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## Dynamic ecology of Aldabran seabird communities

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The characteristics of the present seabird community of Aldabra are described, and compared briefly with others in the tropics. By comparison with Pacific Ocean communities, Aldabra is deficient especially in petrels and shearwaters, which are poorly represented in the western Indian Ocean generally and are absent probably for zoogeographic reasons. Ground-nesting species are also scarce, especially pelagic feeders that form large colonies, and this is attributed partly to their extermination by rats and partly to the proximity of Assumption, and perhaps Cosmoledo, that offer better nesting sites to these species. Inshore-feeding terns are also scarce on Aldabra, probably owing to insufficient areas of shallow water nearby. Relative population sizes are roughly in agreement with those that would be predicted, except for the fairy tern whose population may have been reduced in the past by barn owls. Almost all Aldabran seabirds nest either in mangroves or on small lagoon islets, the habitats in which birds are least vulnerable to introduced rats, which appear to have had a major effect on nesting distribution.

The seabird community is made up of two different trophic guilds, the pelagic feeders which bring in nutrients entirely from outside the ecosystem, and the inshore feeders which cycle nutrients between the intertidal and inshore parts of the system and the terrestrial part. Both result in a net input of nutrients, in the form of bird droppings, to the terrestrial ecosystem. It is estimated that about 1680 t of food are removed from the sea per year, most of the 105 t of guano resulting being channelled into the intertidal, rather than the terrestrial, parts of the ecosystem.

The seabird communities likely to have occupied Aldabra in the past are reconstructed on the basis of the known changes in the atoll's size and structure during the Pleistocene. At most times there would have been more species of seabird using Aldabra than now, and more of their guano would have passed into the terrestrial ecosystem.

Probably the most significant event in the recent history of the atoll was the arrival of rats, which exterminated probably quite considerable colonies of ground-nesting seabirds and drove the survivors into the only places where the rats could not survive – the tall mangroves and the tiny lagoon islets. In so doing, the rats destroyed a significant source of nutrient input to the terrestrial ecosystem, with major consequences for the ecology of the atoll as a whole.

## 1. Introduction

The object of this paper is to attempt to place the present community of seabirds on Aldabra in ecological and evolutionary perspective, and to explore its relation to the ecology and evolution of the Aldabran ecosystem as a whole. In view of the subject of this discussion, the rôle of seabirds in the terrestrial ecosystem will receive most attention. The composition of the present community is first analysed in terms of species number, population sizes and distribution, and the ecological interactions between seabirds and the rest of the ecosystem. The likely composition of former seabird communities during the evolution of the atoll is then suggested, followed by a brief comment on the future composition based on current knowledge

of erosion rates. The picture presented throughout is of a constantly changing, dynamic assemblage of seabirds, responding to, and in part influencing, the changes in the physical environment around them.

#### 2. THE PRESENT COMMUNITY

## (a) Species composition

Eleven species of seabird currently breed at Aldabra (table 2), belonging to five families: five terns (Laridae), two frigatebirds (Fregatidae), two tropicbirds (Phaethontidae), one booby (Sulidae) and one shearwater (Procellaridae). The community is thus dominated taxonomically by larids, but both numerically and in biomass terms by the three Pelecaniform families (frigatebirds, tropicbirds and boobies) which together account for 50 000 of the 55 000 breeding individuals and about 98% of the biomass of breeding seabirds (Diamond 1971 a, b).

Comparisons with the species composition of other tropical seabird communities suggest that the species composition of Aldabra is disharmonic, chiefly in three respects, one zoogeographic and two ecological.

- (i) Although comparing favourably with other Indian Ocean islands, Aldabra has six or seven fewer breeding species than would be expected on an island of similar size in the Pacific, such as Christmas Island where 18 species breed (Schreiber & Ashmole 1970). The chief group lacking on Aldabra is the petrels and shearwaters (Procellaridae); only two species breed widely in the western Indian Ocean, one of which breeds at Aldabra, compared with the five species that nest at Christmas Island. The western Pacific Ocean is the centre of distribution of tropical procellarids, which become progressively fewer westwards towards Aldabra.
- (ii) Apart from procellarids, which are absent chiefly for distributional reasons, the most obvious omissions from the Aldabran seabird community are three ground-nesting species, the white and brown boobies, Sula dactylatra and S. leucogaster, and the sooty tern, Sterna fuscata. There is no obvious reason for any of these to be missing, other than the lack of predator-free nesting space; there is evidently sufficient food since these species frequently feed around Aldabra. All the ground-nesting species that do breed at Aldabra, do so on very small lagoon islets (Diamond 1971a, b); probably none of these islets is large enough to support viable breeding colonies of any of these species. The absence of all ground-nesting species from the main islands of the atoll is one of the most striking features of Aldabra seabird distribution, and must be attributed to terrestrial predators, most of all the introduced rat, Rattus rattus, though the indigenous crab, Birgus latro, may also be implicated.

The sooty tern, and possibly the white booby, may be absent for a second ecological reason. Both these species are pelagic feeders, ranging for probably 160 km (100 miles) or more from the breeding colony to feed. Aldabra is thus within the feeding range of birds breeding on Assumption 27 km to the south, and even Cosmoledo 110 km east; neither species now breeds on Assumption (Stoddart, Benson & Peake 1970) but both do so at Cosmoledo (Bayne et al. 1970). Where several alternative nesting grounds are available within a common feeding area, species probably choose the most suitable breeding ground, rejecting an island that might be used if there were no better alternative nearby. Although Cosmoledo is the only island that might now draw away potential breeding seabirds from Aldabra in this fashion, Assumption carried large populations of seabirds in the past and, being so close to Aldabra, has probably played a larger part than Cosmoledo in determining past seabird community structure on Aldabra, at least until its seabird colonies were destroyed by phosphate mining.

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(iii) There remain several species which are widely distributed elsewhere in the region, and for which there are apparently still suitable breeding sites on Aldabra. These are the black noddy, Anous tenuirostris, and the bridled and roseate terns, Sterna anaethetus and S. dougalli. All of these nest in the central Seychelles, 1000 km to the east, in considerable numbers. The most likely reason for their absence from Aldabra is a lack of suitable feeding grounds; all are inshore feeders and in Seychelles feed chiefly over the very extensive shallow waters of the Seychelles Bank; there is no comparable area of shallow water near Aldabra.

## (b) Population sizes

There are two ecological models that can be used to predict the relative population sizes of species in a seabird community (Preston & Williams's log-normal model is not considered here, being a mathematical model rather than a biological one). The first is MacArthur's 'brokenstick' model (MacArthur 1957), in which species populations are treated as a random sub-set of the total number of individuals in the community. Population sizes of Aldabran seabirds do not differ statistically from those predicted by MacArthur, although one of the chief assumptions of the model, that the species' niches do not overlap, is not met (Diamond 1971a). The second model, which is specific to tropical seabirds, predicts that species with the largest feeding ranges are the most numerous (Diamond 1978); again, the Aldabran community agrees with these predictions, but since this model was formulated partly from these Aldabra data, it cannot strictly be used to interpret them.

One species whose population size is greatly different from that which would be expected, both from the second model and from general knowledge of the natural history of the species, is the fairy or white tern,  $Gygis\ alba$ . This species usually feeds some distance from land around Aldabra, whereas in central Seychelles it feeds chiefly inshore and is very numerous. The population on Cousin Island in Seychelles, which is less than  $\frac{1}{600}$  of the area of Aldabra, is about  $10\,000$  pairs (Diamond  $1975\,a$ ), about 30 times the Aldabran population, whereas its larger feeding area around Aldabra, and the much greater area available for nesting, should support a very much larger population. Its rarity on Aldabra can tentatively be attributed to predation in the past by barn owls,  $Tyto\ alba$ , which used to occur on Aldabra and have greatly reduced fairy tern populations in central Seychelles since they were introduced there in the 1950s.

### (c) Distribution

The distribution of nesting colonies and roosts has been described by Diamond (1971 b). Two habitats are used to the exclusion of almost all others; small lagoon islets, and mangroves on the lagoon shore. A few fairy terns and tropicbirds (*Phaethon* spp.) occasionally breed on the main land rim, and there are regular roosts of frigatebirds (*Fregata* spp.) and brown noddies (*Anous stolidus*) there, but the number of individuals that breed on the mainland rim is very small indeed. Much of it is suitable, in the sense that similar vegetation elsewhere in the tropics is often used by breeding seabirds, including species that occur on Aldabra, and its avoidance by seabirds on Aldabra can be explained only by the presence, on all the main islands of the land rim, of abundant rats (*Rattus rattus*). These are widely held to have exterminated seabird colonies elsewhere in the world, and must be presumed to have done so in the past on Aldabra. Norman (1975) concluded that the influence of rats in destroying seabird colonies has been over estimated, and that cats and man may have been at least equally culpable; this conclusion was based on the paucity of direct evidence of rat predation in seabird colonies, but such evidence is

difficult to acquire, and there is still substantial circumstantial evidence implicating rats in the destruction of seabird colonies.

## (d) Ecological rôles

There are two chief routes by which seabirds interact with the terrestrial ecosystem; by modification of vegetation through guano deposition at the nest or roost, and through nutrient recycling.

## Vegetation modification

Vegetation may be changed radically by the guano deposited at and around the nest or roost. Trees used as roosts by frigatebirds and boobies are often leafless, and a few are apparently dead, but there has been no systematic study of the problem and it is possible that the birds choose bare trees to roost in, rather than that they cause trees in which they roost to become bare. Such effects are not common in trees used for nesting, although the leaves are often liberally splashed with droppings. The ground-nesting colonial terns, especially brown noddies and crested terns (Sterna bergii), undoubtedly modify vegetation; the herb Achyranthes aspera is particularly common and luxuriant on islets used by brown noddy colonies, and in mainland Seychelles shows a similar affinity for the ground beneath colonies of the tree-nesting black noddy (Anous tenuirostris). The seed of Achyranthes is almost certainly transported by seabirds, as is that of Boerhavia repens which commonly occurs on the smaller rocky islets on which noddies and black-naped terns (Sterna sumatrana) breed. No proper studies have been made of seabirdvegetation interactions on Aldabra but, for reasons detailed in the next section, such effects are likely to be very localized and not of major importance to the terrestrial ecology of the atoll. (Gillham's (1977) preliminary study of seabird-vegetation interactions lacks the long-term element necessary to substantiate the seabird-induced cycles proposed.)

## Nutrient cycling

Seabirds obtain their food from the sea, and return to land to nest and roost. They therefore produce a net input of nutrients to the terrestrial ecosystem. However, 89% of the seabird biomass nests in trees, almost all of which are mangroves, so most of the guano will fall, or be washed by rain, into the tidal waters beneath the mangroves; thus the intertidal part of the ecosystem will be much more affected than the terrestrial part. The rich growth of corals and algae on the lagoon floor around the large frigatebird and booby colonies near East Channel may owe their existence partly to nutrient enrichment by the seabird colonies above. As marine predators, seabirds fall into two trophic guilds that play different rôles in the ecosystem as a whole:

- (a) Pelagic feeders, which feed far from land, i.e. well outside the Aldabran ecosystem, returning an unknown proportion of nutrients to the terrestrial system, chiefly on lagoon islets.
- (b) Inshore feeders, which catch prey in shallow waters around the atoll, again returning these nutrients to land; because much of their prey is caught either within the lagoon, or between the land and the seaward reef, they can be regarded as cycling nutrients within the atoll ecosystem although, like pelagic feeders, they produce a net input to the terrestrial ecosystem.

The total amount of nutrients that the seabirds bring in to the system can be estimated, very approximately, as follows.

(1) Mass of food consumed. By using the bird masses and population sizes given by Diamond

# (1971 a, b respectively); and assuming that a bird eats about 10% of its body weight per day (a conservative estimate – for large birds, Hutchinson (1950) gives 17% for the cormorant

(a conservative estimate – for large birds, Hutchinson (1950) gives 17% for the cormorant *Phalacrocorax auritus*, and Houston (1972) 8–9% for two vultures *Gyps* spp.), the total weight of food consumed by Aldabra seabirds is approximately 1680 t per year.

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- (2) Mass of guano produced. Gamarra Dulanto (1941, quoted by Hutchinson 1950) found that 16 t of fish eaten by Peruvian seabirds resulted in 1 t of guano. Hence the 1680 t consumed by Aldabran seabirds would be equivalent to about 1680/16 = 105 t of guano per year.
- (3) Mass of guano deposited on land. Referring to Peruvian guano-producing species, which build nests composed chiefly of their own guano, Hutchinson (1950) estimated that very nearly all of the droppings produced by these birds would be deposited on land at the breeding colony. This is less likely to be true of the species presently breeding at Aldabra, particularly the treenesting species, but there are no data on which to base an estimate of the difference. Hence we can say only that a maximum of 105 t of guano is brought into the atoll ecosystem by seabirds.
- (4) Mass of major nutrients. Again, only maxima can be given. Seychelles guano averages about 24.2%  $P_2O_5$  and 0.98% N (Hutchinson 1950); 24.2%  $P_2O_5$  is equivalent to about 10.5% P, so the mass of P produced by Aldabran seabirds =  $105 \times 0.105 = 11$  t p.a.; and mass  $N = 105 \times 0.0098 = 1$  t p.a. As already pointed out, the great majority of this nutrient input is channelled into the intertidal, rather than the terrestrial, parts of the atoll ecosystem.

In summary, seabirds remove several hundred tonnes of nutrients from the sea and deposit a small fraction of this into the terrestrial ecosystem of Aldabra; this deposition is extremely localized and, as far as the strictly terrestrial part of the ecosystem is concerned, is limited to the small islets in the lagoon.

## (e) Stability

It is 10 years since seabirds began to be studied on Aldabra; these years have presented unique opportunities for long-term work on a tropical seabird community and, in particular, for assessing its stability, in terms of both numbers and of distribution. These opportunities cannot be said to have been fully exploited, but sufficient recent observations have been made to suggest that numbers of at least two species have remained fairly stable over this time, but that the distribution of nesting colonies has changed, in some cases very substantially. These observations, which I hope will be documented fully by the observers concerned, are outlined below.

- (i) Frigatebirds. In a recent census (1976), B. Reville (personal communication) found little change from the population sizes of Fregata minor and F. ariel that I found in 1967 (Diamond 1975b). However, the distribution of species within colonies had changed greatly (figure 1), although the main colonies were still in approximately the same places.
- (ii) Terns. Regular observations by S. Hnatiuk and R. Prŷs-Jones of some of the lagoon islets used by tern colonies suggest little change in the total numbers of either brown noddies, crested terns or caspian terns (Hydroprogne caspia), but major changes in the location of the main colonies of brown noddies and crested terns. These are listed in table 1.

Unfortunately it is difficult to be sure that these changes result from natural causes. Frigate-birds were killed for food by Seychellois fishermen before 1967, and are still very sensitive to human disturbance, particularly during their courtship period. Crested terns in 1967–9 were very prone to desert if disturbed, perhaps because their eggs were taken by the fishermen. Noddy colonies in the north and east part of the lagoon are evidently much more heavily preyed upon by pied crows (*Corvus albus*) now than they used to be (R. Prŷs-Jones, personal

communication); the crows had evidently learnt the location of these colonies, and specialized in preying upon them, in the intervening period. Just how important these human factors might be is impossible to judge; in any case, the efficient way in which the birds do move colonies and yet breed successfully, suggests that such anti-predator behaviour has been selected for in the past, whether by human or other predators.

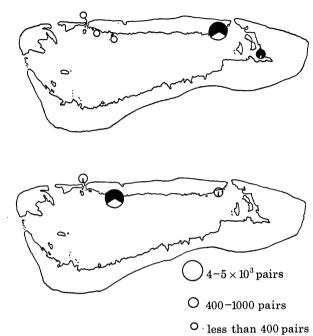


FIGURE 1. Changes in size, location and composition of frigatebird colonies. Upper map: 1967 (Diamond 1975b); lower map: 1976 (B. Reville, personal communication). Fregata minor shown in white, F. ariel in black.

The influences that have shaped the Aldabran seabird community, as we see it today, may therefore be summarized as follows.

- (i) Zoogeography. The species making up the community are drawn from the species pool of the western Indian Ocean which, by comparison with the western Pacific, for example, is relatively poor in species, especially in petrels and shearwaters (Procellaridae).
- (ii) Proximity of alternative breeding sites. The nearness of Assumption (in the past) and Cosmoledo may draw away pelagic feeders to breed there rather than on Aldabra. Since pelagic feeders are more numerous than inshore feeders, which will not be affected in this way (Diamond 1978), the proximity of other islands may have a major ecological effect in significantly reducing the inflow of nutrients (via seabirds) to the ecosystem.
- (iii) *Undersea topography*. The steep offshore gradient of the sea floor around Aldabra allows no extensive shallow-water feeding areas for such species as bridled and roseate terns, and black noddies, which are probably at least partly dependent on such areas.
- (iv) Introduced predators. Rats, accidentally introduced by man, have spread throughout the land rim of the atoll, and have probably exterminated past breeding colonies of seabirds that must have made significant contributions to the nutrient status of the terrestrial ecosystem. They and the barn owl (which probably reached Aldabra naturally), may also have selectively depressed the populations of species particularly sensitive to them.
  - (v) Geological structure. Different rock types on the lagoon islets offer different types of nest

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site, and this influences the nesting distribution of the two species of tropicbird *Phaethon* spp. (Diamond 1975c) and of ground-nesting terns, which breed almost exclusively on Takamaka limestone islets (Diamond 1971a); whether it also affects the total population sizes of these species, as well as their patterns of distribution, is not known.

Table 1. The islets used by brown noddies and crested terms as nesting colonies in 1967–9 and 1975–6

	brown noddy		crested tern	
islet (grid references)	1967-9	1975–6	1967–9	1975-6
228° E, 047° N	0	0	12	3
220° E, 044° N	0	200	26	0
302° E, 091° N	318	50	20	0
229° E, 108° N	23	0	4	0
271° E, 065° N	20	>100	20	ca. 18
338° E, 105° N	79	ca. 10	0	0
317° E, 109° N	20	< 10	0	0
338° E, 105° N	14	ca. 10	0	0
080° E, 066° N	0	0	<b>2</b>	20

Figures shown are the maximum number of occupied sites. 1967-9 figures from Diamond (1971a), 1975-6 from R. Prŷs-Jones (personal communication).

## 3. THE PAST COMMUNITIES

The area and morphology of Aldabra have changed many times during the Pleistocene, and these changes have been reconstructed by Braithwaite, Taylor & Kennedy (1973). Their data (particularly as summarized in table 2) have been used to postulate the likely seabird communities that have occupied Aldabra during that time. Four principles have governed this procedure:

- (1) It is assumed that past zoogeographic influences were broadly the same as now, i.e. the same pool of species was available to colonize the island. The possibility that species that now breed outside the tropics might, during glacial periods, have occupied the tropics, cannot be explored without further evidence.
- (2) It is assumed that islands of a particular structure had a similar fauna then to that which they have now, i.e. a sand cay had the same avifauna 100000 years ago as a sand cay has now.
- (3) The same relation between feeding strategy and population size that holds now (i.e. pelagic feeders and migrants are more abundant than inshore feeders and residents (Diamond 1978)) is assumed to have operated in the past.
- (4) The possible effect, referred to above, of a nearby island in drawing away potential breeders, cannot be taken into account because too little is known of the geological histories of the nearest islands, Assumption, Cosmoledo and Astove.

Braithwaite et al. (1973) inferred seven periods of emergence of land before the appearance of Aldabra in its present form; of these, they were able to suggest a land area, and to describe landforms, sufficiently precisely to identify three different types of land mass for which seabird faunas can be suggested. These are shown in table 2 and described below.

## (a) Sand cays

Aldabra has consisted of sand cays at least three times, all before 125000 a B.P.; the land area is unknown for the first such emergence, and was 20–25 km² on the second and third. Present

caspian tern, Hydroprogne caspia

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sand cay islands are found in the Amirantes (e.g. African Banks) and Cargados Carajos, and their avifaunas suggest that Aldabra would then have had about 13 breeding seabird species, including large colonies of sooty tern, white booby, wedge-tailed shearwater and perhaps roseate tern. If there were sufficient trees, black noddy and fairy tern would also have bred. Species that occur now, but probably did not then through lack of suitable nest sites, include white-tailed tropicbird, Audubon's shearwater (*Puffinus l'herminieri*) and black-naped tern.

TABLE 2. SUGGESTED SEABIRD FAUNAS DURING EVOLUTION OF ALDABRA

	structure of Aldabra				
breeding species	sand cay	rocky islets	high, steep rocky island	present atoll	
sooty tern, Sterna fuscata	×	×	×	•	
red-footed booby, Sula sula	×	×	×	×	
great frigatebird, Fregata minor	×	×	×	×	
lesser frigatebird, Fregata ariel	×	×	×	×	
wedge-tailed shearwater, Puffinus pacificus	×	•		•	
Audubon's shearwater, Puffinus l'herminieri	•	×	×	×	
red-tailed tropicbird, Phaethon rubricauda	×	×		×	
white-tailed tropicbird, Phaethon lepturus		×	×	×	
white booby, Sula dactylatra	×	×	×	•	
brown noddy, Anous stolidus	×	×	×	×	
fairy tern, Gygis alba	(×)	•	×	×	
brown booby, Sula leucogaster	×	×	×		
black noddy, Anous tenuirostris	(×)	•		•	
roseate tern, Sterna dougalli	×	•		•	
bridled tern, Sterna anaethetus		×	×	•	
crested tern, Sterna bergii	×	×		×	
black-naped tern, Sterna sumatrana	•	×		×	

Structure of Aldabra from Braithwaite et al. (1973). Species arranged in descending order of feeding range; species at top are pelagic feeders, those at bottom, inshore feeders. Parentheses denote cases where doubt exists as to whether there were enough trees for species to breed in.

### (b) Low rocky islets

This landform was probably similar to that of Cosmoledo Atoll now, and occupied a land area of about 50 km² about 80 000 a B.P. Large colonies of sooty tern and white booby are likely to have flourished, and smaller numbers of brown booby and bridled tern may also be inferred, though the latter two species also need shallow water in which to feed. Of the present avifauna, fairy and caspian terns are likely to have been absent. Again, about 13 species probably bred.

## (c) High, steep-sided, flat-topped rocky island

About 27000 a B.P., Aldabra was larger (400 km²) and more diversified in structure and habitat than at any other time in its recent history. Its seabird community is likely to have been dominated by species nesting in the trees and shrubs that probably crowded the top of the island; the nearest comparisons at the present day are probably Christmas Island (Indian Ocean) and Monito Island in the Caribbean (C. B. Kepler, personal communication). The vegetation on top of the island would have carried large colonies of red-footed boobies (Sula sula) and great and lesser frigatebirds (Fregata minor and F. ariel). The more open grassy areas would afford nesting sites for sooty terns, white boobies, and smaller numbers of both species of

tropicbirds and, if sufficient shallow water were nearby, bridled terns. Probably about 11 species nested, the most conspicuous losses being the shallow-water feeding terns.

Throughout its history, the avifauna has been dominated by pelagic feeders (except at any time, e.g. when the land area was least, when there were extensive areas of shallow water nearby). On the first two island types, the large colonies of pelagic feeders would have deposited large amounts of guano. The composition of the seabird fauna depends not only on the physical structure of the island, which determines to a large extent the kinds of nest site available, but also on the depth of surrounding water and, for the pelagic feeders, the proximity of alternative nesting sites on other islands.

In discussing both the present and the past seabird communities on Aldabra, I have repeatedly suggested that there have been very much larger numbers of seabirds in the past than there are now, and in particular that ground-nesting pelagic feeders, the kind that produce large amounts of guano, would have been abundant. Yet one of the most striking features of Aldabra's ecology is its lack of guano deposits; indeed this absence may be one of the chief reasons why the atoll has escaped the devastation that most of the others in the region have suffered. However, many of the superficial deposits, as well as several rock formations (e.g. the Esprit phosphorites), do contain substantial quantities of phosphate; these are not sufficiently extensive or concentrated to be of commercial value (Baker 1963), but they do indicate past concentrations of seabirds considerably greater than at present. The chief anomaly is the lack of recent phosphate deposits; if, as I have suggested, large colonies of ground-nesting seabirds were exterminated by introduced rats, where is the guano they deposited? In fact superficial deposits of quite high phosphate content are widespread on Aldabra, but are very thin and usually at the bottom of pockets or pits in the limestone (Baker 1963) and therefore not economic to extract; Hutchinson (1950) suggested that these deposits may be contemporary with those on Assumption and other islands in the region. It seems certain that there were fewer ground-nesting, guano-producing seabirds on Aldabra than on Assumption, even before rats came to Aldabra, for the possible reasons already suggested ( $\S 2a$  (ii)).

## 4. FUTURE CHANGES

Past communities have been reconstructed on the basis of the known physical structure of Aldabra in the past. Since we cannot predict its structure in the future, neither can we predict changes in the seabird communities with any confidence. The only change that seems inevitable is a reduction in the number of small lagoon islets for the ground-nesting birds to breed on. These islets are both destroyed, and produced from the lagoon shore of the land rim, by marine erosion; but whereas the lagoon shore is generally protected from erosion by mangroves, the islets in the open lagoon are not, so islets are probably destroyed faster than they are created. A substantial part of the seabird community, in terms of numbers if not biomass, will then have to seek alternative breeding sites elsewhere.

I thank R. Prŷs-Jones and B. Reville for permission to quote their observations on seabird distribution and numbers in the last few years.

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