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FEEDING OVERLAP IN SOME TROPICAL AND TEMPERATE SEABIRD COMMUNITIES

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ABSTRACT.—Overlap matrices, used to assess feeding relationships in tropical seabird communities, suggest that in species feeding far from shore their prey is restricted in diversity, irrespective of the prey's abundance relative to the predators' needs. Inshore feeders in the tropics take more diverse prey in terms of number of species, and they overlap less than pelagic species. These data suggest that overlap between predators depends on the diversity of prey. Prey size is but weakly related to predator size and the foraging strategy of the seabird is as good a predictor of its prey size as is its own body size. Areas for further profitable research in feeding biology of seabirds are suggested.

The first studies of diet in seabird communities, both temperate (Pearson 1968) and tropical (Ashmole and Ashmole 1967), were concerned chiefly with the phenomenon of ecological segregation between co-existing species, which remains a preoccupation in more recent studies (Schreiber and Hensley 1976, Croxall and Prince 1980).

In this paper I want to explore instead the patterns of dietary diversity and overlap within and between seabird communities in the tropics and to make some comparisons with a community at higher latitudes. My intention is not simply to demonstrate a difference between co-existing congeners, but to measure the overlap between as many members of a community as possible and to look for trends in amount of overlap between different communities. The interpretation of overlap values is difficult, especially since there are as yet no statistical methods for testing the significance of apparent differences between values. At this stage, I attempt to draw attention to trends which, if followed up by further field studies and analysis, promise to increase our understanding of the organization of seabird communities and their relation to marine ecosystems.

The first study of a seabird community's diet was by Ashmole and Ashmole (1967) on Christmas Island (Pacific Ocean). This has become an ecological classic and is widely quoted to support the view that, even where several closely-related species appear to share similar diets, close and careful study will always reveal significant differences between any two species (Lack 1970). Most of the Ashmoles' data were from terns, which probably segregate more clearly than larger species (see below), so their results may not apply to whole seabird communities. However Schreiber and Hensley (1976) also found clear segregation between three of the larger Christmas Island species. Pearson's (1968) work on the Farne Islands seabirds remains the only comparable study of a temperate-latitude community. It has attracted less attention, at least in textbooks, probably because Pearson found much greater overlap between co-existing congeners than theory predicted.

Neither Pearson nor the Ashmoles calculated measures of dietary overlap between the species they studied. From my own data on seabird food samples from Aldabra Atoll and Cousin Island in the tropical Indian Ocean (Diamond 1971a, 1974, 1975a, b, 1976, unpub.) I have calculated dietary overlap and diversity in several different ways. I have also calculated overlap values from Pearson's and the Ashmoles' published data, supplemented by Schreiber and Hensley's (1976) data on species not studied by the Ashmoles. All or parts of three tropical and one temperate sea bird community can therefore be discussed in some detail; comparisons with studies on other communities, such as South Georgia (Croxall and Prince 1980), Ascension Island (Stonehouse 1962), the Galapagos (Snow 1965; Snow and Snow 1967, 1969; Harris 1969, 1970; Nelson 1969), the Bering Sea (Hunt et al. 1981), and the Barents Sea (Belopolskii 1957) are precluded because their data were presented in insufficient detail for quantitative comparison. Harrison et al.'s recent studies of Hawaiian seabird diets are not yet published; the phenomenal sample sizes involved eclipse those of previous studies, but were taken from such a wide geographical range that the species sampled can hardly be said to constitute a community. For practical purposes I treat the seabirds breeding on one island or atoll, or a small but isolated archipelago, as a 'community'; but I recognise that the community concept needs more rigorous consideration in relation to seabirds.

METHODS

COLLECTION AND PRESERVATION OF SAMPLES

I collected food samples from adults and nestlings. Almost all were regurgitated, either by adults caught for banding, or by chicks approached closely on the nest. The only exceptions were some prey items dropped

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by adult White Terns *Gygis alba* and found beneath the breeding site, often in very fresh condition. Young of most species regurgitated when approached closely, but some did so only when handled, and many chicks handled regularly for growth studies became so habituated to handling that they no longer regurgitated.

I inspected all samples in the field, and discarded those that were so digested as to contain no identifiable remains. I kept the others in labelled plastic screw-topped jars, which I filled with 10% formalin solution on return to camp or laboratory. Specimens collected on Aldabra were shipped to Britain before transferral to 70% ethanol solution prior to analysis. Specimens collected on Cousin were analysed there; only reference specimens, preserved in 70% ethanol, were shipped to Britain for identification.

LABORATORY TREATMENT

I first sorted each sample into the categories fish, cephalopod and "others." I identified fish provisionally to family level, by reference to Smith (1949) and Smith and Smith (1969) and representatives of each family were later identified by P. J. Whitehead of the British Museum (Natural History). Cephalopods were identified to family using criteria supplied by Dr. M. R. Clarke, who determined reference specimens; the great majority were squids of the family Ommastrephidae, and all the ommastrephids identified to species were *Symplectoteuthis oualaniensis.* The few other cephalopods were identified by Dr. Clarke. Other invertebrates were identified by R. W. Ingle and Dr. J. D. Taylor of the British Museum (Natural History); most were small gastropods or fish ectoparasites.

I counted the number of items in each food class. Some samples contained material so fragmented that I could not be sure how many different items were present. In these cases I recorded the minimum possible number of items in each food class. If only skeletal or other indigestible remains of a food class were present, e.g., fish vertebrae, otoliths or eye lenses, or squid beaks, then that food class was recorded as present (for frequency analysis) but was not counted since such hard parts might be retained in a bird's stomach long after its original owner had been eaten. This part of my technique differed from Ashmole and Ashmole (1967), who arbitrarily scored one item of any class represented by such hard parts in a sample.

Most items were partly digested, so their volume depended as much on their state of digestion as on their original size; accordingly I did not measure the volume of such fragments, as Ashmole and Ashmole (1967) did, but tried instead to reconstruct the original size of the animal when it was caught.

Each fish fragment carrying at least two different sorts of fin, or one end of the fish and one fin, was measured between the base of one fin and either the end of the fish (tip of nose, or base of tail-fin) or the base of the other fin. These partial measurements could be converted into estimates of the total length of the fish by reference to sets of measurements made on all complete fish obtained (Figs. 1 and 2); where too few were obtained in samples, measurements of complete specimens were supplemented using specimens in the British Museum. Thus, the length of any fish could be estimated if it was sufficiently well preserved to identify and to retain at least two reference points for measurement.

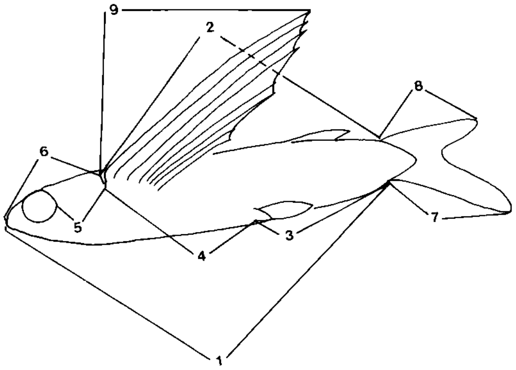

FIGURE 1. Measurements taken on fish specimens: 1: standard length, 2: base of pectoral fin to base of upper caudal fin, 3: base of pelvic fin to base of lower caudal fin, 4: base of pectoral fin to base of pelvic fin, 5: shortest length between eye and base of pectoral fin, 6: tip of nose to base of pectoral fin, 7: length of lower caudal fin, 8: length of upper caudal fin.

Other workers have usually used volume rather than weight to express the bulk of prey items—in Ashmole and Ashmole's case, the volume of the partly digested fragment—but volume is very similar to weight in aquatic animals since their specific gravity is close to 1.0. Volumes of Aldabra specimens were measured by displacement, but the Cousin seabirds took smaller prey which was very hard to measure with any accuracy; these were therefore weighed after drying with absorbent paper until dry to the touch and, in the case of squids, emptying free liquid out of the mantle cavity. All volume and weight data are presented as weights for ease of comparison, irrespective of the method of measurement. The length-weight relationship obtained from complete specimens (Fig. 3) was then used to estimate weights of partly-digested specimens. When comparing my weight data with the Ashmoles' volume figures it is important to note that mine refer to the whole prey item and theirs to the partly digested fragment.

I measured only the dorsal mantle length of squid, since heads were usually detached from mantles. I determined weights as for fish, after emptying the mantle cavity of preservative, and plotted them against mantle length (Fig. 4). Many samples contained squid beaks, which were identified using the key in Clarke (1962); any beaks not from ommastrephids were identified by Dr. Clarke. Beaks of whole specimens were removed and measured. The relation between lower rostral length and mantle length (Fig. 5) provided an estimate of the weights of many more squid eaten by each bird species than could be found whole in the food samples. These estimates have not been included in the species accounts, but the size ranges of squid given by the two methods were not significantly different in any case.

METHODS OF ANALYSIS

Three basic methods can used in analysing food samples (Hartley 1948, Ashmole and Ashmole 1967):

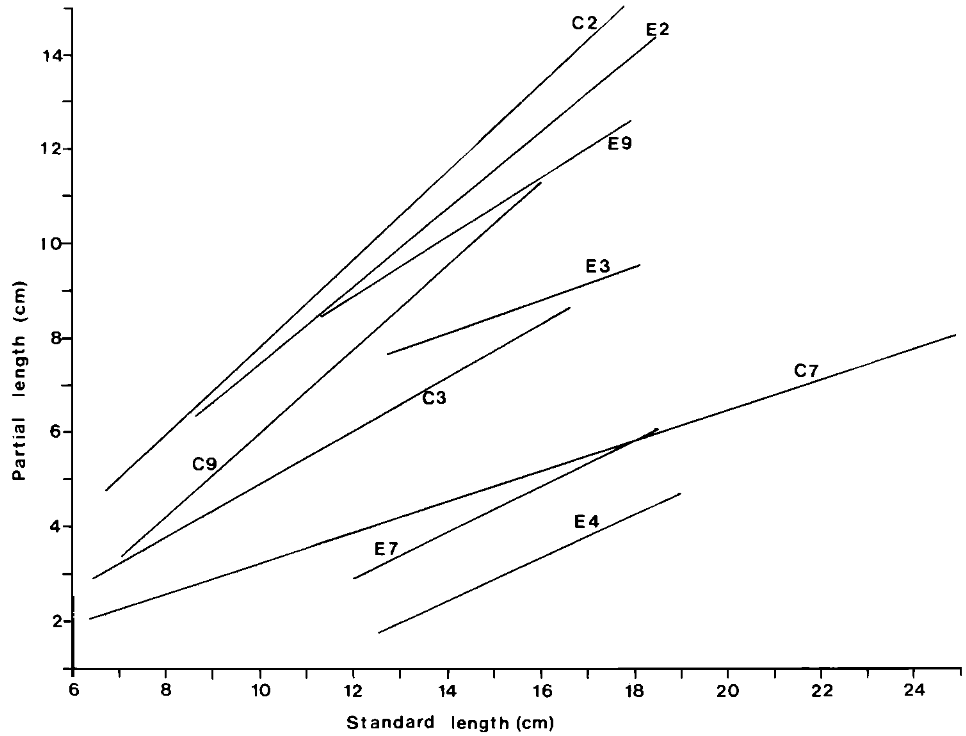

FIGURE 2. Relationships between selected partial measurements and standard length of flying fish in food samples. (Numbers as in Figure 1. E = *Exocoetus volitans*, C = *Cypselurus furcatus*.)

Frequency: the proportion of samples in which a prey category is present;

Number: the number of different items in each prey category;

Size (weight, volume or length) of all items (and, in my study, of items in each prey category).

Each of these methods, used by itself, may give misleading impressions of a species' diet. Even if all methods are used, they may (as Ashmole and Ashmole (1967) pointed out) underestimate the importance of a food class which is eaten only when other food is scarce, but whose presence enables a species to survive where otherwise it might not. For example, snails are apparently important in this way to Song Thrushes, *Turdus philomelos* in Britain (Davies and Snow 1965).

Quantitative comparisons of seabird diets are complicated by a number of factors. First, all samples (except from White Terns, which were the only species to bring back food as bill-loads) were regurgitations and may therefore have been incomplete. This drawback needs to be balanced against the only alternative source of data—stomach contents of dead birds—in which durable parts of prey are likely to be over-represented. Second, some species yielded samples that were consistently more digested than those from other species; this becomes important if different food classes are digested at different rates, or differ in the state of digestion at which they can still be identified. Although fish and squid do not seem to differ significantly in the rate at which they are digested by birds (Ashmole and Ashmole 1967), fish of some families can certainly be identified at far more advanced stages of digestion than others. The pectoral fin rays of flying-fish are diagnostic and very resistant to digestion, and garfish (Belonidae) and half-beaks (formerly Hemirhamphidae, now merged in Exocoetidae) have characteristic body forms which can be recognised at advanced stages of digestion. Fish larvae, on the other hand, can often not be identified, even to family, even when they are intact.

A further possible source of difficulty in comparing different species' diets is that in some studies most samples came from chicks, in others from adults; in practice this is probably not a serious problem because most samples from adults were destined for a chick, and none of the species concerned is known to collect prey for its chicks that is different from that eaten by adults.

A more serious problem is that samples can be obtained most readily (and in some cases, only) during the season when young are in the nest. Non-seasonal nesters can thus be sampled year-round, seasonal breeders in only some months. A complete, year-round picture of the diet of a seabird community is thus an unobtainable goal, at least with present techniques.

These methodological problems apply to all communities studied; there is no reason to suspect that any of them is more serious in one community than another.

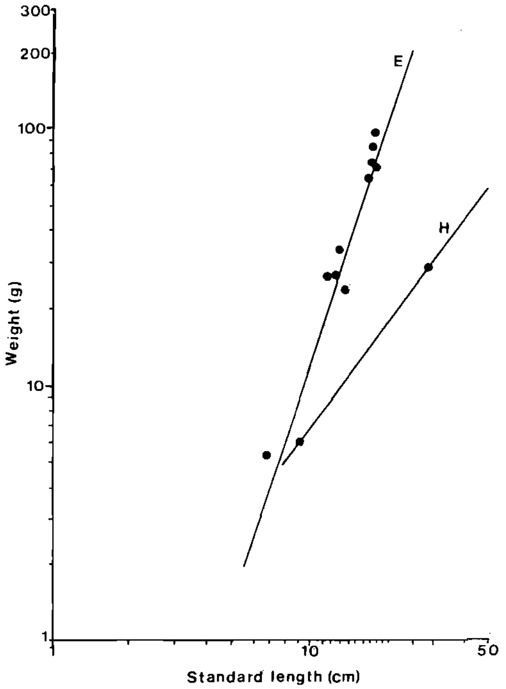

FIGURE 3. Weight/length relationships of Exocoetidae (E) and Hemirhamphidae (H) in food samples.

The purpose of this study is to make comparisons between communities; since these communities have been studied by similar methods, subject to comparable constraints, these methodological problems are unlikely to invalidate such comparisons.

MEASUREMENT OF OVERLAP

Several measures of overlap are available; the one used here is Horn's (1966) modification of Morisita's Index (1959), where Overlap Index, C, is given by:

$$C = \frac{2 \sum_{i=1}^{s} x_i \cdot g_i}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2}$$

where s is the number of prey categories in the two bird species being compared, and category i is represented x times in species x and y times in species y. This index is particularly appropriate where, as here, the data are expressed as the proportions x_i and y_i of the respective samples containing category i. The upper limit, when the two species take exactly the same prey, is 1, and the lower limit, when they have no prey in common, is 0.

The overlap index is a relative measure, not an absolute one. Its value depends on the number of categories used in the particular level of analysis in question (see RESULTS). The mathematical distribution of the index seems to be not well known, and I know of no valid way of testing apparent differences between indices. Accordingly I do not attempt statistical tests of the differences I discuss, relying instead on consistency of trends as a guide to interpretation. This is clearly a weakness of overlap indices as a statistical tool; I hope that its value in ecological interpretation will be apparent, and might stimulate more work on its statistical manipulation.

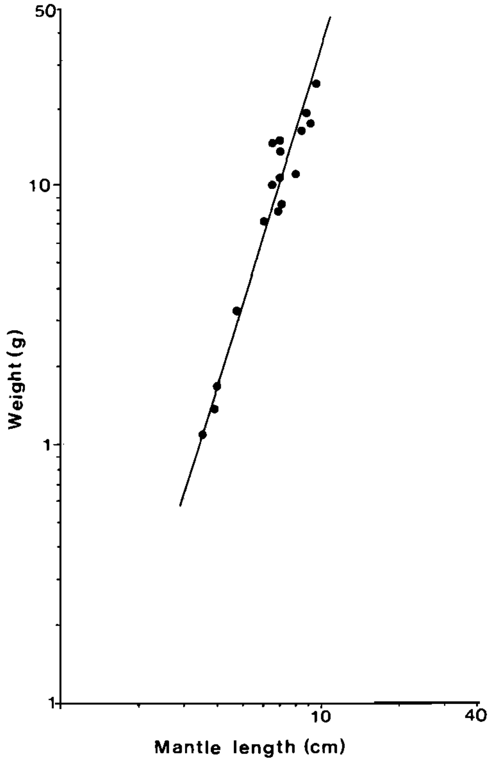

FIGURE 4. Weight/mantle length relationship in squid (Ommastrephidae) in food samples.

It is important to stress that the absolute values of the overlap index depend on the number of categories into which the resource is divided for analysis. Suppose, for example, that we used just one category, "food"; then of course, overlap between all species would be 1 because they all eat food. At the opposite extreme, we might treat each food item collected as a different category; in this case, overlap would be 0, because any individual item of prey could find its way into only one bird's stomach. Both extremes are of course ridiculous, but they are the end-points of a logical sequence from the minimum to the maximum possible number of prey categories. The first, "Level 1" analysis I shall use is based on the percentage by weight found in each length-class of the lowest taxa identified. This will give the lowest absolute values of the index because it uses the greatest possible number of categories. Level 2 analysis uses family as the taxon but retains length-classes; Level 3 combines length-classes and uses only Family as a category. The relation between Overlap Index and category number is illus-

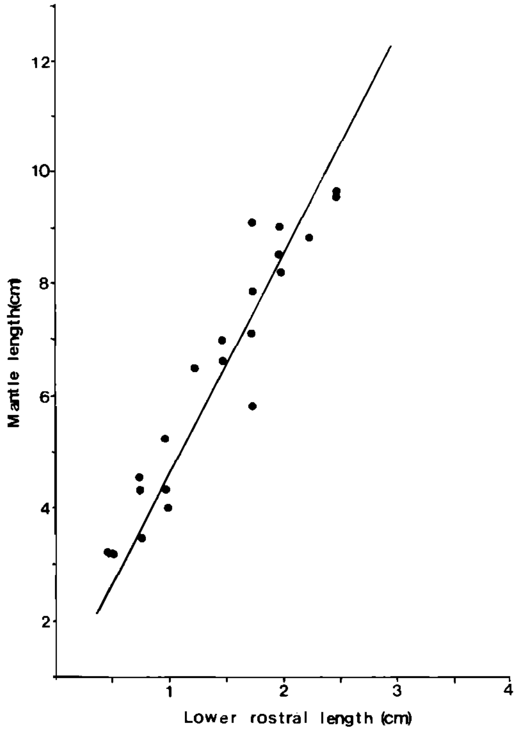

FIGURE 5. Mantle length/beak length relationship in squid (Ommastrephidae) in food samples.

trated in Figure 6; the practical importance of the relationship is that comparisons between indices are valid only if they are measured at the same level. It also invalidates attempts to generalise about the levels of overlap tolerable between co-existing species (Hutchinson 1959, Schoener 1965).

Finally, it is important to note that despite vigorously promulgated arguments to the contrary (e.g., Kohn 1959, MacArthur 1968, Levins 1968), there is no *a priori* relationship between overlap and degree of competition; the value of the overlap index need bear no relation whatever to the competition coefficient.

MEASUREMENT OF DIVERSITY

Species differ in the variety of prey they take; those taking a restricted range are commonly referred to as specialists, those with a wide range as generalists. To express the degree of specialisation on a quantitative scale, I use the Shannon-Weiner information function (Tramer 1969):

$$H' = -\sum_{i=1}^{s} p_i \log p_i$$

where p_i is the proportion of the total prey spectrum belonging to the i th category, and s is the total number of prey categories in the diet sample. S is of course itself a simple measure of the diversity of the diet; H' includes a measure of the relative importance of different prey categories in the diet.

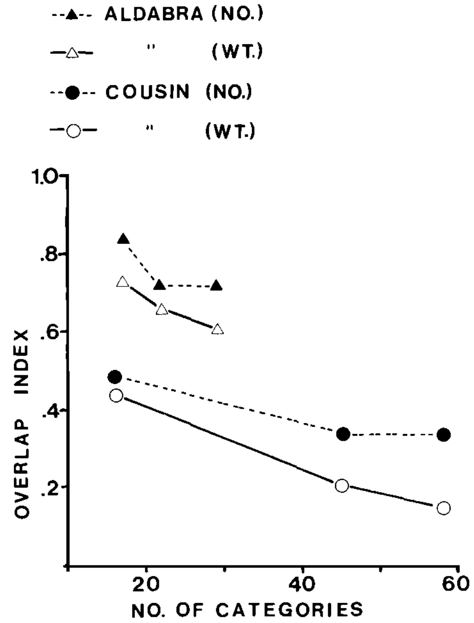

FIGURE 6. Inverse relation between Index of Overlap and number of categories used in comparison (see text for calculation of index).

DESCRIPTION OF STUDY AREAS

THE OCEANOGRAPHIC ENVIRONMENT

Figure 7 shows the location of Aldabra and Cousin in relation to the major currents of the region. Aldabra lies in the path of the westward-flowing South Equatorial current, which flows throughout the year but is stronger during the northwest monsoon (November to March), and is close to an area of upwelling north of Madagascar (Cushing 1975). Pocklington's (1979) maps of surface-water types in the region show that in the northwest monsoon the two islands lie in different water-

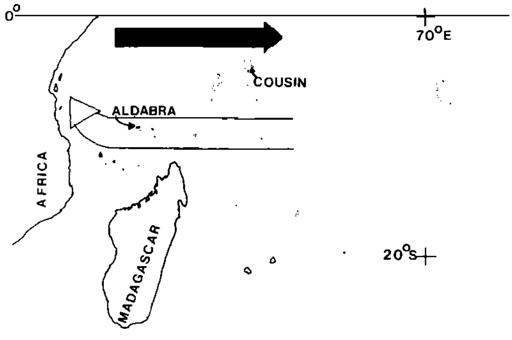

FIGURE 7. Location of Aldabra Atoll and Cousin Island in relation to South Equatorial Current (open arrow) and Equatorial Counter-current (solid black arrow).

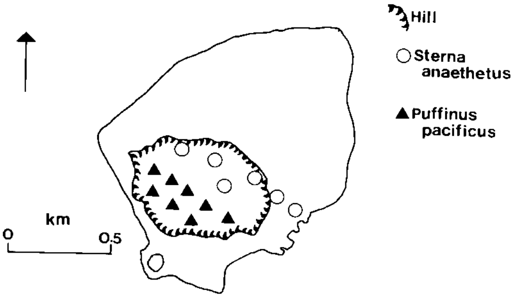

FIGURE 8. Distribution of breeding colonies of Bridled Tern (*Sterna anaethetus*) and Wedge-tailed Shearwater (*Puffinus pacificus*) on Cousin Island. Other seabirds breed in scattered pairs or colonies throughout the island.

types but in the southeast monsoon (April to October), both are near the edge of the same water-type.

A major oceanographic difference between the two islands that is not reflected in either current systems or surface-water types, is that Aldabra is on top of a steep-sided sea mount, causing a very rapid increase in water-depth offshore, whereas Cousin lies on the vast but shallow Seychelles Bank, extending over 120,000 km^2 and rarely exceeding 60 m in depth. Potential feeding areas are therefore much greater for inshore feeders at Cousin, and for pelagic feeders at Aldabra; this difference is likely to influence not only the species composition of the communities, but also the relative abundance of species within them (Diamond 1978).

COUSIN ISLAND

Cousin Island (4°20′S, 55°40′E) is one of the smallest of the central (granitic) islands of the Seychelles archipelago, and is about 1000 km north-east of Aldabra. Its area is about 27 ha and its maximum altitude 69 m above sea level. Most seabirds nest in the dense woodland on the flat plateau and around the coast, but the ground-nesting terns are concentrated in bare rocky parts of the hill and the south coast (Fig. 8). Fuller descriptions were given by Diamond (1975c, 1980a, b).

Cousin's climate is similar to Aldabra's, but the peaks and troughs of rainfall are two to three months earlier on Cousin (December and July, respectively), and Cousin receives about 70% more rain on average (160 cm). Mean monthly temperatures vary from ca 24°C in August and September to ca 26°C in April. The climates of the two islands were compared by Prŷs-Jones and Diamond (In press), who stressed that Cousin lacks a predictably dry time of year comparable to the usual August–October drought on Aldabra. The weather on Cousin during my study (January 1973–January 1975) was not significantly different from the usual pattern.

ALDABRA ATOLL

Aldabra (9°24′S, 46°20′E) lies 420 km northwest of Madagascar and 640 km from the East African coast, in the west tropical Indian Ocean. It is an elevated coral reef, raised 1 to 4.5 m above sea level. Total area is about 365 km^2, about 155 km^2 of which is occupied by land and the rest by lagoon. Aldabra is the largest of a group of raised reefs situated on the summits of undersea mountains about 4000 m high (the others are Assumption, Cosmoledo and Astove); deep blue water is found very close offshore. The atoll has been studied intensively since 1967; this work is reviewed in Westoll and Stoddart (1971) and Stoddart and Westoll (1979). The seabird community was described by Diamond (1971a, b, 1979); here we need note only that tree-nesting seabirds nest almost exclusively in the mangroves fringing the north and east coasts of the central lagoon, and that ground-nesters are confined to the tiny limestone islets scattered around the periphery of the lagoon (Fig. 9). Only the very occasional White Tern or tropicbird (*Phaethon* sp.) attempts to nest on the main islands of the atoll rim, probably because all those islands have been colonised by introduced rats *Rattus rattus*.

Detailed work on particular species or groups was described by Diamond (1974, 1975a, b) and Prŷs-Jones and Peet (1980). Data on diets were summarized in Diamond (1971b, 1974, 1975a, b), where details of ecological segregation between co-existing species should be sought, but are given in more detail here.

Aldabra was described in detail in Westoll and Stoddart (1971) and Stoddart and Westoll (1979). Its climate (Farrow 1971, Stoddart and Mole 1977) is dominated by a marked seasonal change in wind-direction. From April to November winds blow chiefly from the south-east and air temperatures reach their minimum (in July) of about 22°C; in January and February winds are chiefly from the north-west, temperatures rise to a maximum (in February) close to 32°C, and the heaviest rains fall. Intervening months have light but variable winds and intermediate temperatures. The driest months are August to October. Mean annual rainfall is about 941 cm (Stoddart and Mole 1977), and the annual range in mean monthly temperature is about 4°C.

An important feature of the weather during my study (Sep. 1967–Mar. 1968, Mar.–Sep. 1969) was an exceptional failure of the rains in January and February 1968; the total rainfall in those months (3.99 cm) was one-tenth of the average and less than one-third of the lowest value for those two months in any other year.

THE SEABIRD COMMUNITIES

COUSIN ISLAND

Fewer species breed on Cousin than at Aldabra (Table 1), which is not surprising in view of the very much smaller size of the island; what is surprising is the enormous number of individuals, amounting to around one third of a million birds per year. This profusion of seabirds is accounted for chiefly by the enormous population of tree-nesting Black Noddies (*Anous tenuirostris*); to put the size of this colony into a temperate perspective, it is more than twice the entire British breeding population of Lesser Black-backed Gulls (*Larus fuscus*).

Approximate seasonality of laying in relation to climate of the Cousin seabirds is shown in

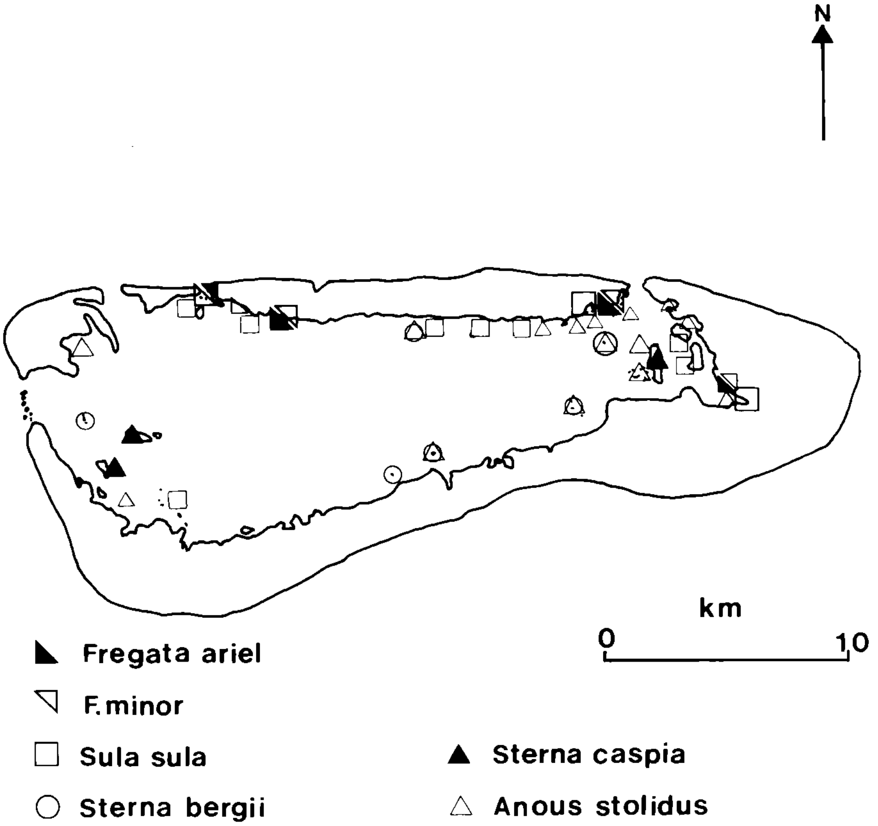

FIGURE 9. Distribution of breeding colonies of seabirds on Aldabra Atoll. Symbol sizes indicate relative sizes of colonies within each species. Locations shown have been used at one time between 1967 and 1976 but not necessarily in same season. Tropicbirds (*Phaethon* spp.) and Audubon's Shearwater (*Puffinus lherminieri*) and Black-naped Terns (*Sterna sumatrana*) breed on islets scattered throughout lagoon, and Fairy Terns (*Gygis alba*) scattered among the northern mangroves. Note restriction of breeding sites to coastal (mangrove) areas and lagoon islets.

Figure 10. The most notable difference between these and Aldabra breeding seasons is in the concentration of laying by terns in the south-east monsoon (April to October), a time generally avoided by Aldabra terns (Diamond 1971a, Diamond and Prŷs-Jones, in prep.). Such an "average-year" diagram cannot, of course, adequately reflect a synchronous but non-annual regime such as that of the Bridled Tern *Sterna anaethetus* on Cousin (Diamond 1976).

ALDABRA

The Aldabra community (Table 1) is similar to those at other major seabird breeding stations in the region, such as Aride (Seychelles), Cargados Carajos or St. Brandon, and the Chagos archipelago, both in the number of species involved and in the predominance of pelecaniforms and terns and the paucity of procellariids. Approximate laying periods are shown, in relation to climate, in Figure 11; breeding seasonality has not been fully studied elsewhere in the region, other than on Cousin, but the data available do suggest that in other breeding stations, laying is restricted more sharply to the dry, cool and windy months of the southeast monsoon. Bailey's (1972) analysis of breeding seasons in the region was based on quite inadequate data and does not inspire confidence; Aldabra seabirds, for example, are quoted there as showing "continuous breeding throughout the year" although this applies to only two of the 11 species concerned.

The Cousin community is dominated by terns, with a substantial population of procellarids and only one pelecaniform; the Aldabra community, by contrast, has smaller tern populations but a rich assortment, and large populations, of pelecaniforms. Large pelecaniforms have suffered greatly

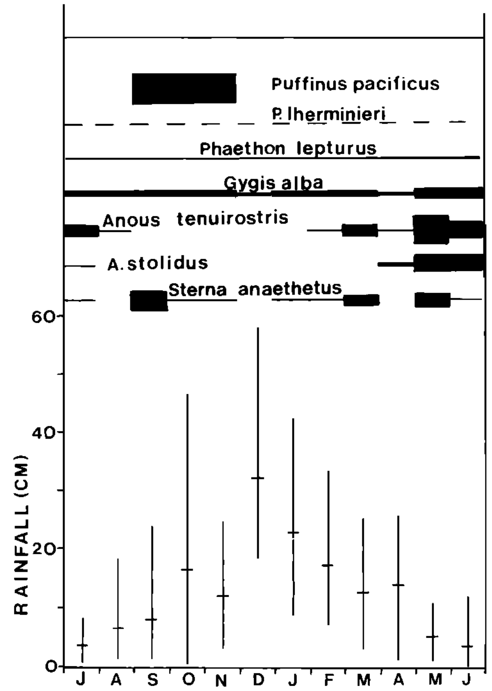

FIGURE 10. Seabird laying seasons in relation to rainfall on Cousin Island. Rainfall data from Prŷs-Jones and Diamond (In press). Depth of solid line indicates degree of restriction to months shown.

from human persecution in the region, and may well have been part of the Cousin community before the Seychelles were settled by man little over 200 years ago (Diamond and Feare 1980). Great and Lesser Frigatebirds (*Fregata minor* and *F. ariel*) are now only nonbreeding visitors, Red-footed and Brown Boobies (*Sula sula* and *S. leucogaster*), and Red-tailed Tropicbirds (*Phaethon rubricauda*), occasional vagrants.

RESULTS

Data on the proportion of each prey category in the diets of all species sampled on Cousin and Aldabra (Tables 2 and 3, respectively) allow analysis of three diet characteristics separately: number of items; length-class of items; and weight of items. Data on numbers are presented chiefly for comparison with other studies, where number is perhaps the most widely-used prey characteristic; however, it tells nothing of the likely relative amount of nutrition contributed by a prey item, which is better indicated by its weight. The presentation of diet data in Tables 2 and 3, which also show the proportion by weight of food in each length-class of each taxon identified, gives the fullest possible picture of the likely relative importance of each size-class of each prey taxon. Yet it can also be analysed in progressively simpler ways, by combining taxonomic and length categories, for comparison with other sets of data.

COUSIN ISLAND

Analysis by percent number of items can give a very different picture from analysis according to percent weight of items (Table 2). The former method, for example, suggests that 8–10 cm squid are an insignificant part of *Gygis alba*'s diet—only 4%—but the latter shows they account for over 31% of prey items by weight. Over half the items identified in *Sterna anaethetus* samples were the marine insects *Halobates micans* and *H. garmanus*, but these are so light that they contributed less than 4% by weight.

Each bird species took a relatively low proportion of the total dietary range of the community as a whole; only *Gygis* took more than half of the taxonomic categories represented in this sample of the community's diet, and the other three tern species took strikingly restricted diets. The tropicbird *Phaethon lepturus* took a notably different range of food from the terns, but this was manifest chiefly as a wider size range rather than different taxa. The two *Anous* terns took similar taxa but the larger *A. stolidus* took larger items; the difference between them was greater than the table suggests, because the numerous unidentified and unmeasured small fish larvae common in *A. tenuirostris* samples, not shown in the body of Table 2 (but see footnotes), were not found in *A. stolidus*. The most striking similarity is between two non-congeners, *A. tenuirostris* and the Bridled Tern *Sterna anaethetus*; both concentrated on young red mullets *Upeneus* sp. and on the unidentified fish larvae, and although *Sterna* took significant numbers of *Halobates*, and *Anous* a number of squid, neither of these prey classes contributed much in terms of weight.

Overlap indices (Table 4) calculated from the data in Table 2 quantify the impressions described above; the extremely similar diets of the *Sterna* and *A. tenuirostris* are reflected in the 96% overlap between them. The tropicbird is very distinctive, with little overlap with terns except for *Gygis*; its diet is sufficiently different from that of the terns to justify recognising two separate guilds, one of surface-feeding terns feeding chiefly inshore, and the other consisting of more far-ranging plunge-divers, represented on Cousin now only by the tropicbird.

ALDABRA

Some differences exist between the percent number and percent weight analyses of Aldabra

TABLE 1
SEABIRD COMMUNITIES OF COUSIN AND ALDABRA

Species	Number breeding pairs	
	Cousin	Aldabra
Wedge-tailed Shearwater *Puffinus pacificus*	30–35,000	–
Audubon's Shearwater *Puffinus lherminieri*	(few hundred?)	not counted
White-tailed Tropicbird *Phaethon lepturus*	(ca. 1,000?)	2,350
Red-tailed Tropicbird *P. rubricauda*	–	2,500+
Red-footed Booby *Sula sula*	–	6,000–7,000
Great Frigatebird *Fregata minor*	–	2,000
Lesser Frigatebird *F. ariel*	–	6,000
Caspian Tern *Sterna caspia*	–	10
Crested Tern *Sterna bergii*	–	60
Bridled Tern *Sterna anaethetus*	(few hundred)	–
Black-naped Tern *S. sumatrana*	–	70
White Tern *Gygis alba*	10,000	10,000
Brown Noddy *Anous stolidus*	3,000	1,500
Black Noddy *A. tenuirostris*	110,000	–

seabirds (Table 3), but they are much less marked than on Cousin and affect mostly the relative importances of middle-sized flying-fish (Exocoetidae) and squid (Ommastrephidae). The Aldabra seabirds each take a higher proportion of the total taxonomic range of the community's diet, none taking less than 25% of the total dietary range and all but one taking over 40%. There are two pairs of congeners in this sample; the two frigatebirds have very similar diets, separable statistically only if analysed seasonally, whereas the two tropicbirds are clearly separated, especially by size of prey (for detailed discussion of these two cases, see Diamond (1975 a, b)). The smaller tropicbird *P. lepturus* differs clearly from the other species, though it is not as distinctively different from them as it is from the terns on Cousin. Only one tern (*Anous stolidus*) is shown in Table 3, and that in only summary form (see footnotes); the very few samples from other terns are listed in the footnotes. In spite of the small sample size, *A. stolidus* is clearly quite different in its diet from the other species, with a high proportion of Gempylidae and Pomatomidae, both families taken rarely or not at all by the other species. These data support the naturalist's intuitive recognition of distinct feeding guilds: the pelagic feeders, ranging far out to sea and taking chiefly flying-fish and flying squid Ommastrephidae; and the terns, feeding chiefly from the surface and much closer to the shore and taking a different range of fish. *A. stolidus* clearly belongs to the second, inshore-feeding guild, and while *P. lepturus* is clearly part of the pelagic guild it is certainly the most distinctive in its diet.

The overlap indices calculated for Aldabra seabirds (Table 5) average strikingly higher than those for Cousin—the overall mean is over three times that of Cousin—and *P. lepturus* is again set apart from the others by a low measure of overlap. The two congeneric pairs are strikingly different in index value (*Fregata* 94%, *Phaethon* 36%).

COMPARISON OF DIETARY OVERLAP

Overlap indices were compared for Cousin and Aldabra at levels 1 (each length class of lowest taxon identified), 2 (each length-class in each family) and 3 (each family only), using both per-

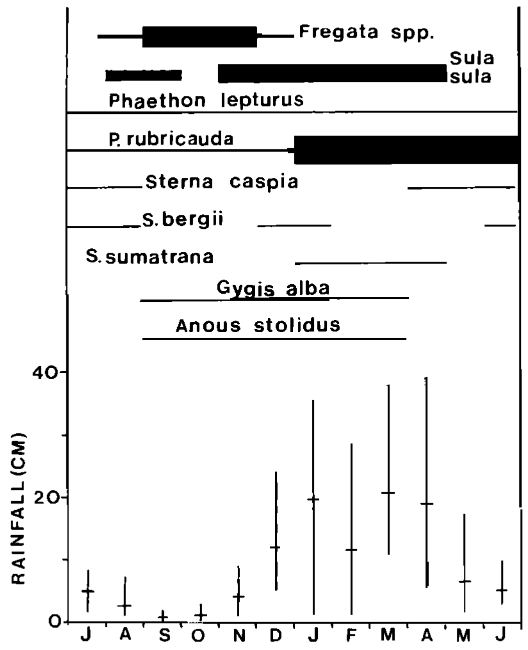

FIGURE 11. Seabird laying seasons in relation to rainfall on Aldabra Atoll. Rainfall data from Prŷs-Jones and Diamond (In press). Depth of solid line indicates degree of restriction to months shown.

cent number and percent weight at each level (Table 6). The figures shown are the mean and one standard deviation of all the species in the community from which diet samples were presented in Tables 2 and 3, and were calculated from those data. Standard deviation is shown simply as a familiar guide to the amount of variation around the mean and is not intended as a statistically rigorous measure.

Several trends are apparent. Overlap is considerably higher between species on Aldabra than on Cousin, by a factor averaging about 2.3. Within the inshore/surface-feeding/tern guild on Cousin, overlap is also higher than within the community (i.e., the terns themselves plus the tropicbird) as a whole. Within both communities, overlap indices are higher in relation to number than to weight, suggesting that prey size is an important component of segregation between species. Indices also show a clear relationship with the level of analysis; this is predictable from first principles (see METHODS), but may also reflect the importance of segregation by prey size.

Overlap in weight

Prey weight may be an important component of segregation between co-existing species (Table 6). To examine this relationship further, I plotted the distribution of weight of prey for each bird species (Fig. 12) and calculated overlap indices for weight-classes alone, irrespective of taxonomy or length-class (Table 7). Close comparison of the data in Table 7 with those in Tables 4 (Cousin) and 5 (Aldabra) shows that Cousin species overlap rather more, on average, by weight than in the level 1 analysis (as expected), but with one striking exception; *Sterna anaethetus* and *Anous tenuirostris,* which overlap by 96% overall, are much more clearly segregated by weight of prey (overlap 38%), reflecting the preponderance of very light *Halobates* in *Sterna*'s diet. Aldabra species are no more or less clearly segregated by prey weight than by the combined characteristics of their prey.

Overlap in prey length

The length of an item may be important independently of its bulk, for example in influencing its catchability, so the distribution of prey lengths in a seabird's diet is of interest. These distributions, and their associated overlap indices, for both Cousin and Aldabra (Table 8), are totally independent of weight. Cousin species tend to overlap less than Aldabra species and, on Cousin, the terns overlap more with each other than with the community as a whole.

Conclusions on dietary overlap

This analysis of diet overlap in these two samples of two seabird communities leads to several questions and tentative conclusions which can be explored further by comparison with other communities:

(1) At both localities, at least one species seems to be quite distinct in its diet from most of the others sampled. This suggests that feeding guilds, which are apparent in the field, can also be reflected in the distribution of indices of overlap calculated from suitably-expressed analyses of food samples. But in both cases, all but one or two species sampled belong to the same guild, and the number of species sampled is too small to support this conclusion unequivocally. The clarity of the feeding-guild concept is also obscured by the close correspondence between taxonomic and ecological criteria; the pelagic-feeding "guild" at Aldabra comprises pelecaniforms, whereas the inshore-feeding guild there and at Cousin are larids.

(2) Overlap within a guild is higher than the mean overlap averaged over all the species.

(3) Overlap between Aldabra species is consistently higher than that between Cousin species (at equivalent levels of analysis). The Aldabra species are large-bodied pelecaniforms, feeding mostly in the pelagic zone, some (the booby and

TABLE 2
Percentage Composition of Food Samples from Cousin Island Seabirds

Taxon	Length class (cms)	*Gygis alba*		*Sterna anaethetus*[a]		*Anous tenuirostris*[a]		*Anous stolidus*		*Phaethon lepturus*	
		No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
EXOCOETIDAE	0–2			1.7	1.9						
	4.1–6	2.7	1.0							4.3	0.4
	8.1–10	1.3	3.6							4.3	2.5
	10.1–12							2.3	29.5		
	12.1–14									2.1	4.2
	14.1–16									4.3	13.4
	16.1–18									4.3	19.4
	?									8.5	
Evolantia micropterus	4.1–6	1.3	0.5								
Parexocoetus brachypterus	2.1–4	1.3	0.04								
	8.1–10	4.0	10.7							2.1	1.3
Cypselurus furcatus	0–2					0.6	0.2				
	2.1–4					1.6	1.0				
	4.1–6							2.3	2.4	2.1	0.2
	8.1–10	2.7	7.1							2.1	1.3
	10.1–12									2.1	2.2
Cypselurus sp.	6.1–8	1.3	1.3					2.3	5.9		
	8.1–10	1.3	3.6							1.1	0.6
	10.1–12									5.3	5.6
C. nigripennis	6.1–8	1.3	1.3								
	8.1–10	1.3	3.6								
HEMIRHAMPHIDAE	10.1–12	1.3	2.9								
	16.1–18									2.1	1.9
? *Hemirhamphus far*	8.1–10	1.3	2.3								
Hemirhamphus sp.	10.1–12	1.3	2.9								
Hyporhamphus sp.	4.1–6	1.3	1.4								
	10.1–12	1.3	2.9								
CARANGIDAE											
Selar crumenophthalmus	4.1–6	1.3									
	6.1–8	1.3									
CARANGIDAE											
Decapterus maraudsi	4.1–6	1.3	4.2					4.6	39.3		
	8.1–10	1.3	8.8								
	10.1–12									2.1	3.7
	12.1–14									4.3	10.4
	14.1–16									2.1	7.5
SCOMBRIDAE[b]	2.1–4	1.3	0.4								
	4.1–6	1.3	0.7								

TABLE 2
CONTINUED

Taxon	Length class (cms)	*Gygis alba*		*Sterna anaethetus*[a]		*Anous tenuirostris*[a]		*Anous stolidus*		*Phaethon lepturus*	
		No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
MULLIDAE											
Upeneus sp.	0–2	2.7	0.04	15.6	8.4	4.9	0.9				
	2.1–4	40.0	3.8	22.5	72.5	60.1	67.3	34.1			
	4.1–6	13.3	5.6	0.6	8.4	23.5	26.3	54.6			
	?					4.9					
HOLOCENTRIDAE[c]	2.1–4	1.3	0.3								
STROMATEIDAE[d]	4.1–6	1.3									
TETRAODONTIDAE[e]	0–2			3.5	0.4						
BELONIDAE	8.1–10			1.7	4.4						
	14.1–16									2.1	1.5
	?									2.1	3.3
BALISTIDAE	2.1–4									2.1	0.01
BLENNIDAE[f]	16.1–18									2.1	8.9
COELENTERATA											
Velella	2.1–4	1.3									
Others		2.7									
SQUID	0–2					0.6	0.1				
	2.1–4					1.1	1.6				
	4.1–6					0.6	2.6			21.3	1.9
	6.1–8									2.1	1.6
	8.1–10	4.0	31.3							4.3	7.5
	?					2.2					
INSECTA											
Halobates				51.5	3.6						
CRUSTACEA-CRABS				2.9							
Number of samples		49		38		57		19		43	
Number of items		105		308		577		83		77	
Percentage of taxonomic categories		78		26		13		17		43	

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[a] Not including over 230 undetermined juvenile fish (mostly 41–60 mm long) in *Anous tenuirostris* samples, and 42 from *Sterna anaethetus*.

[b] *?Rastrelliger* sp.

[c] *Holocentrus* sp.

[d] *?Hyperoglyphe* sp.

[e] *?Arothron* sp.

[f] *Xiphasia setifer*.

TABLE 3
PERCENTAGE COMPOSITION OF FOOD SAMPLES FROM ALDABRA SEABIRDS

Taxon[a]	Length class (cms)	*Fregata ariel* No.	*Fregata ariel* Wt.	*Fregata minor* No.	*Fregata minor* Wt.	*Sula sula* No.	*Sula sula* Wt.	*Phaethon rubricauda* No.	*Phaethon rubricauda* Wt.	*Phaethon lepturus* No.	*Phaethon lepturus* Wt.	*Anous stolidus* No.[bc]
EXOCOETIDAE		53.6	—	65.9	—	72.1	—	45.6	—	14.9	—	8.3
Exocoetus volitans	5.1–10	7.9	2.5	1.9	0.4					3.6	3.0	
	10.1–15	15.0	19.7	16.7	16.0	19.7	16.0	3.1	3.1	3.6	4.8	
	15.1–20	2.4	5.7	13.0	17.0	8.2	9.6					
	20.1–25								3.1	9.3		
Cypselurus furcatus	5.1–10	3.1	0.8			1.6	0.2			7.1	2.5	
	10.1–15	5.5	5.2	1.9	2.1	9.8	8.2	9.4	7.5			
	15.1–20	13.4	32.8	16.7	30.6	34.4	52.9	25.0	41.2			
	20.1–25	0.8	2.7	1.9	5.4							
Evolantia micropterus	5.1–10	0.8	1.5							3.6	3.9	
	10.1–15	3.9	3.8	3.7	5.2							
	15.1–20	1.6	3.2	1.9	2.8	1.6	1.5					
HEMIRHAMPHIDAE		0.4		0.3	2.9	2.5	5.0	0.9	2.1	1.8		2.3
ZANCLIDAE		4.0		2.4				3.1				
GEMPYLIDAE										7.0		37.9
TYLOSURIDAE		0.8	0.4					3.1	2.4			
BELONIDAE		0.3						6.1				3.0
CARANGIDAE	10.1–15	4.1	4.6					2.6				0.8
SCOMBRIDAE	10.1–15	0.7						1.8		0.9		1.5
STROMATEIDAE								0.9				
CORYPHAENIDAE										0.9		
GONORHYNCHIDAE										14.0		
HOLOCENTRIDAE												7.6
POMATOMIDAE												18.2
"Species A"		0.4		3.6								
"Species B"												5.3
OCTOPODA[d]								6.3	7.2			
SQUID		39.4		27.8		25.4		42.1		60.5		15.2
OMMASTREPHIDAE	1–4	1.6	0.1	1.9	0.1	1.6	0.1	0		7.1	0.8	
	4.1–8	26.8	14.0	22.2	10.5	16.4	3.5	18.8	3.6	53.6	45.7	
	8.1–12	13.4	3.2	14.8	7.0	3.3	2.9	28.1	23.5	17.9	39.3	
Number of samples		179		79		78		61		35		19
Number of items		668		334		197		114		114		132
Number of taxonomic categories		12		8		5		11		9		10

[a] Family entries include all items referrable to that family, irrespective of condition. Since some could not be identified to genus, nor measured, there is no entry under "weight," and the total percent number differs from the total under "% No." of individual species.

[b] So many specimens from *Anous stolidus* were well-digested larval fish that could not be identified even to family, nor put reliably into a size-class, that their analysis by weight and length was not attempted. Data on % number are presented for superficial comparison with other Aldabra species, and for comparison with samples from the same species on Cousin.

[c] Also not shown are the few fish regurgitated by other terns: Crested Tern *Sterna bergii*: 1 Acanthuridae (possibly *Acanthurus strigosus*); 4 Labridae (1 *Novaculichthys* sp., 1 *N. macrolepidotus*, 1 ? *N. taeniorus*, 1 *Cheilio inermis*). Black-naped Tern *Sterna sumatrana*: 4 Atherinidae (possibly *Atherina breviceps*); 3 Stolephoridae (*Spratelloides delicatulus*).

[d] *Tremoctopus violaceus*.

TABLE 4
OVERLAP IN DIET OF COUSIN ISLAND SEABIRDS (LEVEL 1 ANALYSIS)

	G.a.	*S.a.*	*A.t.*	*A.s.*	*P.l.*
Gygis alba		.09	.12	.14	.23
Sterna anaethetus			.96	.19	.00
Anous tenuirostris				.24	.00
Anous stolidus					.00
Mean	.15	.31	.33	.14	.06
Overall mean: 0.20 ± 0.28 (Terns only: 0.29 ± 0.33).					

G.a. = Gygis alba, S.a. = Sterna anaethetus, A.t. = Anous tenuirostris, A.s. = Anous stolidus, P.l. = Phaethon lepturus.

TABLE 5
OVERLAP IN DIET OF ALDABRA SEABIRDS (LEVEL 1 ANALYSIS)

	F.a.	*F.m.*	*S.s.*	*P.r.*	*P.l.*
Fregata ariel		.94	.88	.74	.31
Fregata minor			.86	.73	.33
Sula sula				.83	.11
Phaethon rubricauda					.36
Mean	.72	.72	.67	.67	.28
Overall mean: 0.61 ± 0.30					

F.a. = Fregata ariel, F.m. = Fregata minor, S.s. = Sula sula, P.r. = Phaethon rubricauda, P.l. = Phaethon lepturus.

TABLE 6
OVERLAP INDEX OF SEABIRD DIETS ACCORDING TO LEVEL OF ANALYSIS

	Aldabra				Cousin			
	Weight		Number		Weight		Number	
Analysis	$\bar{x}$	±SD	$\bar{x}$	±SD	$\bar{x}$	±SD	$\bar{x}$	±SD
Level 1:								
All spp.:	.61	.28	.72	.16	.15	.14	.34	.33
Terns:					.21	.13	.55	.25
Level 2:								
All spp.:	.66	.30	.72	.19	.21	.26	.34	.32
Terns:					.29	.31	.55	.24
Level 3:								
All spp.:	.73	.30	.84	.17	.44	.33	.49	.35
Terns:					.46	.29	.74	.18

both tropicbirds) by plunge-diving, others (the two frigatebirds) by surface dipping. The Cousin species are mostly terns, feeding almost certainly over the shallow waters of the Seychelles Bank, by surface dipping or plunging to surface—only the tropicbird does not belong to this guild. Is the difference in overlap between these two "communities" one that refers to the two communities, or to these two different guilds? (see Discussion).

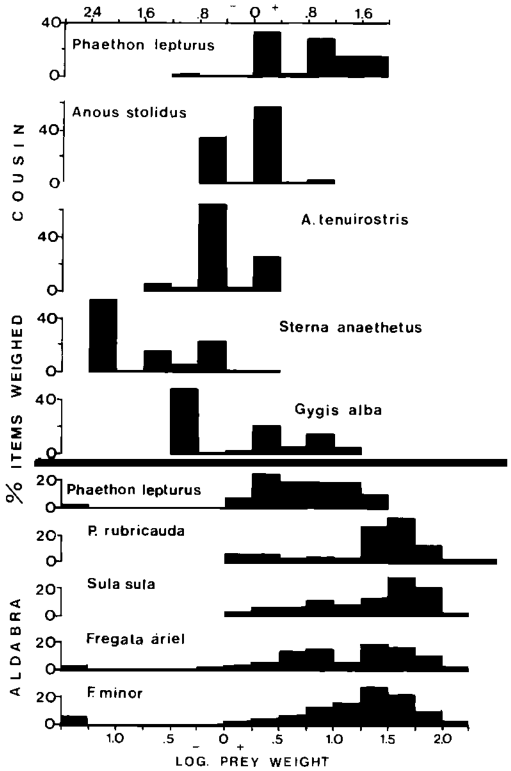

FIGURE 12. Number of prey items in each Log weight-class of Aldabra and Cousin seabirds.

DIET DIVERSITY

Diversity is highest at the highest level of analysis, and there is relatively little difference between the two sets of samples although on average those from Cousin are slightly more diverse (Table 9). Note that the higher number of categories represented in the diet of Cousin birds is partly a reflection of the use in Cousin data of a 2-cm length-class rather than the 5-cm class used for the larger prey taken by the Aldabra species. The number of families of prey represented is an unbiased guide to the possible influence of sample size on diversity index, and is similar in the two communities.

TABLE 7
OVERLAP IN WEIGHT-CLASSES OF PREY TAKEN BY ALDABRA AND COUSIN SEABIRDS[a]

Cousin	*G.a.*	*S.a.*	*A.t.*	*A.s.*	*P.l.*
Gygis alba		.08	.15	.35	.52
Sterna anaethetus			.38	.21	.11
Anous tenuirostris				.79	.24
Anous stolidus					.60
Mean:	.28	.17	.39	.49	.34
Overall mean: .33 ± .25					
Aldabra	*F.a.*	*F.m.*	*S.s.*	*P.r.*	*P.l.*
Fregata ariel		.91	.88	.94	.67
Fregata minor			.87	.88	.52
Sula sula				.90	.44
Phaethon rubricauda					.32
Mean:	.85	.80	.77	.76	.49
Overall mean: .73 ± .23					

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[a] Calculations made on log-transformed weights. In each community, total range of weights covers four orders of magnitude.

TABLE 8
OVERLAP IN LENGTH-CLASSES OF PREY TAKEN BY ALDABRA AND COUSIN SEABIRDS

Cousin[a]	G.a.	S.a.	A.t.	A.s.	P.l.
Gygis alba		.57	.91	.93	.58
Sterna anaethetus			.64	.41	.12
Anous tenuirostris				.83	.29
Anous stolidus					.60
Mean:	.75	.44	.67	.69	.40
Overall mean: .58 ± .26					
Aldabra	**F.a.**	**F.m.**	**S.s.**	**P.r.**	**P.l.**
Fregata ariel		.93	.81	.93	.83
Fregata minor			.96	.98	.61
Sula sula				.93	.44
Phaethon rubricauda					.57
Mean:	.87	.87	.79	.85	.61
Overall mean: .80 ± .19					

[a] Cousin length-classes 2 cm, Aldabra 5 cm. Initials as in Tables 4 and 5.

Thus, the striking contrast between the two communities in amount of dietary overlap is not reflected in the diversity of individual species' diets within the two communities.

DISCUSSION

There are very few analyses of the diets of significant proportions of any seabird community with which to compare these results. Even the pioneering studies by Ashmole and Ashmole (1967) and Pearson (1968) were not presented in sufficient detail for a level one or two analysis; they must be compared at level three, i.e., proportion in each prey family, and by number not by weight because although Pearson gave weight data in suitable form, the Ashmoles did not. These comparisons are therefore at the very crudest level, where overlap values are all biased upwards.

CHRISTMAS ISLAND, PACIFIC OCEAN

Like my study of Aldabra, the Ashmoles' work on Christmas covered only a segment of the seabird community, but the two studies are complementary in that I studied chiefly the larger pelecaniforms on Aldabra and the Ashmoles did not cover this part of the Christmas community (except for the Red-tailed Tropicbird, *Phaethon rubricauda*). Fortunately, three of the large pelecaniforms of Christmas have since been studied by Schreiber and Hensley (1976), whose data have been incorporated with the Ashmoles' to give as complete a picture of Christmas Island seabird diets as is possible. Schreiber and Hensley's data are important in rounding-off this picture; there are still gaps (18 seabird species breed on Christmas but only 11 have had their diets sampled) but this community is now the best-known, in relation to diet, of any seabird community in the tropics.

The mean overall index of overlap between

TABLE 9
DIVERSITY OF DIET OF COUSIN AND ALDABRA SEABIRDS

	From percentage composition by weight			
	Level 1	Level 2	Level 3	$\bar{x}$
Cousin				
Gygis alba	3.59	2.82	2.24	2.88
Sterna anaethetus	1.44	1.41	0.64	1.16
Anous tenuirostris	1.28	1.28	0.24	0.93
Anous stolidus	2.13	2.12	1.55	1.93
Phaethon lepturus	3.79	3.61	2.05	3.15
Mean:	2.45	2.25	1.34	1.85
No. categories:	49	36	13	33
No. prey families:	17	17	17	
Aldabra				
Fregata ariel	3.03	2.22	0.99	2.08
Fregata minor	2.90	1.82	0.87	1.86
Sula sula	2.18	1.46	0.62	1.42
Phaethon rubricauda	2.48	2.38	1.46	2.11
Phaethon lepturus	1.78	1.72	0.59	1.36
Mean:	2.47	1.92	0.91	1.77
No. categories:	19	12	7	
No. prey families:	18	18	18	

TABLE 10
Overlap in Diet of Christmas Island Seabirds (Level 3 Analysis)[a]

	S.d.	*S.s.*	*F.m.*	*P.r.*	*P.n.*	*P.a.*	*S.f.*	*A.s.*	*A.t.*	*G.a.*	*P.c.*
Sula dactylatra		.79	.59	.50	.41	.18	.48	.62	.31	.27	.14
Sula sula			.96	.92	.85	.47	.82	.61	.33	.29	.31
Fregata minor				.99	.94	.84	.86	.48	.27	.25	.35
Phaethon rubricauda					.95	.86	.86	.44	.25	.23	.22
Puffinus nativitatis						.83	.90	.44	.40	.30	.37
Pterodroma alba							.66	.17	.11	.10	.33
Sterna fuscata								.64	.44	.34	.53
Anous stolidus									.60	.47	.37
Anous tenuirostris										.78	.38
Gygis alba											.20
Mean:	.46	.63	.65	.62	.64	.46	.65	.48	.39	.32	.33

Overall mean: .51 ± .26
Within-guild means: Pelagic squid-eaters—.85 ± .13
Non squid-eaters (mostly inshore)—.42 ± .19
Terns (excluding *S. fuscata*)—.47 ± .20.

[a] Sources: Ashmole and Ashmole (1967) (Appendix 3 & 4); Schreiber and Hensley (1976).

Christmas Island seabirds is 51% (Table 10), very close to the 49% of Cousin but substantially lower than the 84% of Aldabra (Table 6). The matrix of overlap indices shows a clear separation into species overlapping with each other by 80% or more and those with much lower indices. High-overlap species (*Sula sula, Fregata minor, Phaethon rubricauda, Puffinus nativitatis, Pterodroma alba,* and *Sterna fuscata*) are an ecologically coherent group of pelagic-feeding species; the remainder, all terns, feed closer inshore (Ashmole and Ashmole 1967). There remain anomalies; *Pterodroma alba* fits less comfortably in the pelagic guild than the others, overlapping much less with *Sula sula* and *Sterna fuscata* than with other species. The most striking anomaly, though, is the Masked Booby (*Sula dactylatra*) which is certainly a far-ranging pelagic feeder, but is not identified in this overlap matrix as a member of this guild. The overlap matrix has evidently sorted species which take a significant proportion (by number in this case) of squid, from those that do not; Masked Boobies take a very much smaller proportion of squid than Red-footed Boobies, not only in this Christmas Island sample but also, apparently, throughout most of the species' range (e.g., Murphy 1936). Yet they feed in the same waters as other species that do take squid frequently (notably Red-foots, two frigates, and two tropicbirds). Why do they too not take squid? The answer appears to lie in the size range of their prey items. They take much larger fish than either Red-foots or frigatebirds; over two-thirds of Masked Booby prey were over 11 cm long, whereas two-thirds of both Red-foot and frigatebird prey were shorter than 11 cm (Schreiber and Hensley 1976); but of 1561 squids measured from seabird stomachs on Christmas, only 5 (0.32%) were longer than 10 cm (Ashmole and Ashmole 1967, Appendix 2b). Whether or not Masked Boobies also discriminate taxonomically against squid in their diet, their size preference alone would lead them to take very few squid because the squid available to seabirds are evidently smaller than most of the prey the boobies take. (Albatrosses of course take much larger squid, but often scavenge them, and at any rate use very different feeding techniques from the tropical seabirds considered here). This seems to be a case of a discrimination based on size having a taxonomic consequence on the composition of the diet; this makes an interesting comparison with the opposite condition of a taxonomic discrimination, also based on squid, having a consequence for the size of prey in the diet (Lesser Frigatebird, *Fregata ariel,* on Aldabra; Diamond 1975b).

The Christmas Island overlap matrix (Table 10), interpreted in relation to the original data (Ashmole and Ashmole 1967, Schreiber and Hensley 1976) suggests that the seabird community can be divided into two groups according to the proportion of squid in the diet, rather than on the basis of feeding range. The correlation between the two is close and only one species (Masked Booby) would change groupings according to the criterion adopted. If we equate groupings within the overlap matrix with the ecological concept of a feeding guild, the matrix would suggest that we recognise a squid-eating guild and a non-squid-eating guild rather than a pelagic and an inshore one. Note that if this were to be the criterion adopted, it would be much better to obtain and use data on the proportion

TABLE 11
OVERLAP IN LENGTH-CLASSES OF PREY TAKEN BY CHRISTMAS ISLAND, PACIFIC OCEAN SEABIRDS

(a) From Ashmole and Ashmole (1967)

	P.r.	*P.n.*	*P.a.*	*S.f.*	*A.s.*	*A.t.*	*G.a.*	*P.c.*[a]
Phaethon rubricauda		.58	.63	.78	.73	.24	.53	.09
Puffinus nativitatis			.97	.85	.96	.66	.95	.20
Pterodroma alba				.96	.98	.56	.93	.26
Sterna fuscata					.97	.47	.85	.26
Anous stolidus						.54	.93	.24
Anous tenuirostris							.75	.91
Gygis alba								.45
Mean:	.51	.74	.75	.74	.76	.59	.77	.34
Overall mean: .65 ± .29								

(b) From Schreiber and Hensley (1976)

	S.d.	*S.s.*	*F.m.*[b]
Sula dactylatra		.52	.46
Sula sula			.84
Mean:	.49	.68	.65
Overall mean: .61 ± .20			

[a] *P.c.: Procelsterna cerulea.*

[b] *F.m.: Fregata minor.*

by weight of squid in the diet, rather than the proportion by number used perforce in this analysis.

The overlap in length of prey items in the diets of Christmas Island seabirds (Table 11) averages 65% in the species studied by the Ashmoles (1967), and 75% in those described by Schreiber and Hensley (1976). These two figures cannot be compared directly, nor can pelagic (or squid) feeders be taken from the Ashmoles' data and combined with Schreiber and Hensley's because these two studies used different size-classes (2 cm and 5 cm, respectively). Nor can overlap in length be said to exceed that in taxonomic classes (Table 10), because the number of categories is so different in the two. A more valid comparison is between these length-overlap figures and those for Cousin and Aldabra (Table 8). The slight difference suggested in the Christmas Island figures (large pelecaniforms perhaps overlapping more than the smaller species) is in the same direction as the difference between Cousin and Aldabra, but the trend is a slight one.

GUILD DIFFERENCES IN OVERLAP

Three tentative questions were raised above (Conclusions on dietary overlap) regarding the apparent differences between degrees of overlap on Cousin and Aldabra. These differences could not be ascribed confidently to inter-community or inter-guild phenomena, because each "community" studied was a sample dominated by a single guild. The comparison with Christmas Island is fruitful because the sample now available for that community includes reasonable numbers of species in two guilds, and therefore illuminates the three problems raised above:

(1) The guild concept is clarified as a reality within a community; two such guilds can be recognised within the Christmas community, corresponding closely with the guild studied on Aldabra (pelagic-feeding squid-eaters) on the one hand, and that on Cousin (more inshore-feeding terns, taking very few squid) on the other.

(2) Overlap is not consistently higher within a guild than within the overall community. On Christmas, overlap within the non-squid-eaters (42%) is lower than the overall average (51%) but that in the squid-eating guild is higher (85%).

(3) The higher overlap on Aldabra, compared with Cousin, is consistent with a guild difference between the two samples, rather than an overall difference between the two communities. The high overlap among the Aldabra species is repeated among the pelagic squid-eaters of Christmas, and the lower overlap between the terns of Cousin is similar to that between the terns (except the squid-eating pelagic Sooty Tern) of Christmas.

This comparison thus suggests that tropical seabird communities may consist of at least two guild-types: far-ranging species, most of which include a substantial proportion of squid in their diet; and others feeding much closer to shore and taking negligible proportions of squid. The classic picture that resulted from the Ashmoles' work, of marked segregation between co-existing species of tropical seabirds, is typical only of the second

TABLE 12

OVERLAP IN DIET OF FARNE ISLANDS SEABIRDS (LEVEL 3 ANALYSIS)[a]

	F.a.	*R.t.*	*P.a.*	*S.s.*	*S.p.*	*U.a.*	*S.h.*	*L.f.*	*P.c.*[b]
Fratercula arctica		.98	.98	.96	.93	.73	.71	.64	.45
Rissa tridactyla			.99	.99	.96	.81	.79	.66	.47
Phalacrocorax aristotelis				.96	.93	.74	.71	.65	.50
Sterna sandvicensis					.98	.86	.84	.65	.48
Sterna paradisaea						.92	.91	.60	.48
Uria aalge							.98	.52	.45
Sterna hirundo								.52	.41
Larus fuscus									.31
Mean:	.80	.83	.81	.84	.84	.75	.73	.57	.44
Overall mean: .73 ± .21									

[a] Source: Pearson (1968).

[b] *P.c.: Phalacrocorax carbo.*

of these guilds; overlap between members of the pelagic or squid-eating guild is much higher, commonly exceeding 90% between guild members, and poses a more serious challenge to competition theory.

FARNE ISLANDS

The only temperate-zone seabird community for which there are data suitable for comparison with the tropical communities described, is that on the Farne Islands (Pearson 1968). The Farnes are a group of small islands (largest 6.5 ha), eight of which support breeding colonies of seabirds, between 1.6 and 7 km off the north-east coast of Northumberland, England. The seabirds breeding there feed in the North Sea, i.e., in shallow waters over the continental shelf. Their feeding environment is therefore much more similar to that of the Cousin Island seabirds, or the inshore feeders at Christmas, than to the pelagic feeders on either Aldabra or Christmas. By analogy with tropical seabirds, all these temperate species are inshore feeders, none pelagic.

The overlap matrix (level 3, % number) of the nine species whose diet Pearson studied (Table 12) shows strikingly high overlap values; of 36 overlaps, 13 exceed 90% and only half are below 70%. There is not such a sharp division into guilds as on Christmas Island, but Lesser Black-backed Gulls (*Larus fuscus*) and Cormorants (*Phalacrocorax carbo*) are distinct and Kittiwakes (*Rissa tridactyla*), Puffins (*Fratercula arctica*), Shags (*Phalacrocorax aristotelis*), and Sandwich and Arctic Terns (*Sterna sandvicensis* and *S. paradisaea*) form a very tight-knit group. Pearson's (1968) Table 2 shows that the fish families dominant in all diets are juvenile sand-eels (Ammodytidae) and young herrings (Clupeidae). Sand-eels predominate by number in all species but herring predominate by weight in Arctic and Common Terns. Cormorants are distinctive in taking no clupeids but many Pleuronectidae; Lesser Black-backs take very few clupeids but much offal and many invertebrates, and Puffins, Kittiwakes and Shags are almost toally dependent on sand-eels.

Pearson did not measure overlap values as such, but the extraordinary similarity of the birds' diets was obvious. He sought to explain it by suggesting that, in addition to some segregation by feeding range, the supplies of juvenile sand-eels and herrings are superabundant during the summer months and so there is little or no competition between the different species of seabird. Outside the breeding season, these fish become unavailable around the Farnes and most of the seabirds disperse or migrate elsewhere.

Farne Island seabirds' diets overlap, on average, by the same amount as Cousin Island terns and by rather less than the pelagic-feeding squid-eaters of Aldabra and Christmas Island. Are food supplies for the tropical species, too, super-abundant in the breeding season (when diet samples were perforce collected)? Clearly they are not: whereas most Farne Island seabirds rear broods of two or three, with a high breeding success, tropical seabirds notoriously suffer much lower breeding success. None of the species whose diets are reported here ever raises more than one chick. Many aspects of the breeding biology of tropical seabirds are apparently adaptations to—or consequences of—food shortage, so their commonly high feeding overlap with coexisting species cannot be due to a superabundance of food. I must stress that these high overlaps occur even *within* guilds of species that feed at similar ranges from land, so they already take into account possible differences in feeding range. We must conclude that very high levels of dietary overlap between co-existing species are commonly tolerated in tropical seabird species. This is particularly true in those that feed far out at sea and include significant proportions of squid in their diet.

The highest levels of overlap—in pelagic trop-

TABLE 13
DIVERSITY OF DIET (LEVEL 3, % NUMBER) OF SEABIRDS SAMPLED IN MORE THAN ONE COMMUNITY

Species	Locality			
	Christmas	Cousin	Aldabra	Hawaii
Sula sula	.39	—	.29	.88
Fregata minor	.45	—	.35	.84
Phaethon rubricauda	—	—	.67	.75
Phaethon lepturus	—	2.36	.52	—
Anous stolidus	.86	.61	.79	.87
Anous tenuirostris	.90	.21	—	.88
Gygis alba	.74	2.08	—	1.07

ical squid-eaters, and temperate species dependent on sand-eels and herring—are associated with a very low diversity of prey; the tropical squid-eaters concentrate on one or two families of fish (chiefly flying-fish) and one of squid, the temperate species on two families of fish. The fact that bird predators of these families are so restricted in their diet suggests that these are the only prey available and, in turn, that the high overlap found within these guilds is an inevitable consequence of a limited diversity of prey. The theoretical problems of the possible relationship between overlap and competition, and of just what level of overlap is theoretically permissible between co-existing species, are beyond the scope of this paper, though I have considered them elsewhere (Diamond 1971a). However, tropical seabirds, and particularly pelagic squid-eaters, are commended to theoreticians wishing to explore these problems as clear cases where high overlaps are the norm rather than the exception.

DIET DIVERSITY

The studies used here contain enough data to enable a comparison between the diets of more than one population of seven species (Table 13). Some species vary relatively little between sites (*Anous stolidus*) but others vary by a factor of three to five times (*Gygis alba, Phaethon lepturus*). Clearly no consistent trend exists, and a species' dietary diversity is an adaptable feature of its biology.

SEASONALITY

The method of collecting food samples used in the studies described here confines sampling to times when young are being fed in the nest. My own sampling was not distributed evenly throughout the year (Table 14). It would, therefore, be rash to attempt any statement on seasonal variation in food supply around either Aldabra or Cousin. The only species for which sufficient samples were available even to attempt such an analysis (*Fregata* spp.) showed variation which was slight, but significant (Diamond 1975b). Very little is known of seasonal variation in fish stocks, (even of the migratory tunnies (Scombridae) and jacks (Carangidae) which are so important in making fish available to pelagic seabirds in the tropics, but because they are poorly known should not lead us to ignore their possible significance. Current techniques for sampling seabird diets are too insensitive to detect the more subtle differences in feeding strategy

TABLE 14
SEASONALITY OF COLLECTION OF SEABIRD FOOD SAMPLES ON COUSIN AND ALDABRA ISLANDS

Species	Months											
	1	2	3	4	5	6	7	8	9	10	11	12
Cousin												
Gygis alba	4	3	4	2	5	12	4	2	7	2	1	1
Sterna anaethetus	5	1	4	2	7	7	3	3	3	2	0	1
Anous tenuirostris	0	1	0	0	9	17	12	14	3	0	0	1
Anous stolidus	0	0	0	0	5	8	7	3	1	0	0	0
Phaethon lepturus	4	3	2	0	5	10	8	4	0	6	1	0
Total	13	8	10	4	26	54	34	26	14	10	2	3
Aldabra												
Fregata ariel	15	35	15	88	19	4	0	1	2	0	0	0
Fregata minor	3	0	15	44	5	2	0	1	0	0	0	9
Sula sula	14	6	4	31	0	15	0	1	0	1	4	2
Phaethon rubricauda	2	8	2	6	5	5	18	5	4	2	0	4
Phaethon lepturus	2	1	3	3	2	0	6	8	1	4	2	3
Anous stolidus	4	3	1	9	0	2	0	0	0	0	0	0
Total	40	53	40	181	31	28	24	16	7	7	6	18

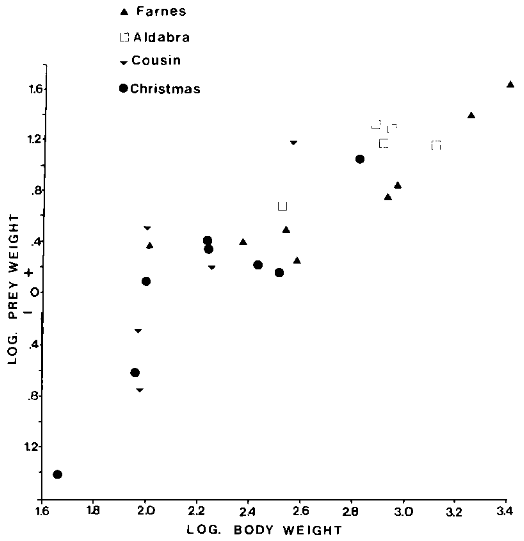

FIGURE 13. Relationship between body weight of seabirds and mean weight of their prey in four communities. Data from Ashmole and Ashmole (1967), Pearson (1968) and this study.

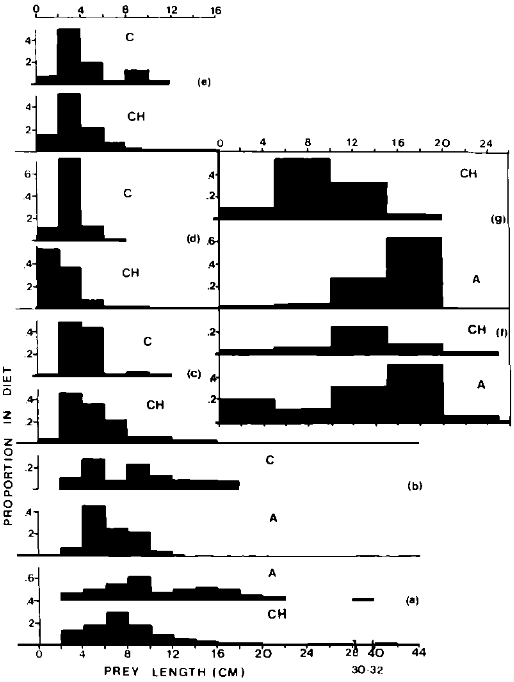

FIGURE 14. Lengths of prey taken by seven species of seabird in each of two different localities. (a) *Phaethon rubricauda* (b) *P. lepturus* (c) *Anous stolidus* (d) *A. tenuirostris* (e) *Gygis alba* (f) *Fregata minor* (g) *Sula sula.* A = Aldabra, C = Cousin, CH = Christmas Island (Pacific). Data from Ashmole and Ashmole (1967), Schreiber and Hensley (1976), and this study.

and technique that no doubt help to segregate co-existing seabirds in the tropics. Since birds simply do not produce sufficient samples year-round, future studies would do well to concentrate instead on obtaining large numbers of samples from several species as nearly simultaneously as possible. Differences between species which, over a year, show very little difference in diet may well be manifested more conspicuously as significant differences in efficiency at feeding in different weather conditions, or at different times of day.

PREY SIZE AND THE SIZE AND BEHAVIOR OF THE PREDATOR

Big birds eat bigger food than little birds—as a rule. At that very broad level—comparing, say, a Masked Booby with a White Tern—such a conclusion is as obvious as it is uninteresting. The general relationship between predator weight and mean prey weight of the seabirds in this study (Figure 13) shows a clear general trend, but the enormous amount of variation around the trendline, especially near the origin, is also impressive. The smallest seabirds in these communities can eat prey varying in mean weight (between species) by more than an order of magnitude. The three smallest terns on Cousin, for example, all average 93–98 g in weight, yet their mean prey weight varies from 0.2 g in *Sterna anaethetus* to 3.45g in *Gygis*. The variation in mean prey weight between species of the same size, in the same community, is surely at least as striking as the very crude relationship between body weight and prey weight over the whole range of body size from terns to boobies.

Another guide to the importance of predator size is the variation in prey weight between populations of the same predator. Distributions of prey-size for a number of seabirds sampled at different sites (Fig. 14) shows a substantial—and surely significant—degree of variation within species.

A predator's behavior is of course important in determining the prey it takes; whether more or less important than its body size we do not yet know for tropical seabirds. As yet, the field has barely begun to be explored. One of the few things we can reasonably assess about a species' feeding behavior is the distance from land at which it forages while breeding, at least in terms of the time it spends away from the nest, and relative to other species if not in absolute terms (Diamond 1978). Recent developments in the

TABLE 15
SPECIES RANKS ACCORDING TO MEAN PREY WEIGHT, BODY WEIGHT AND FORAGING RANGE

Species	Rank[a] prey weight	Rank body weight	Rank foraging range
Cousin Island			
Phaethon lepturus	1	1	1
Gygis alba	2	3	3
Anous stolidus	3	2	2
Anous tenuirostris	4	5	4
Sterna anaethetus	5	4	5
Christmas Island			
Phaethon rubricauda	1	1	2
Sterna fuscata	2	2=	1
Anous stolidus	3	2=	?
Gygis alba	4	4	3
Anous tenuirostris	5	5	5
Procelsterna cerulea	6	6	4

[a] Rank 1 = heaviest (weights) or furthest (foraging range).

theory of feeding behavior stress the importance of travel time in relation to handling time (the time taken to capture and consume prey once it has been detected). Our small knowledge of tropical seabird feeding behavior thus does include a parameter of central importance. A prediction shared by all central-place foraging models is that the size of a prey item is related to travel time; a predator with a long travel time should take larger prey than another with a short travel time. This, therefore, gives us an alternative model for predicting prey size; pelagic feeders should take larger prey than inshore feeders. While we cannot measure foraging distance precisely, we can rank species within a community according to foraging distance, and we can also rank them according to body weight, and the weight of their prey, with much greater confidence. These three rankings are compared in Table 15, for Christmas Island and Cousin (foraging ranks for Aldabra species are all very similar) and show that foraging range is as well correlated as body size with prey size. This comparison is made simply to demonstrate that better knowledge of the behavior of the bird is as likely to lead to greater understanding of its feeding ecology as the more traditional zoologists' emphasis on body size.

SUMMARY

The use of overlap matrices to assess feeding relationships in tropical seabird communities suggests a number of interesting relationships beyond the further demonstration of differences between closely related co-existing species. Overlap between species feeding far from land, and taking significant proportions of squid can regularly average over 90%. These values are higher even than some reported in temperate communities, where they have been explained by a seasonal superabundance of food. There is clearly no such superabundance for tropical pelagic species but they share with temperate seabirds a very limited diversity of available prey. Such high overlap is therefore seen as a consequence of restricted diversity in prey, irrespective of the prey's abundance relative to the predators' needs.

Inshore-feeding seabirds in the tropics take more diverse prey in terms of number of species, though not when measured taking evenness of distribution among prey categories into account. They overlap less than pelagic species, which is consistent with the suggestion that overlap between predators depends on the diversity of the prey.

Prey size is but weakly related to predator size, especially among small predators. The foraging strategy of the seabird is as good a predictor of its prey size (relative to that of other seabirds in the community) as is its own body size.

Future work could profitably concentrate on three areas: 1) comparing large samples from different species in a community, taken simultaneously rather than spread out over a long period; 2) more detailed work on foraging behavior in relation to prey size and behavior; and 3) parallel sampling of high-latitude communities to determine the relationships between seabird communities and the very different ecosystems they inhabit at different latitudes.

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