed in one open colony on Nake that extended nearly 1,000 m, beginning approximately 150 m south of Transect 2 and extending about 50 m north of Transect 4 (Pt. I, Fig. 8). Here a nearly unbroken *Heliotropium* mat 30-80 m wide, with patches of *Tournefortia*, occupied the area between the leading edge of the *Tournefortia* scrub and the beach crest. Nests were 20-30 m apart in the densest section (near Tr. 3). All nests were exposed to the sun, unlike those of the Brown Boobies. Some adults and juveniles roosted under the scrub; guano deposits indicated regular occupancy.

A loose group of 7 breeding pairs was scattered on a broad plain of low herbs along a partially filled old interislet channel 370 m south of the north end of Long Island (Tr. C, Pt. I, Figs. 8, 40). Four more pairs nested in coral rubble along the channel separating Nake and Long,
Figure 4. Distribution map of breeding Masked Boobies on Caroline Atoll, September 1988.
Figure 5. Approximate laying dates for Masked Booby nests found on Caroline Atoll in September 1988. See Fig. 3 for explanation.
one pair with a downy young only 2-3 cm above high-tide flow on an "islet" between fingers of the channel, a precarious location where nesting surely must fail in stormy periods. No birds were seen there in March and May 1990, following a severe storm in February 1990. Four pairs nested singly along a leeward 1,000 m stretch of lagoon shore on the northern end of Long (Fig. 4); hardpan was the primary substrate.

**Numbers:** In September 1988 we found 189 Masked Booby pairs (Table 3), including those on territory (with or without nest scrapes) and juveniles (with or without attending adults). We found no "clubs" of nonbreeding birds. We covered most of the habitat favored by this species except the northern 300 m of Nake Island; in 1990 a few scattered pairs nested there. Our population estimate, including pairs we might have missed, was approximately 200 breeding pairs. Other population estimates were "ca. 10" birds (Clapp & Sibley 1971a) and 50 ± 15% (Grossman & Grossman 1974). In 1965 POBSP biologists (F. Sibley, pers. comm.) surveyed all locations where we found breeding pairs. Thus, 200 pairs represents a major increase in the population on Caroline Atoll.

**Phenology:** In June 1965 only 4 Masked Booby nests containing eggs were found (Clapp & Sibley 1971a), indicating that nesting began in May or June. On 9-10 September 1974, Grossman & Grossman counted 23 nests containing "eggs and nestlings" on windward Long and part of Nake. We found nests in all stages in September 1988 (Table 3, Fig. 5). The large age class in April may include some juveniles that could fly (i.e. were older than 180 days). We may have undercounted naked chicks, not wishing to expose them to the sun by frightening the brooding adult. Laying began in April or earlier, peaked in June and July (Fig. 5), and continued until our survey in late September. The 34 pairs on territory, many with nest scrapes (Table 3), indicated that laying was still in progress and would continue into October.

Table 3. Stages in the breeding cycle of the boobies of Caroline Atoll, 21-29 September 1988.

<table>
<thead>
<tr>
<th>Species</th>
<th>Flying Juv.</th>
<th>Juv.</th>
<th>Scapulars</th>
<th>Remiges</th>
<th>Downy</th>
<th>Naked</th>
<th>Eggs</th>
<th>Pairs on Territory</th>
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<tr>
<td>Masked</td>
<td>&gt;164</td>
<td>145-164</td>
<td>115-144</td>
<td>89-114</td>
<td>55-88</td>
<td>45-54</td>
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<tr>
<td>Brown</td>
<td>&gt;164</td>
<td>144-164</td>
<td>114-144</td>
<td>88-114</td>
<td>54-88</td>
<td>44-54</td>
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<tr>
<td>Red-footed</td>
<td>-</td>
<td>&gt;150</td>
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<td>75-110</td>
<td>54-74</td>
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No. nests in each stage

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<td>Brown</td>
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<td></td>
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</tr>
<tr>
<td>Red-footed</td>
<td>many</td>
<td>-</td>
<td>-</td>
<td>29</td>
<td>-</td>
<td>919</td>
<td>1,270</td>
</tr>
</tbody>
</table>

1 For descriptions of nest stages see C. B. Kepler (1978).
In March 1990, 31 pairs were on territory or were attending nests, eggs, or older chicks, indicating that a new breeding season was underway as the previous season was ending. By May 1990 there were 63 nests, mostly with eggs, and there were no older chicks. Thus, the 1990 season augments the 1988 data and suggests an annual cycle with egg laying beginning slowly in February and March, peaking in June and July, and declining to a low ebb from December to February.

The large number of fledged juveniles and nests with older chicks, in both September 1988 and in March 1990, indicated that the 1988 and 1989 breeding seasons were very successful. It also suggested that potential predators (rats and coconut crabs) posed little hazard to this hardy species.

**BROWN BOOBY (Sula leucogaster)**

This widely distributed pantropical species has an estimated population in the Line and Phoenix Islands of about 3,200 (Clapp 1967, Perry 1980), with over half of them (2,000) recently found on Malden Island, in the Southern Line Group. However, all other estimates of this species on Malden from 1964 to 1980 (the 16 years after pigs were eliminated) are below two hundred.

**Distribution and habitat preference:** Breeding Brown Boobies on Caroline were restricted to the windward edges of *Tournefortia* scrub and forest, generally within 15-20 m of high water. In 1988 we found nests on 4 islets (Fig. 2, Table 1). Long, with 12 pairs, was the only islet supporting more than a single pair. They were located on the northern two-thirds of the island: 4 pairs formed a loose colony near the head of Transect A (Pt. I, Fig. 8). All nests were under *Tournefortia* bushes approximately 3 m tall. In March 1990, we found 20 pairs of Brown Boobies, all on windward Nake as far as the islet’s northern extremity. There was no evidence of nesting on Long Island. On May 22, 1990, only 3 nests, all with eggs, were found on Nake.

On 22 September 1988, we saw 2 birds plunge-diving with Masked and Red-footed Boobies approximately 500 m west of South Island. On the atoll, flying Brown Boobies were observed soaring only along the windward beaches. Two birds roosted on the south-central beach of South, and another was found roosting on Kota.

**Numbers:** We counted 15 pairs during perimeter surveys in 1988, yet found none on the transects. Since we covered virtually all the windward beaches (Pt. I, Fig. 9), we are confident that fewer than 20 pairs nested on the atoll. Our population estimate for 1990 was 25 pairs.

The POBSP (Clapp & Sibley 1971a) found 3 nests on Nake in June 1965, estimating a population of 15 birds, while the Grossmans (1974) found 8 nests on Long Island, estimating a similar population. Even though our surveys triple the known population, the Brown Booby remains a rare seabird on Caroline.
Phenology: With the exception of one recently fledged juvenile, all nests contained eggs in September 1988 (Table 3). Clapp & Sibley (1971a) found eggs in June; the Grossmans found eggs in September. In March 1990, the 20 pairs were all on nests whose contents ranged from eggs to an older juvenile. However, 2 months later, only 3 nests containing eggs, could be found. These data from 4 years suggest that the species may have trouble rearing young. More juveniles should have been encountered, especially in May 1990. However, cyclonic weather in February 1990 brought torrential rains and severe winds (Falconer, pers. comm.) which defoliated and uprooted the strand vegetation of Long and Nake (Pt. I, Pl. 33), deposited storm blocks on the windward reef flats and tons of sand over the existing beaches and old interislet channels of Long (AKK, pers. obs.). Brown Booby eggs and chicks would have experienced great difficulty at this time, as the region hardest hit was their sole nesting area. During February 1990, 640 mm (25.2") of rainfall fell in 10 days (Pt. I, App. II). Predation by Polynesian rats or coconut crabs could also limit reproduction on the atoll.

RED-FOOTED BOOBY (Sula sula) Figs. 6, 7

This pantropical booby numbers over 55,000 individuals in the Line Group (Clapp 1967, Perry 1980), making it one of the most important regions in the world for this species. Caroline holds the fifth largest known Red-footed Booby colony (see Nelson 1978). The largest known colony (140,000 pairs) is found on Tower Island (Galapagos): three of the 5 biggest colonies occur in the Line Group.

Distribution and habitat preference: In 1988, the Red-footed Booby bred on 28 islets, ranging in size from Nautonga (0.34 ha) to Nake (107.46 ha) (Fig. 6). On the Windward Islands, Red-foots occurred from Nake to Tridacna, absent only from the smallest islets (Noddy Rock, Skull Islet, Motu Atibu). The species was also widespread on the leeward islets, extending from Pandanus to Eitei. The tiny islets (Fishball, Azure, Reef-flat) were not occupied.

Red-foots are tree nesters whose distribution on Caroline closely matched that of Tournefortia scrub and forest. They sometimes utilized smaller Pisonia or Cordia trees where they intermingled with Tournefortia, and occasionally built nests in the tallest (>15 m) Pisonia. They nested in smaller Tournefortia patches within the peripheral scrublands, especially those not directly exposed to the trade winds. They clearly avoided smaller islets because of the lack of suitable Tournefortia in which to breed. They nested inward from the vegetated edges of the islets, generally at 3-6 m in height, and were distributed in broken rings around the smaller motus in areas of moderate winds. A higher percentage of the population occurred on perimeter surveys than on cross-island transects.

Red-foots were absent from South Island, which was primarily covered with Cocos (Pt. I, Figs. 50, 51). Even though Tournefortia occurred on all its coastlines, no boobies nested in them. Ana-Ana was also unoccupied: the presence of a family of 4 people, a cat, and a dog (all removed in 1991) undoubtedly discouraged nesting attempts. Red
Figure 6. Distribution map of breeding Red-footed Boobies on Caroline Atoll, September 1989.
Figure 7. Approximate laying dates for Red-footed Booby nests found on Caroline Atoll in September 1988. See Fig. 3 for explanation.
foots also avoided the mixed forests of south Nake, which contained much Cocos and Pandanus (Pt. I, Fig. 37). Red-footed Boobies were thus found only in Caroline’s indigenous woodlands, primarily in Tournefortia >2 m tall; they avoided anthropogenic plant communities and man.

Red-footed used a wider range of habitats for roosting. Nonbreeding birds were found throughout the taller indigenous trees, even in leeward situations where Pisonia and Cordia overhung the lagoon (as on Long Island).

**Numbers:** The POBSP (Clapp & Sibley 1971a) estimated 5,000 ± 25% Red-foots on Caroline in June 1965, with about 2,000 ± 25% nesting pairs. The Grossmans estimate was 3,000 ± 25% and 2,500 pairs in September 1974. In 1988 we sampled systematically more than 7% of the available habitat on all motus except Crescent (4.6% sampled) and North Arundel, and estimated that 2,221 pairs of Red-footed Boobies nested on 27 of Caroline’s islets (Table 1). We found an additional 1,234 roosting, nonbreeding birds. We know (C. Kepler 1969, Nelson 1978) that fewer boobies remain in their colonies during the day than at night. Thus an unknown fraction of the population was at sea when we conducted our counts. Impressive flights of Red-footed Boobies returned each evening: 3-4 birds arrived for each one that had remained behind, many undoubtedly mates of incubating birds. To approximate the number of returning nonbreeding birds, we doubled the number of roosting adults to allow for an additional 1,234 adults and juveniles. Thus, our conservative estimate was at least 7,000 individuals.

Because Red-footed Boobies were so dependent upon Tournefortia, we determined the nesting population on each islet by multiplying the number of nests found on transects by the ratio of sampled to total Tournefortia area. Perimeter counts (Pt. I, Fig. 9) were used if the number of Red-foots observed exceeded the number calculated from the cross-island transects.

Long Island held the greatest number of nests (659), mostly in the leeward Tournefortia and Tournefortia-Pisonia edge. Bird densities were typically highest on the largest islets: Windward and Tridacna, the largest Windward Islets, held 163 and 111 nests, respectively; and Mannikiba, the biggest leeward islet, harbored the largest population (184) of the entire leeward side. There were exceptions, however: Pandanus, with 4 times the area of Tournefortia of any of the South Nake Islets, held fewer birds than 3 much smaller islets (Table 1).

Tournefortia scrub and forest covered approximately 125.25 ha (Pt. I, Table 9). Overall, there were 1.75 Red-footed Booby nests/1,000 m² of Tournefortia forest. Nest densities for occupied islets by island groups (Table 4) showed that Red-foots favored areas less exposed to the trade winds: most nests on the windward motus were protected by well-developed Pisonia forests. The exposed Central Leeward Islets held the lowest nest densities (1.2 nests/1,000 m²), far less than on the South Nake Islets (5.3/1,000 m²), which are protected by the northege edge of Long. The greatest densities (7.8 nests/1,000 m²) occurred on the South Nake Islets south of Pandanus.
Table 4. Density of Red-footed Booby nests in occupied Tournefortia habitats on islet groups, Caroline Atoll, September 1988.

<table>
<thead>
<tr>
<th>Islet Group</th>
<th>Number Occupied Islets</th>
<th>Estimated Number Nests</th>
<th>Area of Tournefortia (m²)</th>
<th>Nests/1,000 m² of Available Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nake</td>
<td>1</td>
<td>496</td>
<td>300,650</td>
<td>1.6</td>
</tr>
<tr>
<td>Long</td>
<td>1</td>
<td>659</td>
<td>322,000</td>
<td>2.0</td>
</tr>
<tr>
<td>Windward Islets</td>
<td>8</td>
<td>434</td>
<td>251,900</td>
<td>1.7</td>
</tr>
<tr>
<td>South Nake Islets</td>
<td>7</td>
<td>319</td>
<td>59,800</td>
<td>5.3</td>
</tr>
<tr>
<td>Central Leewards</td>
<td>6</td>
<td>239</td>
<td>197,500</td>
<td>1.2</td>
</tr>
<tr>
<td>Southern Leewards</td>
<td>4</td>
<td>74</td>
<td>39,600</td>
<td>1.9</td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>2,221</td>
<td>1,170,550</td>
<td>1.9</td>
</tr>
</tbody>
</table>

Broadly speaking, Red-foots bred in well-dispersed colonies. A record density of 600 nests/1,000 m² on Tromelin Island (Indian Ocean) is exceptional. Elsewhere, 53 pairs/1,000 m² on Tower Island (Galapagos), 40/1,000 m² on Moku Manu (Oahu, Hawaii), and 27/1,000 m² on Half Moon Cay (Honduras) are more consistent high-density colonies (Nelson 1978). Only on tiny Motu Kota (Pt. I, Fig. 52), with 12 nests in 303 m² of Tournefortia (40/1,000 m²), did we find such density, and for this reason we named the islet "Kota" (Gilbertese for Red-footed Booby).

**Phenology:** In September 1988, we located 339 nests. Of the 152 whose contents could be determined, 87 were empty, 63 contained eggs, and 2 held downy chicks. We saw dozens of flying juveniles along the windward coasts. Most pairs were building or guarding their nests during a prelaying stage that lasts from 11-35 days (Nelson 1969). Of the pairs with nests, 57.2% had yet to lay and 41.4% had laid their eggs between mid-August and late September (Fig. 7). Applied to the total breeding population, approximately 1,270 nests were in the prelaying stage and would be expected to produce eggs throughout October. An additional 919 nests had a mean laying date in early September (Fig. 7). Red-footed Boobies were synchronous with Brown Boobies but delayed relative to Masked Boobies.

In June 1965, nests containing prelaying adults, eggs, and young in all stages indicated that the birds were in the midst of a protracted breeding season extending from January to June. In September 1974, eggs and "young at nearly all stages" were present. Our data reveal that no successful nesting occurred in May-June 1988. Data from March and May 1990 indicate that nest-building began in January (or earlier), with eggs laid from January to May. However, perimeter counts and cross-island transects on 11 windward motus found virtually all Red-footed Boobies either nest-building or sitting on eggs. Chicks were found only on the leeward islands. This asynchronous breeding suggests that
breeding activities were curtailed by the cycloonic weather two weeks earlier, which was particularly violent on the windward beaches harboring brown booby nests. Red-footed Boobies in other tropical locations have variable, opportunistic breeding seasons that depend upon food availability (Nelson 1978; F. Sibley, pers. comm.); our data suggests that similar pressures could be operating at Caroline.

**Color morphs:** Red-footed Boobies are polymorphic (Nelson 1978). The basic plumages are brown or white, with brown morphs having many combinations of tail, back, scapular, foot, and bill colors. A variety of brown forms and white forms occurred on Caroline, with a ratio of 9:1 (337 brown to 35 white), which contrasts sharply with Nelson's (1978) statement that "in the Line and Phoenix Islands all birds are white morphs." Most of the dark morphs were the "white-tailed" form (see Nelson 1978, pp. 660-661). The variations and proportions of plumage types show clinal change in the Line and Phoenix Islands (F. Sibley, pers. comm.), thus the question of plumage morphology needs much more study in the Central Pacific.

**GREAT FRIGATEBIRD** (*Fregata minor*), Figs. 8, 9 and Pt. 1, Pl. 42

The Great Frigatebird breeds at widely scattered locations throughout tropical waters in the Atlantic, Pacific, and Indian Oceans. It is known to breed on all of the Line Islands except Starbuck (Perry 1980).

**Distribution and habitat preference:** Great Frigatebirds nested on 22 islets, including Nake, Long, and most of the larger islets (Fig. 8, Table 1), ranging in size from Azure (0.20 ha) to Nake (307.46 ha). Every occupied islet had some *Pisonia* forest, even if only a single tree (Azur). The larger islets lacking *Pisonia* forest (Arundel, 7.34 ha, Tidacra, 9.08 ha) lacked frigatebirds in 1986, although frigatebird chicks were present on Arundel in early 1989 (Anne Talcomer, pers. comm.).

Although Great Frigatebirds were similar in nest requirements to Red-footed Boobies, there were significant differences: the frigates tended to nest higher in, and closer to, the outer edge, of the canopy (although nests were found as low as 1.3 m). Nest sites were more sheltered from the wind than those of Red-foots, and in locations where the birds could take flight easily. Such site preferences may explain the association with *Pisonia*. *Pisonia* reaches 21 m on Caroline, taller than other tree species, providing a windbreak on most islets. The largest colonies (Nake, Long, Fig, Manuskea) were found leeward of these stands. We found nests in *Tournefortia*, *Pisonia*, and *Cardia*. They were often in the *Tournefortia-Pisonia* interface, generally in the taller *Tournefortia*. One colony on south Long overhung the lagoon in a dense *Pisonia* stand. Frigates were not found in any anthropogenic forests and were absent from then-inhabited Ana-Ana.

**Numbers:** The previous population estimate for Great Frigatebirds on Caroline was 10,000 birds (Clapp & Sibley 1971a, Perry 1980). The Grossmans (1974) estimated 5,000-6,000 birds, with 4,000-6,000 nests.
Figure 8. Distribution map of breeding Great and Lesser Frigatebirds on Caroline Atoll, September 1988.
Figure 9. Approximate laying dates for Great Frigatebird nests found on Caroline Atoll in September 1988. See Fig. 3 for explanation.
We calculated that 2,427 pairs bred or attended territories. An additional 617 birds roosted, thus the entire population was approximately 5,471 individuals. A large but undetermined number of birds soared over the atoll throughout the day, and an uncountable number of birds, including fledged juveniles that would ultimately return to the island to nest (Diamond 1971), were undoubtedly at sea. Because this species is difficult to count accurately, it is unclear if the population has changed since 1965.

Phenology: In frigatebirds, the scapulars, which first appear at 81 days in *Fregata magnificens* (Diamond 1973), erupt before the primaries. Because we lack chick stage data for *F. minor* and *F. ariel*, we have modified ages from Diamond (1973) for *magnificens*, using the hatching times for *F. ariel* and *F. minor* from Nelson (1976), and fledging ages from Diamond (1975b), to construct very approximate development stages for the species on Caroline. Since they fledge at an earlier age than *F. magnificens*, we have reduced the ages for chicks with erupting primaries for *F. ariel* and *F. minor*, kept the duration of the earlier stages approximately the same, and reduced the period in juvenile plumage.

We found 214 nests in 1988. Of the 144 in which we determined contents, 49 contained eggs or young chicks, 27 held chicks with developing scapular feathers, and 68 contained older chicks (Table 5). The additional 70 adults occupied nests of unknown contents. We saw fewer than 10 displaying males and a high proportion (87%) of nests with chicks, many of them old, indicating that the breeding season was nearly over. A major laying effort had begun in March-April (Fig. 9) and continued into September. In March 1990, an abundance of flying juveniles and occasional larger chicks down to the downy stage indicated that the previous year's breeding season was ending. Of all the seabird species affected by the February 1990 storm, Great Frigatebirds suffered

<table>
<thead>
<tr>
<th>Table 5. Stages in the breeding cycle of frigatebirds on Caroline Atoll, 21-29 September 1988.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nest stage/Approximate age in days from laying</strong></td>
</tr>
<tr>
<td>Species</td>
</tr>
<tr>
<td>Great</td>
</tr>
<tr>
<td>Lesser</td>
</tr>
<tr>
<td><strong>No. nests in each stage</strong></td>
</tr>
<tr>
<td>Great</td>
</tr>
<tr>
<td>Lesser</td>
</tr>
</tbody>
</table>

1 Duration of naked and downy chick stages are lumped because it was often impossible to see into canopy nests.
the most obvious mortality. We found at least 10 adults and flying immatures recently dead, either draped in partly defoliated Tournefortia shrubs or lying on the ground. A small number of males were beginning another courtship cycle. By May 1990, courtship and egg-laying were still underway, and nests contained eggs or small chicks up to the "remiges" stage. Peak laying on Christmas Island (Pacific Ocean) occurs from March-May (Schreiber & Ashmole 1970), the same laying cycle observed on Caroline in 1988 and 1990.

LESSER FRIGATEBIRD (Fregata ariel)  

The Lesser Frigatebird is a pantropical species. It breeds and disperses widely within the tropical Pacific (Sibley & Clapp 1967). One of the largest populations in the world (30,000-85,000) breeds on McKean Island, in the Phoenix Group (Garnett 1983). Lesser Frigatebirds breed on 4 of the Line Islands, with the population on Malden (7,000) the largest in the archipelago (Perry 1980).

Distribution and habitat preference: In June 1964, Lesser Frigatebirds were found nesting in one compact colony on the leeward north end of Long (Clapp & Sibley 1971a). In September 1974, adults and flying immatures were observed flying and resting (Grossman & Grossman 1974), but no nests were found, most likely because the western side of the atoll was not surveyed. A population of 200 was estimated. We found a single colony in leeward Pisonia forest on western Nake (Fig. 8), both in September 1988 and May 1990. The birds nested high (to 18 m) in the Pisonia and Pisonia-Cordia edge facing an open Tournefortia savannah. Although primarily composed of F. ariel, a few F. minor were scattered along all but the eastern edge of the colony. West of the birds, across the open forest, F. minor and Sula sula nested in a mixed colony in a denser stand of Tournefortia. Birds were seen soaring over Nake, Long, and the leeward islets but were not found roosting or nesting away from the colony on Nake. However, in March 1990, approximately 650 Lesser Frigatebirds were swarming above and roosting on Motu Nautonga in a tight cluster, possibly preparing for nesting.

Numbers and phenology: P08SP biologists estimated a population of 1,000 Lesser Frigatebirds on Caroline in June 1964, with 400 ± 10% breeding: only eggs were found (Clapp & Sibley 1971a). On Christmas Island, F. ariel laid in May and June in 1959, 1963, 1964, and 1967 (Schreiber & Ashmole 1970). Of 46 nests found in 1988, we could inspect the contents of only 26: all contained feathered chicks (Table 5). Laying dates ranged from March through July (Fig. 10), with a peak from April to June. Our limited data on Caroline's Lesser Frigates indicates, therefore, that they may be synchronous with those on Christmas. In larger Central Pacific colonies, large subpopulations of this species have differing breeding regimes (F. Sibley, pers. comm.).

Because we did not determine the colony limits, we cannot provide a population estimate. There was a minimum of 200 birds in 1988 (46 nests, plus roosting and flying individuals) and ca. 1,000 in 1990.
Figure 10. Approximate laying dates for Lesser Frigatebird nests found on Caroline Atoll in September 1988.
SOOTY TERN (*Sterna fuscata*) Figs. 11, 12

This tern is the most widespread and abundant tropical seabird in the world. Under favorable conditions it forms immense colonies numbering into the millions. It is known to breed on 7 of the Line Islands: the largest population in the Pacific is found on Christmas Island (15,000,000 at highest count), and 3,000,000 have been recorded on Starbuck (Perry 1980).

**Distribution and habitat preference:** To date, 21 colonies from 10 islets are known for the years 1965, 1974, 1988, 1989, and 1990 (Fig. 11). In September 1988, we found 3 colonies, 2 on the northern half of Long and one on Bo'sun Bird Islet; all fit the general habitat description in Clapp & Sibley (1971a). Colony A, nearly square, was 210 m on a side. Eggs were placed under a savannah-type *Tournefortia* scrub, from 1-4 m tall with approximately 60% canopy cover. The substrate was coral rubble mixed with sand, covered by *Heliotropium* (5%), *Portulaca* (1%), *Laportea* (<1%), and *Lepturus* (<1%), typical of old interisland channels. Colony 1 was located in a broad sandy corridor with 2 large "groves" of *Tournefortia*. The northern subpopulation extended 116 m along the windward beach, but 248 m along the lagoon. The southern subpopulation began 28 m further south along the beach, fronted the seaward reef for 86 m, and was shaped like a blunt triangle, its apex pointing toward the lagoon. Most chicks were under *Tournefortia*, which consisted of shrubs 2-4 m high with 80% canopy cover. The substrate was also older beach sands mixed with coral rubble, and covered with *Portulaca* (40% cover), *Lepturus* (<5%), and *Heliotropium* (<5%). The Bo'sun Bird colony, a rough oval approximately 55 m wide by 70 m long, was under 2-3 m high *Tournefortia* with 75% cover, on coral rubble/sand sparsely carpeted with *Portulaca* and *Heliotropium*. 

**Numbers:** Populations were determined by measuring colony dimensions, then counting eggs and/or chicks in 9 m² sample plots located at random points along a compass line. Because juveniles moved as we approached, they were counted 6 m ahead of us in estimated 3 m x 6 m plots. The Colony 1 subcolonies (North, South) were treated separately.

Colony size (rounded) in 1988 ranged from 127,000 ± 30,000 "nests" (Colony A) to 1,500 ± 750 new eggs on Bo’sun Bird Islet (Table 6). There were an additional 6,900 ± 1,600 nearly-fledged chicks in the Bo’sun Bird colony, resulting from eggs laid 3 months earlier.

The total number of eggs and chicks was 188,000 ± 40,000. Actual numbers of adults are difficult to estimate, but in other studies have exceeded the number of eggs and young by factors of more than 2 because innumerable eggs and chicks were lost, colonies often overlapped, and many nonbreeding adults joined the prebreeding swarms or associated with breeding birds. Schreiber & Ashmole (1970), relying on POBSP data from Johnston Atoll (North-central Pacific), estimated that 4 adults were present for each egg laid. POBSP data from Johnston (Amerson & Shelton 1976) indicated that about 600,000 adults were present in a colony with 105,000 eggs, or approximately 5.7 adults/egg. If we assume that real
Figure 11. Distribution map of breeding Sooty Terns on Caroline Atoll, September 1988 to July 1990.
Figure 12. Approximate laying dates for Sooty Tern young found on Caroline Atoll in September 1988. See Fig. 3 for explanation.

<table>
<thead>
<tr>
<th>Colony Location</th>
<th>Area</th>
<th>Calculated Population (Mean Pairs ± SE)</th>
<th>Nest Stage</th>
<th>Approx. Weeks From Laying</th>
</tr>
</thead>
<tbody>
<tr>
<td>Long Island, A</td>
<td>44,100 m²</td>
<td>127,449 ± 30,429 hatching eggs, downy chicks</td>
<td>4-5</td>
<td></td>
</tr>
<tr>
<td>Long Island, 1 N</td>
<td>24,200 m²</td>
<td>41,382 ± 5,808 chicks with short tails, juv. plumage</td>
<td>7-10</td>
<td></td>
</tr>
<tr>
<td>Long Island, 1 S</td>
<td>6,400 m²</td>
<td>10,944 ± 1,536 &quot;</td>
<td>7-10</td>
<td></td>
</tr>
<tr>
<td>Bo'sun Bird Islet, old</td>
<td>3,375 m²</td>
<td>6,883 ± 1,575 fledglings</td>
<td>11-12</td>
<td></td>
</tr>
<tr>
<td>Bo'sun Bird Islet, new</td>
<td>3,375 m²</td>
<td>1,538 ± 758 new eggs</td>
<td>1-2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>75,075 m²</td>
<td>188,196 ± 40,106</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Numbers of terns in our colonies lay midway between 4- and 5.7 times the number of eggs and chicks, then the number of Sooty Terns using Caroline Atoll would have ranged between 720,000 and 1,100,000 birds (911,800 ± 21%). This is twice the estimate provided by Clapp & Sibley (1971a), even though we found fewer colonies. However, if the POBSP had used the criterion of 4 adults present for each egg laid, their total population figures would have exceeded ours, hence the two estimates are not strictly comparable (F. Sibley, pers. comm.).

In March 1990, laying was just beginning in 2 colonies on Long Island, (625 m x 150 - 315 m wide and 180 m long x 160 m wide). Enormous numbers of birds, both on the ground in densities up to 9 or 10 pairs/m² and in the air, made it impossible to calculate a reasonable population figure. According to Anne Falconer, these 2 colonies were very successful. Similarly, counting was difficult in May 1990 when 6 large prebreeding swirls hovered like huge clouds of gnats over discrete islets and islet groups (Fig. 11). Our 1988 estimate of approximately one million birds is probably a conservative count for the atoll as a whole on an annual basis.

**Phenology:** The incubation period in Sooty Terns is about 4 weeks (Dinsmore 1972). Young fledge 7-8 weeks after hatching, although fledging ages, dependent upon food supply (Schreiber & Ashmole 1970), are highly variable.

Four separate Sooty Tern colonies had been started over the 12-week period prior to our study in 1988 (Table 6). On Bo’sun Bird Islet a new wave of laying was just beginning in an open area immediately southwest of most of the colony, while nearly fledged chicks scurried about beneath the *Tournefortia*. Undoubtedly many young had already fledged, so many more eggs would have been laid in early July by this colony than indicated (Fig. 12). The 2 colonies on Long were established at different times: the short-tailed juveniles in Colony 1 preceded the large number of eggs, hatching eggs, and downy chicks of Colony A by 3-4 weeks.
The July-September laying period on Caroline in 1988 is very different from the bimodal breeding (May-June, December-January) reported from Christmas Island, Pacific Ocean (Schreiber & Ashmole 1970), and the May laying dates noted for Caroline by the POBSP in 1965. In September 1974, "innumerable large unfledged chicks and juveniles" were present in colonies at the tip of Long Island and on Tridacna Islet (Grossman & Grossman 1974). Additional data (Anne Falconer, pers. comm.) indicate that Sooty Terns may lay any time (Fig. 11), certainly January through September (1988 to 1990). Severe storms, which destroyed large Long Island colonies in February 1990, were likely responsible for reinitiating breeding activities on the leeward side of the atoll within the next few months. A great deal more research will be needed on Caroline before the breeding seasons for this species are fully understood. The phenomenon of several colonies on each island breeding at different times is considered the norm for the Line and Phoenix Groups (F. Sibley, pers. comm.), so the situation on Caroline is not unusual.

**BROWN NODDY** (*Anous stolidus*)

This tern, primarily a tree nester, is widely distributed throughout the warm oceans of the world. It is abundant in the Line and Phoenix Groups, with an estimated total population exceeding 40,000 birds. Brown Noddies are most abundant on Palmyra Island (10,000 birds).

**Distribution and habitat preference:** The Brown Noddy is second only to the White Tern in the number of motus (28) upon which it is known to breed (Fig. 13). It utilized the smallest (Noddy Rock, 0.02 ha) and largest (South, 104.41 ha) motus, nesting upon coral rubble and in plant communities ranging from the simplest herb mats to *Tournefortia*, *Pisonia*, *Cordia*, *Cocos*, and the mixed anthropogenic forests of South and Nake. Most pairs were well dispersed, nesting from the outer edges of *Tournefortia* to the central, inner branches of *Pisonia*, and from the ground to the crowns of 25-m *Cocos*. When nesting sympatrically with Black Noddies in *Pisonia*, the Brown Noddies typically occupied portions of branches closest to the trunk. Brown Noddies nested almost solitarily in the *Cocos* canopy on South, were found within dense colonies of Black Noddies and White Terns in tall *Pisonia* forests, with Red-footed Boobies and Great Frigatebirds in *Tournefortia*, and amidst Sooty Terns and Red-tailed Tropicbirds (Bo’sun Bird Islet). Apart from a few ground nesters on Raurau and Fishball, the only ground-nesting colony (80 nests) was located on a Portulaca mat on Noddy Rock—a site free of predators, although flooded during storms.

Brown Noddies often formed loose roosting "clubs" on the atoll's beaches. Aggregations of 15-20 birds were found on the west coast of South and on Sandy Inlet, south-central Nake.

**Numbers:** Clapp & Sibley (1971a) estimated a population of 1,000 birds in June 1965, with about 800 birds breeding (with eggs and young). The Grossmans estimated 400 ± 15% in September 1974. We estimated a total population of 1,491 breeding pairs (Table 1). Because nests high in
Figure 13. Distribution map of breeding Brown Noddies on Caroline Atoll, September 1988.
Cocos palms were difficult to detect, we undoubtedly overlooked many, thus our estimate of approximately 3,000 birds is conservative. Although larger than the population estimated by POBSP (Clapp & Sibley 1971a), uncertainties about the 1965 survey coverage (F. Sibley, pers. comm.) prevent us from knowing if Caroline's population has changed over the past 25 years.

**Phenology:** This is another species whose breeding cycle is irregular in the Central Pacific: during the 1963-1965 POBSP surveys, egg-laying was found in every month of the year somewhere in the Line and Phoenix Groups (F. Sibley, pers. comm.). On Christmas Island, which has received more attention than any other Central Pacific island, the timing of egg laying varies between colonies. In general, peak laying occurs from March to May, and from November to December. On Caroline, mating and nest-building were found in March 1990, but by May only a few eggs had been laid. Eggs and young were found in June 1965 (Clapp & Sibley 1971a) and in September 1988 (present study). Only eggs were present in September 1974. We found 246 nests in September 1988 and determined the contents of 106: 103 held eggs, 3 held downy chicks. The incubation period is 35-37 days (Dorward & Ashmole 1963), so all viable eggs had been laid within the previous 40 days--mid-August to late September. Because many nests were being built, we feel confident that laying continued into October. Clearly more research is needed to determine whether laying occurs in regular cycles.

**BLACK NODDY (Anous minutus)**

The Black Noddy is widely distributed in the tropical Atlantic and Pacific. It is abundant in the Line and Phoenix Groups, with populations of 16,000 estimated in the Phoenix Islands (Clapp 1967) and over 46,000 in the Line Group. Centers of abundance are Palmyra (20,000) and Christmas (14,500) (Perry 1980).

**Distribution and habitat preference:** The Black Noddy is a tree-nesting species that on Caroline prefers tall stands of *Pisonia*. The largest colonies (61% of the population) were found in the grand *Pisonia* forests (to 25 m) on Pig and North Pig. We found breeding birds on 18 motus, with populations exceeding 800 pairs in the *Pisonia* on Nake, Long, North Pig, and Pig (Fig. 14). The only significant colony not primarily associated with *Pisonia* was found on Tridacna, where approximately 230 pairs nested in the tallest (ca. 8 m), most central *Tournefortia-Morinda* forest. Black Noddies always nested in dense colonies near islet centers and were integral components of these plant communities: their droppings, coating the ground with a film of guano, constantly enriched the islet's meager soils.

**Numbers:** Clapp & Sibley (1971a) estimated that 7,000 ± 25% birds were on Caroline. The Grossmans (1974) estimated 500 ± 20%. During our visit the population was much larger: 5,122 pairs were estimated for Pig and North Pig alone (Table 1). Basing our numbers primarily on the densities of sampled colonies in *Pisonia*, we estimated that nearly 8,400 pairs were nesting during our 1988 visit. Our population estimate approached 17,000 birds, to which an unknown number of nonbreeding birds
Figure 14. Distribution map of breeding Black Noddies on Caroline Atoll, September 1988.
could be added. These values place the Caroline population far above that for Christmas, making it the largest known population in Kiribati.

**Phenology:** Black Noddies were just beginning a new breeding season, as was also found in September 1974. On 27 September we observed hundreds of birds gathering *Tournefortia* leaves floating along the windward shore (Long) or flying with fresh leaves to their nests (Pig, North Pig). Of the 1,085 pairs counted on transect, 536 (49%) perched as pairs, were defending nest sites, or were building nests. An additional 273 pairs were attending nearly-completed nests but were not incubating. The remaining 276 pairs were incubating, thus 75% of the pairs had not laid eggs. The contents of 230 nests were unknown, although we assumed they contained eggs because of the incubating positions of the adults. Of 46 nests whose contents were visible, 45 held a single egg, and one contained a downy chick less than 5 days old.

The breeding seasons for Black Noddies on Christmas Island and Johnston Atoll peak in April and May (Schreiber & Ashmole 1970, Amerson & Shelton 1976), where pairs are highly synchronous, laying most of their eggs within a 2-3 month period. The Caroline colony, also synchronous, but beginning egg-production in September, would be expected to peak in October/November, 6 months out of phase with the colonies further north. In 1990, however, Black Noddies were just beginning to mate and nest in March, and by May some were still sitting tightly on nests, while others had chicks in all stages. This was most likely the result of the stormy weather which affected all seabirds.

**BLUE-GRAY NODDY (Procelsterna cerulea)**

Blue-gray Noddies nest widely across the Pacific from the Kermadec Islands to Hawaii. They are scattered throughout the Line and Phoenix Groups. In the Line Islands, they were formerly known to breed only on Christmas and Malden (Perry 1980). Eggs are placed in nests minimally provided with twigs and may be on coral rubble, sheltered under vegetation, or under coral slabs to depths of one meter (Rauzon et al. 1984).

The Blue-gray Noddy was recorded as "present" on Caroline by Perry (1980). Clapp & Sibley (1971a) noted birds over the lagoon but saw none on land. When we approached Caroline, we saw 2 from the ship and later observed 3 flying across the lagoon. We also saw 3 birds perched on reef flats of the leeward motus Nautonga and Eitei. A third bird flushed repeatedly from a small clearing around a pile of bottles on Raurau, but we failed to find a nest. In March and May 1990, we observed Blue-gray Noddies on all of the Southern Leewards, plus Azure and Nautonga in the Central Leewards.

In summer 1990, Alexandre Falconer, resident on Caroline at that time, found one small chick, attended by its parents, on an open expanse of coral rubble on Motu Eitei, the first breeding record for Caroline. Eitei is adjacent to Raurau, which we predicted was the most likely breeding location for this species.
Blue-gray Noddies must breed in very small numbers on Caroline. Nests are hard to find, given their cryptic placement, the small number of birds present, and the extent of open habitat (67.7 ha of herb mats and 41.4 ha of consolidated coral rubble). F. Sibley (pers. comm.) suggests that Blue-gray Noddies are extremely vulnerable to predators, since they were observed on 12 of 20 islands visited in the Line and Phoenix Groups, but nested on only three. Where they did nest, Blue-gray Noddy colonies contained hundreds or thousands of birds.

WHITE TERN (Gygis alba)  


Distribution and habitat preference: White Terns, the most widely distributed breeding bird on Caroline, nested on 32 of the 39 motus (Fig. 15), avoiding only those which were tiny and sparsely vegetated.  

White Terns nested from one to 15 m above ground, wherever a branch or frond provided a relatively stable platform in Tournefortia (Pl. 3), Pisonia, Cordia, Pandanus (Pt. I, Pl. 35), or Cocos. They did not form dense colonies but were scattered throughout each motu, normally selecting sites sheltered from the prevailing trade winds. They utilized isolated trees, scrub, or forest. An unusual departure from the White Tern's usual mode of "nesting" was an egg laid in an old Black Noddy nest, 6 m up in an 8-m-tall Tournefortia on Tridacna Islet.

White Tern densities varied from islet to islet (Table 7). At one extreme we found only 2 nests on Raurau (0.07/1,000 m²). Densities on

<table>
<thead>
<tr>
<th>Islet Group</th>
<th># Islets</th>
<th>Vegetated Area (ha)</th>
<th># White Tern Pairs</th>
<th>Density (pairs/1,000 m²)</th>
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</thead>
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<tr>
<td>Nake</td>
<td>1</td>
<td>66.63</td>
<td>1,094</td>
<td>1.64</td>
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<tr>
<td>Long</td>
<td>1</td>
<td>49.60</td>
<td>751</td>
<td>1.51</td>
</tr>
<tr>
<td>South</td>
<td>1</td>
<td>86.10</td>
<td>381</td>
<td>0.43</td>
</tr>
<tr>
<td>Windward Islets</td>
<td>9</td>
<td>36.09</td>
<td>1,164</td>
<td>3.23</td>
</tr>
<tr>
<td>South Nake Islets</td>
<td>6</td>
<td>8.50</td>
<td>122</td>
<td>1.44</td>
</tr>
<tr>
<td>Central Leeward Islets</td>
<td>9</td>
<td>33.56</td>
<td>408</td>
<td>1.22</td>
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<tr>
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<td>4</td>
<td>6.47</td>
<td>37</td>
<td>0.57</td>
</tr>
<tr>
<td>All Occupied Islets</td>
<td>31</td>
<td>286.88</td>
<td>3,957</td>
<td>1.38</td>
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</table>
Figure 15. Distribution map of breeding White Terns on Caroline Atoll, September 1988.
other islets ranged from 0.75/1,000 m² (Shark) to 6.67/1,000 m² (Nautonga) with a mean density of 1.38 pairs/1,000 m² of woodland. Overall, the lushly vegetated Windward Islets supported the highest densities. Although White Terns also nested in anthropogenic forests, their densities were low: we believe that their low densities on South Island and the Southern Leewards (Table 7) are attributable to man. Of South's 104.47 ha of vegetated land, only 4.2 ha (4.4%) was native woodland (Pt. 1, Fig. 50); fully 84% was either Cocos (18.3 ha) or dying Cocos-Ipomoea (62.5 ha) forest. Although most of the Southern Leewards are covered in virgin forests, central Ana-Ana has been partly cleared (0.21 ha) to accommodate thatched huts and a garden. The activities of a family of 4, with a dog and cat (until October 1990), apparently depressed the White Tern population on Ana-Ana and, perhaps, even on nearby islets. We found no White Terns on Ana-Ana during our visit, although the Falconers, who vacated the atoll in summer 1991, assured us that they occasionally nested.

**Numbers:** We used the total woodland area of each islet, coupled with transect data, to calculate bird populations (Table 1). More birds were found on the largest islets except South Island (see above). We estimated 1,094 pairs for Nake, 751 pairs for Long, and nearly 400 pairs for Tridacna; these 3 islets accounted for over half the population (and over half the indigenous woodlands). We estimated that 3,957 pairs bred on Caroline, which doubles the numbers of Clapp & Sibley (1971a) and Perry (1980) and exceeds by 3,000 the largest population formerly known for the Line Islands.

**Phenology:** Of 569 pairs of White Terns recorded on transect, 437 were roosting without obvious signs of eggs or chicks, 107 were incubating, and 25 had chicks (often adults were not present). Of the 25 chicks recorded, 17 were downy, 7 retained extensive traces of down with remiges, and one was almost ready to fly. Incubation takes about 36 days (Ashmole 1963); young may require from 40-96 days to fledge (Gibson-Hill 1950, Ashmole 1968). Nearly all chicks were less than 4 weeks old.

On Christmas Island, Schreiber & Ashmole (1970) found that peak laying occurred in April-August each year, with some laying in each month. On Caroline, Clapp & Sibley (1971a) noted that about half of the birds had eggs, half had young in June 1965. In September 1974, White Terns had eggs only (Grossman & Grossman 1974). In March 1990, we found very few eggs and downy chicks, but in May a larger number of pairs were breeding, with eggs and chicks in all stages. Again, the February storm had most likely interrupted breeding activities, as only 2 juveniles were found on the windward side. These were in the interior Pisonia forests of Brothers and North Brothers Islets, which suffered less damage than motus further north. Therefore, although White Terns on Caroline do lay during the peak period on Christmas Island, laying appears to be heaviest after mid-August.
D. OTHER BIRDS ON CAROLINE ATOLL

Seven species other than seabirds have now been recorded on Caroline. Six of them are migrants (5 shorebirds and Long-tailed Cuckoo). The few shorebirds encountered (except for Bristle-thighed Curlews) and their lack of increased numbers in the fall suggest that there is only a small migration to Caroline. The Reef Heron is apparently resident, although no nest has been found.

REEF HERON (*Egretta sacra*)

We found 15 Reef Herons scattered on 8 islands: Nake (1), Long (2), Pig (1), Brothers (3), South (2), Mannikiba (2), Matawa (1), and Emerald (2), as well as on the open reef flats (1). Although birds were found on both the seaward and lagoonward sides of the islets, most were along the lagoon edge, as also found by POBSP in 1965 (Clapp & Sibley 1971a) and the Grossmans (1974). We estimated that approximately 30 birds were using the atoll. We found no signs of breeding. Of the 15 individuals we observed, 5 were dark, 8 were white, and 2 were of the pied morph.

LESSER GOLDEN-PLOVER (*Pluvialis dominica*)

This plover used the beaches and herb mats, generally to seaward. In September 1988, we found them on Nake (1), Long (4), Tridacna (4), and Mannikiba (1), estimating a total population of 20-30 birds, the same number found by POBSP (Clapp & Sibley 1971a). In March 1990, we observed 8, and in May, 3, all in winter plumage. In September 1974, 3 were seen on the windward coast (Grossman & Grossman 1974).

WANDERING/GRAY-TAILED TATTLER (*Heteroscelus incanum or H. brevipes*)

In September 1988, we located 18 tattlers on 6 different islets: Nake (3), Long (3), Crescent (1), Arundel (2), South (7), and Emerald (2). All birds were either alone or in pairs and generally remained in the intertidal zone, although they often foraged on herb mats close to the beach scrub. The total population was approximately 40 birds. Those few birds heard were all *H. incanum*. We saw 6 tattlers in March 1990 and several in May of the same year. The Grossmans (September 1974) observed 12 on the windward coast and around the lagoonward shore of the windward islets and South.

RUDDY TURNSTONE (*Arenaria interpres*)

One turnstone was found on the windward beach of Motu Mannikiba in September 1988, and 5 on atoll beaches in March 1990. The Caroline population probably does not exceed 15 birds.

BRISTLE-THIGHED CURLEW (*Numenius tahitiensis*)

The Bristle-thighed Curlew, common in the Line and Phoenix Groups, is a widespread migrant to atolls of the Central and South Pacific...

We counted 83 birds on 12 of Caroline’s islets in 1988, including the 3 large islands (Nake, Long, South) and motus in the Windwards, Central Leewards, and Southern Leewards. In March 1990, we saw 20 curlews on 10 islets during incidental observations throughout the atoll, bringing the total number of islets on which they have been recorded to sixteen (41%). On our return trip (May 1990) we only saw 3 curlews (8 motus visited). Undoubtedly, curlews occur throughout, utilizing essentially all plant communities (for details, see Pt. I, Sect. E). Although they are most conspicuous on the beaches and reef flats, higher numbers may actually forage inland during the day. Small numbers of curlews remain all year, being least common from April to August and most abundant after September/October (R. and Anne Falconer, pers. comm.). This correlates with preliminary information from Rangiroa Atoll, Tuamotu Archipelago (Gill 1990; Gill & Redmond, in prep.).

Unvegetated perimeter habitats: On a complete perimeter count of South Island in 1988, we found 29 curlews. Twenty-one were foraging and loitering on the windward east coast, principally above the beach crest on coral rubble interspersed with herb mat. Similarly, 14 of 20 curlews found on Long and the Windward Islets foraged along the windward beach crest, with only 6 birds found on the lagoonward shores. Curlews were equally common on windward and leeward shores in the leeward islets, occupying habitats composed of coral rubble and sand. While the numbers indicate that curlews preferred windward shores, they may be biased because most birds were seen there in the late afternoon (13, 14, 19). Perhaps they use the relatively open areas for roosting and foraging at dusk. Our largest flock (14, Sandy Inlet, Nake) was found at 16:00, foraging on compacted, silty sand at the lagoonward end of the inlet, while single curlews dotted the interislet channels and shallow tidal reef flats (Pt. I, Pl. 22).

Vegetated habitats: We found Bristle-thighed Curlews on natural herb mats, in Tournefortia scrub, Pisonia forest, and in Cocos habitats, both in the healthy peripheral plantations and within the dying Cocos-Ipomoea woodlands (Pt. I, Fig. 36, Pl. 34). One was captured in a mist net under a dense Cocos canopy. Disintegrating plantations in the center of South (54 ha) held a large population: calculated numbers produced an estimate of 154 curlews. They foraged over the Ipomoea-strewn ground (interspersed with Boerhavia and Phymatosorus), frequently using broken-topped coconut trunks as lookouts. We also found 5 curlews on transects in Pisonia forests up to 20 m tall on Nake (calculated population, 41). They were foraging on the relatively open, although dimly lit, forest floor (Pt. I, Pl. 42).

Numbers: From the 1988 data we estimated a population of 300+ curlews: 41 birds in Pisonia, 154 in Cocos-Ipomoea, 43 on the beaches of South,
14 at Sandy Inlet, Nake, and 62 scattered over the remaining motus. Because 154 were calculated from a single flock of 7 curlews on one transect on South, there may be a bias in our population estimate. However, this habitat covers 80 ha, 77% of South’s total area, and incidental observations made off-transect indicated that curlews commonly foraged in Cocos-Ipomoea woodlands. We believe that our estimated density, about 1.5 birds/ha, is reasonably correct.

**Bill length:** Bristle-thighed Curlews show great variation in bill length immediately after the breeding season. Because birds of the year migrate south before their bills reach adult length (R. Gill, pers. comm.), the ratio of "long" to "short" bills provides a rough estimate of juvenile survival. Of 31 curlews seen in September, 20 were clearly adult length, 7 were conspicuously shorter, and 4 were "intermediate" (probably young birds). All March and May birds had long, adult-sized bills.

Some subadults remain on their Pacific wintering grounds for up to 3 years, during which time they pass through a flightless phase (Gill 1990, Marks et al. 1990). No flightless birds were seen.

**Foraging:** We saw one curlew chase and capture a small Polynesian rat at dusk on the south shore of South Island. The bird bashed the rat on the coral rubble, then ran rapidly about with the rat dangling from its bill. After about 5 minutes, the bird swallowed the rat with vigorous gulps.

Polynesian rats, abundant on Caroline (especially in *Pisonia* and *Cocos*-dominated habitats), remain within the forest during the day, but many move to the beach crest and tide line at dusk. They provide abundant potential prey for curlews, which can easily capture them on the open rubble. The synchronous appearance of rats and curlews at the beach-woodland interface at dusk may be part of the foraging strategy of this large shorebird. The presence of curlews beneath the forest canopy may also be partly associated with this source of food.

**SANDERLING (Crocethia alba)**

One Sanderling in winter plumage was seen at water’s edge on the windward beach of Long Island on 27 September 1988. Although Sanderlings are well-known fall migrants in the Line and Phoenix Islands (Clapp & Sibley 1967, 1968), this is the first record for Caroline Atoll.

**LONG-TAILED CUCKOO (Eudynamis taitensis)** Fig. 16

The Long-tailed Cuckoo breeds in New Zealand and winters in the southwest Pacific. The center of its winter range lies in central Polynesia, but birds have been recorded as far as Palau in the northwest and Pitcairn Island in the southeast. Although occurring throughout French Polynesia and the Cook Islands, it had not been recorded from the Line Islands prior to our expedition (Bogert 1937; Clapp & Sibley 1971a, 1971b; Pratt et al. 1987; Ellis et al. 1990).
Figure 16. Preliminary distribution map of the Long-tailed Cuckoo on Caroline Atoll. The species most likely utilizes all well-wooded motus.
We found Long-tailed Cuckoos on 4 of Caroline’s 39 motus (Fig. 16). We heard its distinctive mono- and disyllabic call notes on South, Long, and Pisonia, identified one on Nake, and on 28 September collected a male in a mist net on Transect 4, Long Island (USNM 607191). Soon after our return home we sent a description and photograph of this species to the Falconers: they, and AKK, have since seen them several times on Motu Ana-Ana in March, April, and May 1989-90.

All the cuckoo sightings were at canopy or subcanopy level, and 3 of the 4 1988 birds were in Pisonia forests. The individual on South foraged in a Cocos canopy 21 m tall. The netted male flitted secretively within an undisturbed, tangled low-canopy (4-6 m) Pisonia-Tournefortia interface. We suspect that this elusive migrant occurs throughout the mid-to-upper levels of Caroline’s forest canopy.

These records establish the Long-tailed Cuckoo as a winter visitor to Caroline Atoll. Our observations on 4 motus in 8 days, including the southernmost, northernmost, windwards, and leewards, indicate that many individuals were present. A March 1990 first sighting on Vostok (J. Phillips, pers. comm.) further suggests that the species disperses regularly to the Southern Line Group.

E. OTHER VERTEBRATES

Lizards

Although "small lizards" were observed on Caroline in 1825 (Paulding 1931), it wasn’t until 1965 that the first collections were made (Clapp & Sibley 1971a). We collected 4 lizard species, increasing the known terrestrial herpetofauna from 3 to 6 (Table 8). Although all are indigenous, the azure-tailed skink (Emoia cyanura) is particularly widespread in Oceania, and is suspected of being partly dispersed by man (Brown 1956, Crombie & Steadman 1986). Recent data from Flint suggest that E. cyanura may have been introduced by Tahitian copra laborers this century (Kepler, in prep.). The same situation may be true on Caroline, especially since this easily-identifiable species was not seen or collected by POBSP personnel in 1965 (Table 8). All but 2 of the lizard species known from the Line Islands (Crombie 1990) have now been found on Caroline. It is perhaps noteworthy that we added 3 species to the atoll list but failed to find 2 species collected in 1965. Since both groups collected lizards opportunistically, rather than systematically, there is evidently much need for further study in this area.

Turtles

We found 3 Pacific green sea turtles (Chelonia mydas), a threatened species (McKeown 1978), at Caroline in 1988. Two were swimming over the lagoon reef flats, one west of Arundel, the second east of Ana-Ana. The third was in the open sea about 100 m west of South Island near the "boat entrance." Ron Falconer has seen up to 7

<table>
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<th>Species</th>
<th>Specimens:</th>
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</thead>
<tbody>
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<td></td>
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<tr>
<td>Lepidodactylus lugubris</td>
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<td>USNM 299773</td>
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<tr>
<td>Polynesian gecko</td>
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<td>Gehyra oceanica</td>
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<tr>
<td>Snake-eyed skink</td>
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<td></td>
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<tr>
<td>Cryptoblepharus poecilopleurus</td>
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<tr>
<td>Moth skink</td>
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<td>Emoia cyanura</td>
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1USNM 158358 has recently been reidentified by R. I. Crombie as Lipinia noctua, not Emoia nigra, as reported in Clapp & Sibley (1971a).

turtles in the lagoon in a single day. In April and May 1990, AKK saw workers from Tahiti capture and kill a minimum of 4 green turtles in the lagoon, and 2 more were in fishtraps on our departure. Two others entered the lagoon during the following 4 months (R. Falconer, pers. comm.).

In March 1990, AKK and G. Wragg found 3 old nests, presumably of this species, on the northwest coast of Nake within 100 m of the northern tip of the islet. These are the first known turtle breeding records for the atoll. Young (ca. 1922) notes that the copra plantation laborers ate green turtles from September to December each year, and members of the Line Islands Expedition (Grossman & Grossman 1974, Vickers 1974) saw fresh turtle tracks either on South or Nake. The February 1990 storm added large amounts of sand to Caroline's shorelines, providing potential new habitat for turtle nesting.

Terrestrial Mammals

None of the terriers (see Pt. I) that were introduced to control rats on South Island early this century (Young ca. 1922) have survived (F. Sibley, pers. comm.; R. Falconer, pers. comm; pers. obs.). In May 1990 the Falconers kept a dog and cat on Motu Ana-Ana. The dog regularly visited all the Southern Leewards and accompanied the family in their sailing canoe throughout the atoll. As a result of our
recommendations, the cat was removed from Caroline in October 1990. The
dog, with the family, vacated Caroline in summer 1991.

Bennett (1840) noted "rats of a red-brown color," the first
reference to rodents on Caroline. Dixon (1884) found that rats were
"not numerous" and that they nested "just at the base of the fronds" of
the coconuts. Two specimens collected by the POBSP proved to be *Rattus
exulans* (Clapp & Sibley 1971a), an uncommon mammal restricted to South
Island.

The 19th and 20th century settlers found rats (presumably
*R. exulans*) to be extremely abundant and very destructive to the coconut
plantations; they contributing greatly to the twice-abandonment of copra
enterprises on Caroline (Young ca. 1922, Maude ca. 1938). They
voraciously devoured both growing and fallen nuts, as well as dried
copra. Being arboreal, they also lapped the juices of the flower
stalks, preventing nut development. In 1920 alone, over 4,600 were
trapped on South (Maude ca. 1938). Thousands more were killed by
terriers introduced in a vain attempt to control them.

We found rats on almost every islet, especially in or near coconut
palms and *Pisonia* trees. We recorded them during daylight hours on most
transects. Each night at our campsites on Long and South we noticed
groups of 10-20, so tame as to approach within one meter while we were
eating. Rats evidently undergo wide population fluctuations, as they
were less abundant in March and May 1990 than in September 1988.

We suspect that rats periodically reach most motus, and that those
apparently lacking rats (such as Noddy Rock) are too small and/or
depauperate to support a resident population. Because *R. exulans* is a
known seabird predator (C. Kepler 1967, Fleet 1972, Norman 1975), the
restriction of some species (i.e. Red-tailed Tropicbird) to small islets
may be due to rat populations on larger islets.

Rats were an abundant nuisance on Ana-Ana; the Falconers trapped
over 1,300 animals in 2 years and, like the pioneers before them, relied
upon a dog to help keep them at bay.

**Marine Mammals**

On March 14, 1990, members of the Line and Phoenix Islands
Expedition observed a minimum of 10 Pacific bottlenose dolphins
(*Tursiops gilli*) in the open sea about 500 m off the southeast corner of
South Island.

**F. COCONUT CRABS**

The coconut crab (*Birgus latro*, Coenobitidae), the largest
terrestrial invertebrate on earth, ranges throughout the tropical Indo-
Pacific (Pt. I, Pl. 21). It is highly esteemed as a source of food
throughout its range, and for this reason is rare or absent on or near most inhabited islands. Because it is heavily exploited by man, it is under consideration for endangered species status (E. Reese, pers. comm.). Since March 1990, dozens of Caroline's coconut crabs have been killed for food and for preservation in formalin as curios for the Tahiti tourist market. Because of the increasing numbers of visitors to Caroline, it is important that Caroline's coconut crabs receive protection.

History: A Californian malacologist, C. D. Voy, was the first to collect coconut crabs (Birgus latro) on Caroline in 1875 (Pilsbry & Vanatta 1905). They are not mentioned again until 1910, when Young (ca. 1922) wrote that "hundreds of great Coconut Crabs were seen: 40 large ones were caught by the crew of the schooner in an hour" on South Island. Young also noted that coconut crabs were considered a great nuisance by plantation laborers, who killed them mercilessly. Evidently they dug up newly planted nuts and snipped off emerging shoots. On smaller motus, visited less frequently than South, Nake, and Long, these depredations were difficult to control. Thus the small motu plantations were abandoned soon after initial planting, resulting in a remarkably rapid recovery of the original vegetation (see Pt. I, Sect. G). Today large crabs once again burrow beneath the boles of well-maturing Pisonia forests which their ancestors helped recreate less than 70 years ago.

It is hardly credible that these enormous crabs, the dominant terrestrial animal of the atoll environment, could have been overlooked by almost all visitors prior to the 20th century. The only plausible explanation is that coconut crab populations were reduced drastically each time Caroline was inhabited: 1846 to at least 1852, 1885 to 1901, and 1916 to 1929. Voy collected them in 1875, 10 years before initial land clearing began; Young noted them in a 1910 visit 9 years after the first abandonment of the plantations, and again from 1916 on when copra enterprises were begun anew. From 1916 to 1920 land clearing was far more extensive, involving most of the area of the Windward Islets and Nake (Pt. I, Table 13), and thus a very large number of homeless coconut crabs would have been evident at that time. Again, mass slaughter reduced their numbers until the main group of copra-cutters left in 1929. Since then, occasional Polynesian and other visitors have taken crabs, but since the island was basically uninhabited for 60 years, their numbers have recovered substantially. "Great numbers" were seen in 1974 (Gilbert and Ellice Is. Govt. 1974). However, activities since 1990 do not bode well for the species (see Sect. G). It is of interest in this regard that members of the 1934 Mangarevan Expedition saw no coconut crabs on nearby Flint Island (R. Fosberg, pers. comm.), nor were they mentioned in an historical summary paper on Flint by Maude (ca. 1942), but some were found at the southern tip of the island in 1906, which at that time was covered in virgin mixed broadleaf forest, including large Pisonia grandis trees, within whose boles the crabs burrowed (E. Campbell 1908; A. Kepler, in prep.). Today Flint has perhaps the greatest density of coconut crabs in the world (A. Kepler
1990b). Human pressures have likely operated on Flint as on Caroline (A. Kepler, in prep.).

**Distribution and habitat preference:** In 1988 and 1990, coconut crabs were abundant in the Cocos plantations of South and Nake, and present, in varying densities, on 12 other motus (Fig. 17). Although generally associated with Cocos, we found them in woodlands of *Pisonia*, *Cordia*, and *Tournesol*ita, as well as on rubble beaches (especially after dusk). Although capable of surviving without coconut palms, these crabs appear to seek them out. In the open understory of the tall plantations, or in groves of only one or 2 palms, telltale piles of shredded coconut husk fibers (Pt. I, Pl. 53) disclosed the crab’s presence.

Because the prevalent coarse rubble substrates on Caroline are hard to burrow into, coconut crabs occupied a variety of shelters: mounds of fallen coconuts and rotting palm fronds (to 1.5 m high), piles of rubble pushed against tree roots, sand burrows, tunnels within the *feo* (Pt. I, Pl. 21), or large cavities in the boles of mature *Pisonia* trees. Coconut crabs also use a variety of shelters on the Tokelau Islands (Yaldwy & Wodzicki 1979), Flint, and Palau (AKK, pers. obs.).

**Numbers:** Though conspicuous and slow-moving, coconut crabs are very difficult to count. Environmental variables such as rainfall, tide, lunar cycle, and population size and age classes all affect their activity (Reese 1965; Helfman 1977a, b). Although unable to conduct mark-recapture studies, we did make incidental observations on the numbers of individuals seen during transect and perimeter surveys. Coconut crabs are generally nocturnal, but we often found them during daylight, at times exposed on coral gravel beaches close to the waterline. E. Reese (pers. comm.) suggests that the abundance of rats occupying the same habitat may “force” the crabs to be more diurnal, as has been reported from the Indian Ocean. Our estimate of the population on Caroline is approximately 2,200 individuals, based on the number of daytime observations, the area covered, and the fact that only one out of every 3 or 4 individuals may be present on any given night (Helfman 1977b, Reese 1987).

**Foraging:** Since the first detailed description of coconut crabs in 1705, their shy, curious habits have been the subject of folklore, speculation, and misinformation (see Reyne 1939). No scientist has yet published a documented account of a coconut crab actually opening a coconut (Helfman 1979), which is widely held to be their consummate foraging behavior. Helfman is convinced that they do so, as he has found piles of coconut fiber and observed crabs walking with husked, opened nuts in places where he was the only other possible coconut husker. We repeat Helfman’s (1979) assertion that coconut crabs do husk fallen coconuts. The piles of finely separated fibers (Pt. I, Pl. 53) we encountered are totally different from those produced by stick or machete husking, the 2 methods commonly employed by Pacific peoples. The crab tears virtually every fiber off individually, a process so painstakingly slow it probably takes days. We did not observe this on Caroline, but in March 1990 AKK, on uninhabited Flint Island, observed a large male coconut crab that had just husked a coconut and was enlarging
Figure 17. Distribution map of coconut crabs on Caroline Atoll.
a small crack in the center of the smooth nut in a manner similar to that described by Gardiner (1907) in Reyne (1939, p. 297). In June 1992, AKK also encountered large males eating coconut meat and husking fibers in the Southwest Palau Islands, Micronesia.

On Caroline we observed the aftermath of coconut crab-Sooty Tern predation or scavenging. On Brothers Islet, several entrances and pathways leading to coconut crab holes were strewn with the feathered skeleta of adult Sooty Terns (and possibly Brown Noddies), along with numerous, freshly snipped branches of *Pisonia* up to 0.7 m long (Pt. I, Sect. H). This was also recorded on Tridacna Islet by Clapp & Sibley (1971a) for Sooty Tern eggs and chicks, and by Helfman (1979) and Reese (1987) on Enewetak, Micronesia.

**Sizes:** Living in a rich environment free of predators, coconut crabs attain huge sizes on Caroline. The bodies of the largest males were as wide as a full-sized, unhusked coconut, giving them weights of at least 4 kg (G. Helfman, pers. comm.). Thorax widths for 10 crabs (2 females with eggs, 8 males) averaged 129 mm. The thorax of the largest male measured 200 mm across, making it, along with many measured on Flint in 1990 (A. Kepler 1990b), one of the largest recorded coconut crabs in the world (the previous record was 178 mm in Helfman 1977a), with an age estimated to exceed 40 years (E. Reese, pers. comm.).

**G. CONSERVATION: ATTRIBUTES OF INTERNATIONAL SIGNIFICANCE**

Caroline's exceptional attributes need to be elucidated, for the atoll has remained essentially unknown, even to some who have evaluated its worth (King 1973; Stoddart 1976; Garnett 1983, 1984). There are few, if any, islands remaining in the Pacific that can claim the impressive array of natural features exhibited by Caroline (Nicholson & Douglas 1969). We believe that it is imperative that this atoll, which has managed to escape large-scale, permanent human disturbance, should remain undeveloped.

Currently Caroline is uninhabited and has been since ca. 1930 except for a single family from 1987-1991. There are no roads, vehicles, stores, jetties, or services (water, sewage, or food), and no communication. There is no passage into the lagoon or safe sea anchorage.

**Lack of Major Disturbances**

Man’s presence anywhere--especially on pristine or near-pristine islands--generally brings rapid, often irreversible, changes. One of the most important of Caroline’s attributes is its relative lack of disturbance and very few exotic plant species. Aside from obvious human impacts on South, Nake, and Ana-Ana, the majority of its motus are dominated by indigenous vegetation and its reefs are basically pristine. There is no obvious pollution to alter the chemistry of the lagoon,
beyond the flotsam and jetsam that litter the beaches. It is thus an exceptionally clear and clean ecological laboratory that presents a lagoon ecosystem before extensive disturbance by man, providing marine biologists with opportunities to study undisturbed natural communities; for example, the maze of patch reefs in the lower half of the lagoon has the highest recorded density of living Tridacna (20/.25 m²) ever recorded (Sirenko & Koltun 1992). This is one of the few undisturbed world populations of this species (Pt. I, Pl. 25). In addition to conventional ecological studies, biomedical research could investigate the causes and treatment of ciguatoxicity of fishes and crabs. Such topics are increasingly important as more islands are subjected to disturbance and pollution. For example, the abundant red snapper (Lutjanus vaigiensis) and red spotted crab (Carpilius maculatus), both notoriously poisonous, are safe to eat on Caroline. Caroline, lacking the problems and pollution that beset many other Pacific islands, could serve as a "control island."

Terrestrial Ecosystems

Caroline's motus of varied age and size classes provide excellent examples of substrate and vegetation development, accompanied by an increasing diversity of bird life. On account of its relatively low human disturbance and rapid forest recovery, especially since 1920, Caroline is thus also an outdoor laboratory for terrestrial ecosystems: many motus have recovered so remarkably they are almost indistinguishable from those which have remained pristine, while others are in different stages of recovery resulting from varied management (or non-management) practices.

Caroline's concentric pattern of plant community development and the relationships of these communities to motu size, shape, and location on the atoll rim could continue to provide insight into evolutionary processes on atolls that are left undisturbed.

Physiography

Caroline offers many opportunities for geological research, under reasonably unmodified conditions. Valuable clues as to the nature of underground water supplies may lead to a better understanding of the regulation of water supplies on inhabited islands. Notable physiographic features include inland upraised reefs (feo) and deep sand deposits, coalesced islets, exposed older reefs, lithified beachrock, a conglomerate platform, a "perched lagoon," patch reefs, a nonfunctional hoa, and changes in motu size and shape during the past century.

Flora

Caroline's insular flora, typical of central equatorial islands in their natural state and covering 70% of the atoll's land area, is of both national and international importance. The 26 extant plant species
are 89% indigenous (possibly 92%), an extremely high figure for anywhere in the world. Six of the 7 plant communities are natural. Lushly wooded, Caroline possesses tall *Pisonia grandis* forests (Pt. I, Pl. 43), reaching 21 m and occurring on 29 islets. Although less majestic than the prime forests of Washington and Fanning (Northern Line Group), which enjoy a heavier rainfall, those on Caroline are notable: Caroline's 62 ha of *Pisonia* forest may well cover a larger area than on any other Pacific atoll.

Caroline also possesses significant stands of the hardwood kou (*Cordia subcordata*), which ranges from Africa to Polynesia, but is now rare in the Pacific. Caroline's groves (Pt. I, Pl. 26), although small and often mixed with other indigenous trees, total 26 ha, possibly the greatest area on any Pacific atoll. The extensive presence of tree heliotrope (*Tournefortia argentea*) is also notable: scrub and forests of this species form 40% of the atoll woodlands (Pt. I, Pl. 47). Caroline's large groves are some of the most unmodified in the Pacific, as elsewhere *Tournefortia* is typically restricted to coastal fringes surrounding anthropogenic plantations (personal observations; Wiens 1962; R. Fosberg, pers. comm.).

Caroline, and its neighbor Flint, are also ideal islands in which to monitor the transition from Cocos plantations to a more natural state: rainfall regimes, intensity of management, underground water reserves, slightly differing plant communities, and a wide range of island/islet sizes have resulted in marked differences in revegetation pattern only 60 years after the atoll was abandoned.

**Seabirds**

Associated with Caroline's plant communities are 11 species of breeding seabirds numbering well in excess of 1,000,000 individuals. Almost every islet harbors nesting populations of up to 9 species (Fig. 18). The populations of most of these species are of national importance (Table 9). For example, Caroline has the fifth largest Red-footed Booby colony in the world. Its Black Noddy and White Tern (Pl. 3) populations are the largest in Kiribati. Under the 1975 Republic of Kiribati Wildlife Conservation Ordinance (amended in 1979), all known seabirds, migrant shorebirds, and endemic land birds are "fully protected throughout the Gilbert Islands" (Garnett 1983, p. 128). However, their protected status is in doubt on Caroline, due to attempts to commercially develop the island. Caroline deserves protection similar to the 5 closed areas on Christmas Island and the 7 island sanctuaries in the Line and Phoenix Groups (Garnett 1983), preferably accompanied by on-site enforcement.

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1In 1992, these forests were evidently altered considerably by immigrant Gilbertese and cyclonic weather.
Figure 18. Seabird breeding species diversity by islet, Caroline Atoll.
Table 9. Comparative abundance of Caroline’s breeding seabirds in the Line Group.

<table>
<thead>
<tr>
<th>Species</th>
<th>Estimated Population</th>
<th>Comparative Abundance in the Line Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red-tailed Tropicbird</td>
<td>300²</td>
<td>Second largest population</td>
</tr>
<tr>
<td>Masked Booby</td>
<td>400</td>
<td>Fourth largest population</td>
</tr>
<tr>
<td>Brown Booby</td>
<td>40</td>
<td>Third largest population</td>
</tr>
<tr>
<td>Red-footed Booby</td>
<td>7,000</td>
<td>Third largest population</td>
</tr>
<tr>
<td>Great Frigatebird</td>
<td>6,100</td>
<td>Third largest population</td>
</tr>
<tr>
<td>Lesser Frigatebird</td>
<td>200+</td>
<td>--</td>
</tr>
<tr>
<td>Sooty Tern</td>
<td>912,000</td>
<td>Third largest population</td>
</tr>
<tr>
<td>Brown Noddy</td>
<td>3,000</td>
<td>Third largest population</td>
</tr>
<tr>
<td>Black Noddy</td>
<td>17,000</td>
<td>Largest population (largest in Kiribati)</td>
</tr>
<tr>
<td>Blue-gray Noddy</td>
<td>&lt;10</td>
<td>--</td>
</tr>
<tr>
<td>White Tern</td>
<td>8,000</td>
<td>Largest population (largest in Kiribati)</td>
</tr>
</tbody>
</table>

² Based upon nest count in 1990.

Shorebirds

Caroline is an important wintering ground for the Bristle-thighed Curlew, a rare shorebird and candidate for the U.S. Fish and Wildlife Service Endangered Species list. Some subadults remain all year on the atoll. As adult curlews pass through a flightless phase on their Pacific wintering grounds, islands such as Caroline provide a predator-free environment for this vulnerable phase of their life history.

Coconut Crabs

Caroline is exceptional in harboring a robust population of coconut crabs (Fig. 17; Pt. I, Pl. 21). These large invertebrates are abundant in the Cocos plantations of South and Nake and are found in good numbers in the indigenous Pisonia forests on most larger motus.

Turtles

Although green turtles are not abundant on the atoll, worldwide populations of these marine reptiles have suffered so greatly from overexploitation that remote, predator-free islands such as Caroline provide important, though small, sanctuaries. Since 1978 the Pacific green sea turtle has been reclassified by the United States Department of the Interior as threatened and the Pacific hawksbill sea turtle as endangered.

Archaeology

From an archaeological point of view, Caroline houses one intact Tuamotuan marae (ancient religious site) and another smaller site, partly destroyed by storms. The main site (Pt. I, Fig. 3, Pl. 36), basically undisturbed since the 1870s, is a relic of prehistoric occupation worthy of protection and study, being the only one of its kind in the Line and Phoenix Islands.
Current Conservation Status

Caroline Atoll is owned by the government of the Republic of Kiribati and does not enjoy any legal protection (Garnett 1983, Ministry of the Line and Phoenix Islands, pers. comm.). Over the last 50 years it has been leased to private individuals who have scarcely altered the atoll. The benign management of the past is no guarantee for the future, and from October 1989 to the present, pressures to develop the atoll have mounted rapidly. Proposed schemes included an airstrip, a blasted channel through the reef, a hotel, a casino, logging, and commercial harvest of fish and lobsters. In March 1990, commercial harvesting of fish, the taking of coconut crabs, and illegal killing of green turtles began, emphasizing that no island, however remote, is guaranteed protection through isolation.

In addition, during the past 3 years Caroline has become more visited than ever before, mostly without the knowledge or consent of the Kiribati government. During 1990 yachts were present almost the entire year, and in 1989 a cruise ship landed tourists who visited several seabird colonies during midday heat. At this time Polynesian crewmen presented some passengers with fresh tail feathers from Red-tailed Tropicbirds (B. Danielsson, pers. comm.). There are many reasons why Caroline is inappropriate for resident tourists or development (remoteness, distance from medical aid, no regular water supply, no passage into the lagoon, mosquitos, etc.; see A. Kepler 1990a). Caroline could support a limited number of ship-based ecotourists each year, but indiscriminate visitation by yachts or other craft, such as developed into an increasing problem at Suvarov, in the Cook Islands (G. MacCormack, pers. comm.), should be discouraged.

Recommendations for an international preserve began in January 1989. During the 1990 ICBP expedition to the Line Islands, team leaders discussed conservation matters with Kiribati government officials and key scientists in French Polynesia. We obtained photodocumentation of illegal land clearing and wildlife disturbance during the last 2 visits to Caroline (A. Kepler 1990a, b, c). As a result, the Kiribati government considered altering their plans for the development of Caroline in favor of wildlife preservation.

In 1990 and 1991, The Nature Conservancy of Hawaii attempted to establish a triple-island preserve on Caroline, Vostok, and Flint through negotiations with Kiribati officials on Tarawa. These negotiations failed, and the Kiribati government leased Caroline (and Flint) for 55 years to the person responsible for the schemes and illegal activities noted above.
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APPENDIX

Preliminary List of Arthropods

The knowledge of Arthropods on Caroline is limited to 15 Lepidopterans collected by Dr. Palisa during the Solar Eclipse Expedition (Dixon 1884), a scant list of common insects (beetle, gnat, etc.) in the same paper, and a preliminary collection of 82 specimens made by Graham Wragg and AKK in 1990. The latter, identified by David Preston and Scott Miller (B. P. Bishop Museum, Honolulu, Hawaii), contained no endemics, consisting primarily of widespread Pacific species and immatures identifiable only to family level.

Although our collection is also scant, it is the second collection of Arthropods from Caroline and the only one containing species other than Lepidoptera: Isometrus maculatus (scorpion), Scolopendra subspinipes (centipede), Anoplolepis longipes (long-legged ant), Isopoda, lepidopterans (larvae and pupa), dermestid beetles (larvae and adults), cockroaches (Dictyoptera), Hibboscidae adult (Diptera), Isopoda, Nitidulidae (immature and adults, Coleoptera), Curculionidae (Coleoptera), immature Hemiptera (Lygaeidae), Scolopendriidae immature, spiders (Arachnida).
Plate 1. Incubating Red-tailed Tropicbird, Bo'sun Bird Islet, Caroline Atoll, 25 September 1988. The nest scrape is in fine coral rubble under a Tournefortia shrub.