Tropical Seabird Biology

RALPH W. SCHREIBER

EDITOR

Studies in Avian Biology No. 8

A PUBLICATION OF THE COOPER ORNITHOLOGICAL SOCIETY

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LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY
900 EXPOSITION BOULEVARD
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Cover Photograph: White Tern (Gygis *alba*) on Christmas Island, Central Pacific Ocean by Elizabeth Anne Schreiber.

STUDIES IN AVIAN BIOLOGY

Edited by
RALPH J. RAITT
with assistance of
JEAN P. THOMPSON
at the
Department of Biology
New Mexico State University
Las Cruces, New Mexico 88003

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INTRODUCTION

RALPH W. SCHREIBER[1]

The Pacific Seabird Group (PSG) formed in December 1972. The organizers wished to study and conserve marine birds in the waters of the Pacific region and the PSG was to serve to increase communication between various persons and organizations. The founders placed a special emphasis on cold and temperate water systems, especially in Alaska, western Canada, and California, in relation to the offshore oil development in progress or contemplated at the time. Many early members of the PSG worked on government studies related to the effects of oil development in the marine environment on birds. An outlyer group of students of tropical marine birds also became interested in the PSG at this early stage. As PSG matured, and funds for offshore oil development waned, those of us specifically interested in tropical or subtropical systems took a more active role in the organization.

This symposium is a direct result of this interest in warm water seabirds. Craig Harrison urged the Pacific Seabird Group to hold an annual meeting in Hawaii. From those meeting plans evolved the idea of a symposium focusing on seabirds of the low latitudes and the relationship between those species and the various components of the marine ecosystem found along the temperature-salinity gradient to the north and south. Communication began between persons working on tropical seabirds about their willingness to participate in a symposium and publishing their results. The papers presented herein resulted from those efforts.

ACKNOWLEDGMENTS—I acted as coordinator and editor to produce this publication. I want to thank especially Craig S. Harrison (present Chairman of the Pacific Seabird Group), Harry M. Ohlendorf (former Chairman of the PSG), Ralph J. Raitt (Editor, Studies in Avian Biology), and Elizabeth Anne Schreiber for various assistance. N. Philip Ashmole, R. G. B. Brown, Cynthia Carey, Wayne Hoffman, Thomas R. Howell, Donald F. Hoyt, George L. Hunt, Jr., and Mary K. LeCroy served as referees. Guy Dresser and the staff of Allen Press performed in an accurate and expeditious manner. Without the timely work by those persons and the authors of the symposium manuscripts, this publication would have experienced considerable deferred maturity.

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[1] Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007.

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AN ECOLOGICAL COMPARISON OF OCEANIC SEABIRD COMMUNITIES OF THE SOUTH PACIFIC OCEAN

David G. Ainley and Robert J. Boekelheide[1]

Abstract.—Five cruises in the Pacific Ocean, passing through Antarctic, subantarctic, subtropical and tropical waters, were completed during austral summers and falls, 1976 to 1980. Over equal distances, species appeared or disappeared at a rate proportional to the degree of change in the temperature and salinity (T/S) of surface waters. In oceanic waters, the most important avifaunal boundaries were the Equatorial Front, or the 23°C isotherm, separating tropical from subtropical waters, and the pack ice edge. Much less effective boundaries were the Subtropical and Antarctic Convergences. The number of species in a region was likely a function of the range in T/S.

Antarctic pack ice and tropical avifaunas were the most distinctive in several respects, compared to Antarctic open water, subantarctic and subtropical avifaunas. Several factors were used to characterize seabird communities: varying with T/S and latitude were the number of seabird species, seabird density and biomass, feeding behavior, flight behavior, the tendency to feed socially and the amount of time spent foraging. There was little pattern in the variation of species diversity. Differences in the above characteristics of seabird communities were probably functions of the abundance and patchiness of prey, the availability of wind as an energy source, and possibly the number of available habitats.

How can one answer the question, "What is a tropical (or polar, etc.) seabird?" Is it merely a seabird that lives in the tropics, or are there distinctive characteristics that make a species supremely adapted to tropical waters but not to waters in other climatic zones? The question, though having received little attention, seems to us to be rather basic to understanding seabird ecology for a fairly obvious reason. The majority of seabirds that migrate, like their terrestrial counterparts, are not tropical. Rather, they nest in polar or subpolar regions. Unlike most landbird migrants, however, the majority of migrant seabird species avoid tropical/subtropical areas, fly quickly through them in fact, and spend most of their nonbreeding period in antipodal polar/subpolar areas. Thus, seabirds that frequent polar/subpolar waters while nesting "avoid" tropical waters. Conversely, seabirds that frequent tropical waters while nesting "avoid" polar/subpolar waters. Why this is so is at present difficult to say. This basic question, which it would seem concerns the characteristics that make a tropical, subtropical, subpolar or polar seabird so special, is difficult because we have few studies that compare regional marine avifaunas, or even that compare seabird species within families or genera across broad climatic zones. Instructive are analyses such as that by Nelson (1978), who compared a small family of tropical/subtropical seabirds on the basis of breeding ecology, or those by Storer (1960), Thoresen (1969), Watson (1968), and Olson and Hasegawa (1979) who, among others, described the convergent evolution of penguins and diving petrels in the south with auks and pelecaniformes in the north polar/subpolar zones. Not available are studies designed to compare the marine ecology of seabird groups that span disparate climatic zones. To help alleviate this situation, we undertook a series of cruises that stretched from tropical to polar waters in the South Pacific Ocean. We compared characteristics of regional avifaunas to determine whether tropical marine avifaunas actually did differ in important ways from those in the subtropics, subantarctic and Antarctic. We were also curious about what ecological/behavioral/morphological factors might underlie any differences that became apparent.

METHODS

Data Collection

We made cruises aboard small U.S. Coast Guard ice breakers, 70–90 m in length, and aboard R/V *HERO*, about 40 m long, with the following itineraries (Fig. 1): NORTHWIND 1976 = USCGC NORTHWIND from Panama City, Panama (10 Nov 1976) to Wellington, New Zealand (30 Nov) and from there (12 Dec) to the Ross Sea, and ultimately Ross Island, Antarctica (19 Jan 1977); HERO 1977 = R/V HERO from Anvers Island, Antarctica to Ushuaia, Argentina (8–10 Feb 1977); GLACIER 1977 = USCGC GLACIER from Long Beach, California (11 Nov 1977) to Papeete, Tahiti (29–30 Nov) to Wellington (9 Dec) and from there aboard USCGC BURTON ISLAND by way of Campbell Island to Ross Island (12–25 Dec 1977); GLACIER 1979 = USCGC GLACIER from Ross Island (15 Feb 1979) to Wellington (25 Feb–3 March) to Sydney, Australia (8–13 March) to Pago Pago, Samoa (22–23 March) to Long Beach (5 April); NORTHWIND 1979 = USCGC NORTHWIND from Wellington (20 Dec 1979), by way of Campbell Island to the Ross Sea, and ultimately to Ross Island (8 Jan 1980); and HERO 1980 = R/V HERO from Ushuaia (17 April 1980) to Lima, Peru (3–10 May) to Long Beach (28 May). We will not discuss here portions of cruises in subpolar waters of the northern hemisphere (a total of about six

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[1] Point Reyes Bird Observatory, Stinson Beach, California 94970.

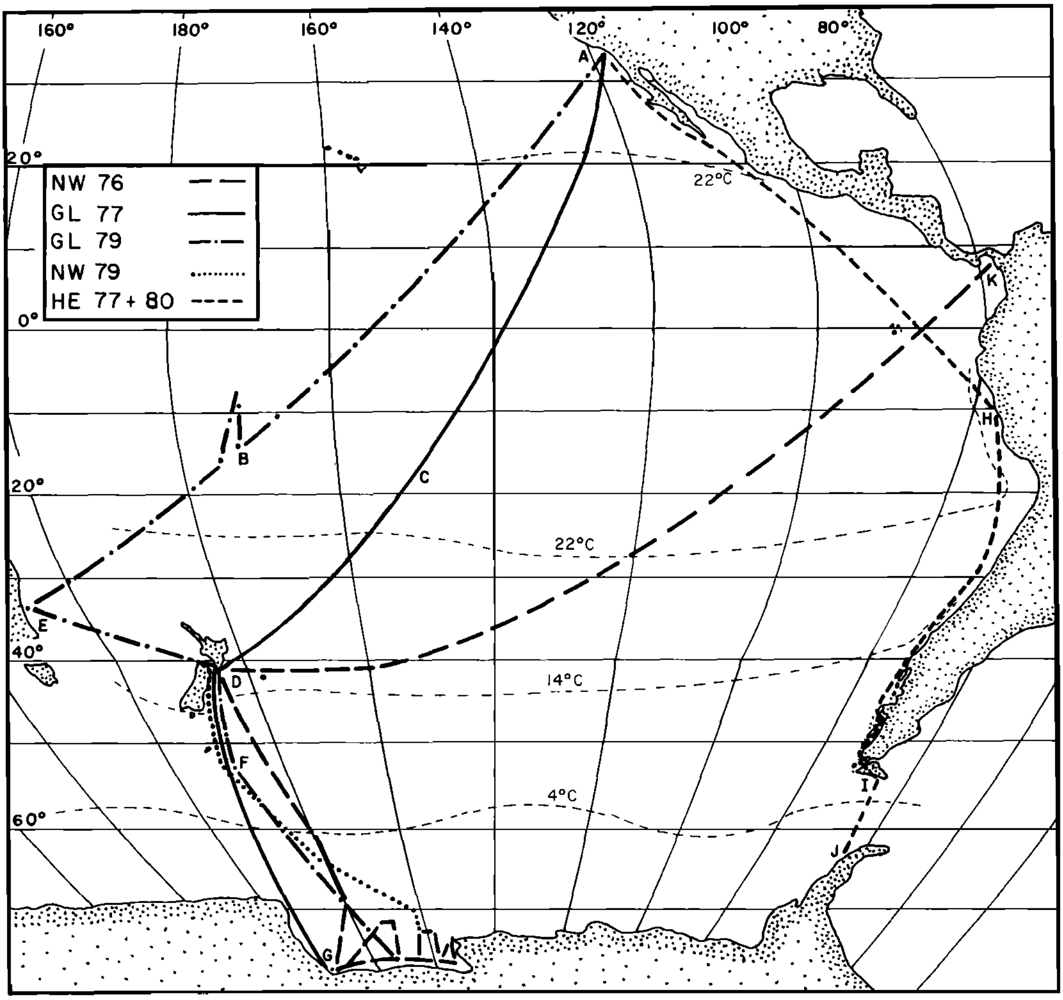

FIGURE 1. Routes of cruises; letters indicate stopping-off points: A, Long Beach, California; B, Pago Pago, Samoa; C, Tahiti; D, Wellington, New Zealand; E, Sydney, Australia; F, Campbell Island; G, Ross Island, H, Lima, Peru; I, Ushuaia, Argentina; J, Anvers Island; K, Panama City, Panama. Drawn according to Goode's homolosine equal-area projection.

days). Thus, from an austral perspective, all cruises occurred within the late spring to fall period. We generally had clear and calm weather, and on each cruise lost the equivalent of only one or two days of transects to poor visibility or impossible sea conditions. Virtually all the "lost" transects were in subantarctic waters.

On ice breakers, we made counts from the bridge wings, where eye level was about 16 m above the sea surface; on R/V HERO, we observed from the wings or front of the upper wheelhouse about 8 m above the sea surface. One 30-minute count, or "transect," was made during every hour that the ship moved at speeds of ≥6 kts during daylight (which increased from about 12 hours at latitude 0° to 24 hours south of latitude 60°S). In water free of pack ice, ice breakers cruised at 10–12 kts and R/V HERO at 8–9 kts. The total number of transects (=30-min count periods) was as follows: NORTHWIND 1976 = 696, HERO 1977 = 46, GLACIER 1977 = 484, GLACIER 1979 = 544, NORTHWIND 1979 = 247, and HERO 1980 = 364. We made no counts when visibility was less than 300 m. We tallied only birds that passed within 300 m of whichever side (forequarter) of the ship we positioned ourselves to experience the least glare. Census width was determined using the sighting board technique described by Cline et al. (1969) and Zink (1981). We used binoculars (8 × 40) to visually sweep the outer portion of the transect zone every two to three minutes to look for small birds and for birds on the water. We firmly believe that transect widths wider than 300 m would strongly bias the data in favor of large birds, and that binoculars must be used to search for birds, instead of using them merely as an aid to identification; otherwise, serious underestimates of bird density result (Wahl and Ainley, unpubl. data). On most transects, two observers searched for birds simultaneously. This was especially important in tropical waters where many species fly well above the sea surface. Distance traveled during each half hour transect, multiplied by census width, provides a strip of known area. This area divided into bird numbers provides an index of density. We counted birds that followed or circled the ship only if they initially flew to it out of the forequarter being censused; even so, each was allowed to contribute only 0.25 individuals assuming that they were likely attracted to the ship from up to 1 km or more away (i.e., about four times the census width away). The 300 m wide transect allowed inclusion of most birds that avoided approaching the ship closely. Density indices of a few species, however, in particular the Sooty Tern (*Sterna fuscata*) and some gadfly petrels (*Pterodroma* spp.), probably were slightly underestimated because of their tendency to avoid ships (R. L. Pitman, pers. comm.; Ainley, pers. obs.).

Immediately following each transect we measured sea surface temperature (SST) using a bucket thermometer, and on all cruises except the first halves of NORTHWIND 1976 and GLACIER 1977 we also collected a water sample to measure sea surface salinity (SSS), determined aboard ship using a portable salinometer. Following each transect, we recorded ship's position and speed, wind speed, sea conditions, depth, and distance to nearest land. All ships were equipped with satellite navigation. Every six hours, or sometimes more frequently, we recorded the thermal structure of the upper 400 m of the ocean by using an expendable bathythermograph. We entered all data into a SOLOS II microcomputer taken aboard ship on all cruises except those on R/V HERO (where data were entered after the cruise finished).

During transects, we kept a minute-by-minute tally of birds in a notebook, including information on behavior, molt or age, and later also entered these data into the computer. We recognized eleven feeding behaviors, as defined by Ashmole (1971) and modified by Ainley (1977) and Ainley et al. (1983). DIPPING: the bird picks prey from the sea surface, or just beneath it, either while remaining airborne (true *dipping*), contacting the water with the body for an instant (*contact dipping*), or contacting it with the feet (*pattering*). PURSUIT PLUNGING: the bird flies from the air into the water and then pursues prey in sub-sea surface flight. DIVING: the bird submerges from the surface to pursue prey beneath it using wings and/or feet for propulsion. SURFACE SEIZING: the bird catches prey while sitting on the surface although the bird could submerge much of its body in reaching down for prey. SCAVENGING: in which the bird eats dead prey, was included in surface seizing. SHALLOW PLUNGING: the bird hurtles head-long into the sea and submerges one to three body lengths as a result of momentum from the "fall." DEEP PLUNGING is similar but the bird "falls" from a greater height, assumes an extremely stream-lined posture, and consequently reaches much deeper depths. AERIAL PURSUIT: the bird catches prey that have leaped from the water and are airborne. PIRATING: where one bird chases another to steal its prey, was observed too rarely to be significant relative to other methods.

DATA ANALYSIS

We assessed bird abundance by determining density (birds per km) and biomass. We used bird weights from the literature and from collected specimens in the case of several Antarctic species (Ainley et al. 1983), and multiplied density by weight to determine biomass. We calculated an index to species diversity using both density and biomass estimates. The Shannon-Weiner diversity formula is:

$$H = -\Sigma\, p \log p$$

where p is the proportion of the total density or biomass contributed by each species.

We compared feeding behavior on a zonal basis by determining the amount of avian biomass involved in various methods of prey capture. We were most interested in the relative aero- or hydrodynamic qualities of various methods which explains why we combined certain similar feeding methods (see above). For many species, the method used was determined by direct observation. If a species fed in more than one way its biomass was partitioned accordingly (Table 1). In the species for which we had no or only a few observations of feeding, we relied on data in Ashmole (1971).

We used the method of Cole (1949), which was also used by Harrison (1982), to determine the degree of species association in feeding flocks. The Coefficient of Interspecific Association, $C = (ad - bc)/(a + b)(b + d)$, and the variance, $s = (a + c)(c + d)/n(a + b)(b + d)$ where a is the number of feeding flocks (equals two or more birds feeding together) in which species A (the least abundant of the two species being compared) is present in the absence of B, b is the number of flocks where B is present in the absence of A, c is the number of flocks where both A and B occur together, d is the number of flocks where neither occur, and n equals the sum of the four variables a, b, c, and d. We divided species among certain oceanographic zones before comparing their associations (see below).

MAJOR ZONES OF SURFACE WATER

We discuss here climatic zones, avifaunal barriers and species turnover relative to gradual changes in sea surface temperature (SST) and salinity (SSS). Of importance in the following discussion are Figures 2 and 3, which show the correspondence of climatic zones, as we define them, and various water masses. We define tropical waters as those having a SST of at least 22.0°C. These waters include the Tropical Surface Water

TABLE 1

PERCENTAGE OF INDIVIDUALS OBSERVED FEEDING BY VARIOUS METHODS[a]

		Method						
Species	*n*	DIP	SEIZE	SHAL-LOW PLUNGE	DEEP PLUNGE	PUR-SUIT PLUNGE	DIVE	AERIAL PUR-SUIT
Diomedea melanophris	3		100					
Daption capense	3		100					
Pterodroma lessoni	6		100					
Small *Pterodroma*[b]	9	33	67					
Medium *Pterodroma*[c]	12	56	9					35
Large *Pterodroma*[d]	10		100					
Procellaria aequinoctialis	3		100					
Pr. westlandica	6		100					
Puffinus griseus	383		11	29		60		
P. pacificus	71	78				17		
P. bulleri	28	80				20		
P. nativitatus	10	100						
Bulweria bulwerii	3	100						
Pachyptilla turtur	3	67	33					
Storm-Petrel[e]	26	100						
Storm-Petrel[f]	639	5	95					
Oceanodroma leucorhoa	49	88	12					
Sula dactylatra	12				100			
S. sula	15				60			40
Phaethon rubricauda	5				100			
Ph. lepturus	3				67	33		
Fregata spp.[g]	5	100						
Stercorarius parasiticus	5	100						
Sterna fuscata	210	91						9
Sterna lunata	12	58		42				
Gygis alba	14	100						
Anous stolidus	10	100						

[a] See also Ainley et al. (1983) for similar observations on Antarctic species.

[b] *Pt. longirostris, Pt. cookii*, and *Pt. hypoleuca/nigripennis*.

[c] *Pt. e. externa, Pt. e. cervicalis*.

[d] *Pt. phaeopygia, Pt. rostrata/alba*.

[e] *Pelagodroma marina, Fregetta grallaria*.

[f] *Oceanodroma markhami, O. tethys*, and *O. castro*.

[g] *Fregata minor* and *F. ariel*.

(T ≥ 25°C, S < 34 ppt) and Equatorial Surface Water (T ≥ 23°C, S 34–35 ppt) masses described by Wyrtki (1966), as well as "semitropical water," i.e., warm, saline Subtropical Surface Water (T ≥ 22°C, S ≥ 35 ppt). Characteristics of the thermocline also figure in defining tropical surface waters (e.g., Ashmole 1971), but we will not consider them in detail here; suffice it to say that our bathythermograph data roughly support the SST/SSS delineations of various climatic zones. The 23°C isotherm is usually considered to correspond approximately to the tropical-semitropical boundary in the South Pacific (Wyrtki 1964, Ashmole 1971). The 23°C isotherm is also at the cooler edge of the Equatorial Front. Because in our data, highly saline waters ≥22°C shared Sooty Terns and Red-tailed Tropicbirds (*Phaethon rubricauda*) with "tropical waters," we chose to include waters of that temperature in the tropical zone. This in practice is not a significant departure from the usual definition. Perhaps because of our cruise tracks or when darkness happened to force our daily census efforts to end, we experienced SSTs between 22.0 and 22.9°C on only 2.5% of our transects (22 on NORTHWIND 1976, 4 on GLACIER 1977, 6 on GLACIER 1979, and 26 on HERO 1980; none on NORTHWIND 1979 or HERO 1977). Thus, in effect, our division of data between tropical and subtropical zones corresponded to Wyrtki's definitions of the two zones. Pocklington (1979) also used the 22°C isotherm for the lowest temperature limit of tropical waters in the Indian Ocean.

At the other end of the marine temperature scale, the Antarctic Polar Front marks the transition between Antarctic and subantarctic waters. Within this frontal zone, where the really important features are subsurface (see Ainley et al.

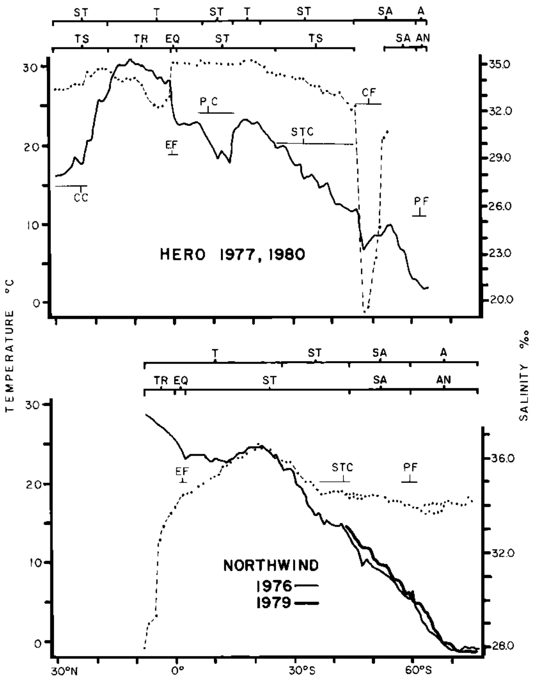

FIGURE 2. Change in sea surface temperature and salinity (T/S) with latitude along cruise tracks of NORTHWIND 1976 and 1979 and HERO 1977 and 1980. The two scales above each graph indicate the correspondence of T/S characteristics along cruise tracks with climatic zones (upper scale) and water masses (lower scale). Symbols for upper scale are: ST = subtropical zone, T = tropical zone, SA = subantarctic zone, and A = Antarctic zone; for lower scale: TS = Transitional Surface Water (SW), TR = Tropical SW, EQ = Equatorial SW, ST = Subtropical SW, SA = Subantarctic SW, and AN = Antarctic SW. Other symbols denote additional oceanographic features and translate as follows: CC = California Current, ECC = Equatorial Counter Current, EF = Equatorial Front, PC = Peru Current, CF = Chilean fijords, STC = Subtropical Convergence, and PF = Polar Front.

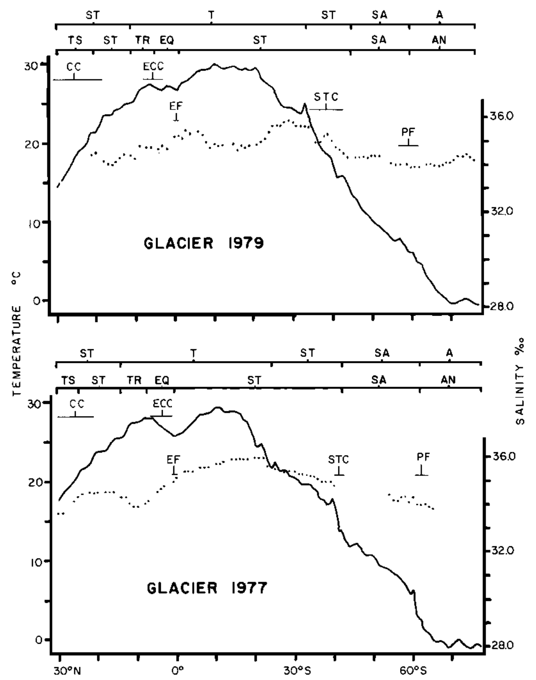

FIGURE 3. Change in sea surface temperature and salinity with latitude along cruise tracks of GLACIER 1977 and 1979. See Figure 2 for definition of symbols.

1983), SSTs drop rapidly from 5 to 3°C. Within this range we arbitrarily considered Antarctic waters to be those colder than 4.0°C.

The tropical and Antarctic zones were relatively easy to define. More difficult was the task of dividing those waters from 4.0 to 21.9°C between the subtropical and the subantarctic regions. The Subtropical Convergence is usually used by oceanographers and zoogeographers as the dividing "line," but using it did present some difficulties. According to Ashmole (1971), the Subtropical Convergence in the South Pacific is characterized at the surface by rapid north-south gradients in SST, the 34 ppt isopleth, and is located at about latitude 40°S. Rapid transitions from 18 to 14°C and from 35 to 34 ppt occurred between 40 and 45°S along cruise tracks in the western South Pacific and Tasman Sea (Figs. 2 and 3) and at about 26–45°S farther east. In the far eastern South Pacific the Subtropical Convergence is rather indistinct. Ashmole (1971) rather arbitrarily placed the boundary of subtropical waters at the 19°C isotherm, but in fact drew the line in his figure 3 coincident with the 14°C isotherm in the western South Pacific (compare Ashmole 1971: fig. 3 with charts in Sverdrup et al. 1942, Burling 1961, and Barkley 1968). Burling (1961) and others, in fact, place the southern edge of the Subtropical Convergence Zone approximately coincident with the 14°C isotherm in the western South Pacific and consider the zone itself to be subtropical in character. This is the definition we shall follow. Pocklington (1979) did not distinguish between subtropical and subantarctic waters in his Low Temperature Water-Type. However, in the Indian Ocean the Subtropical Convergence appears to be absent (J. A. Bartle, pers. comm.).

In summary, major zones of surface water in the South Pacific Ocean have the T/S characteristics outlined in Table 2. These zones are shown

TABLE 2
TEMPERATURE AND SALINITY CHARACTERISTICS OF WATERS IN FOUR CLIMATIC ZONES

Zone	Temperature (°C) Range	Temperature (°C) Spread	Salinity (‰) Range	Salinity (‰) Spread
Antarctic	(−)1.8 to 3.9	7	33.8 to 34.6	0.8
Subantarctic	4.0 to 13.9	10	33.8 to 34.8	1.0
Subtropical	14.0 to 21.9	8	34.4 to 35.8	1.4
Tropical	≥22.0	8	29.0 to 36.2	6.2

graphically in relation to cruise tracks in Figures 2 and 3, which also show the major current systems and water masses that we crossed.

SUMMARY OF SPECIES OCCURRENCE

Considering only oceanic waters, we identified a total of 23 species in the Antarctic, 39 in the subantarctic, 52 in the subtropics, and 51 in the tropics (Table 3). Considering distinctive subspecies as being equivalent to a species (for the purposes of this analysis), no oceanic seabird was confined entirely to subantarctic waters (diving petrels, most species of which are indistinguishable at sea, might eventually prove to be exceptional), four (8%) were confined to subtropical waters, four (17%) to Antarctic waters (all but one to the pack ice), and 19 (37%) to tropical waters. Except for the Antarctic, the increase in the number of distinctive species with increasing water temperature may be a function more of salinity than temperature, or better, a combination of both. Although approximately equal ranges in temperature occurred among zones (Table 2), subantarctic waters had the narrowest range of salinities (1.0 ppt), the subtropics a broader range (1.4 ppt), and the tropics an even broader range (6.2 ppt). This broadening of the T/S regime probably increases the number of surface water-types and in effect increases the number of distinctive habitats (Pocklington 1979). In the Antarctic, with its narrow range of sea surface temperatures and salinities, species-groups separate by specific habitats defined largely by ice characteristics (Ainley et al. 1983). The extensive sharing of species between the open-water Antarctic zone and the subantarctic, and between the subantarctic and the subtropics, is evidence that the Antarctic and Subtropical Convergences are not the avifaunal barriers that we heretofore thought them to be. This conception is based largely on the zoogeographic analysis of seabird *breeding* distributions (see also Koch and Reinsch 1978, Ainley et al. 1983) and must now be re-evaluated.

Our results show tremendous overlap in species among the four major zones of marine climate. Thus, we suggest that the major, classical oceanographic boundaries have few outstanding qualities as avifaunal barriers in the South Pacific. As we journeyed north or south on the various cruises we experienced a sometimes varying but mostly regular change in SST and SSS (Figs. 2 and 3). Coincident with this, species appeared or disappeared regularly as well (Fig. 4). Among all cruises, with each degree change in latitude, SST changed an average 0.67 ± 0.42°C, SSS changed an average 0.13 ± 0.15 ppt and an average 1.8 species appeared and/or disappeared (Table 4). Slight but consistent peaks in species turnover did occur in conjunction with continental shelf breaks, boundary current systems (which have large numbers of endemic species), the Equatorial Front, equatorial currents, the Subtropical Convergence, and the Antarctic Convergence. This species turnover is not surprising because SST/SSS also changed more rapidly as we passed through these areas; nevertheless, three-fourths of the species remained the same across these frontal zones. Equal turnover occurred in the equatorial currents, where we did not cross any classical zoogeographic "boundaries" but remained entirely in equatorial waters. These transitional areas were thus no less or more important than such classical avifaunal barriers as the Subtropical and Antarctic Convergences. Only in the Drake Passage, where a tremendous amount of water moves rapidly through a narrow space between major land masses, and where an extremely sharp horizontal gradient in SST/SSS exists also (S. S. Jacobs, pers. comm.), did the Antarctic Convergence approximate the avifaunal barrier it has been fabled to be. Even there, however, a notable overlap in species existed between zones.

CHARACTERISTICS OF SEABIRD COMMUNITIES IN DIFFERENT ZONES

In the above analyses, it appeared that avifaunas in the Antarctic and in tropical waters may be somewhat more distinctive than those in subantarctic and subtropical waters. To examine this

TABLE 3
Summary of the Zonal Occurrence of Seabirds in Oceanic Waters.

Species	Antarctic		Subantarctic	Subtropical	Tropical	
					Salinity	
	Pack ice	Open water			Low	High
Emperor penguin *Aptenodytes forsteri*	*					
King Penguin *A. patagonicus*		*	*			
Adélie Penguin *Pygoscelis adeliae*	*					
Chinstrap Penguin *P. antarctica*		*				
Crested Penguin *Eudyptes* spp.		*	*			
Royal Albatross *Diomedea epomophora*			*	*		
Wandering Albatross *D. exulans*		*	*	*		*
Black-browed Mollymawk *D. melanophris*		*	*	*		
Gray-headed Mollymawk *D. chrysostoma*		*	*			
Buller's Mollymawk *D. bulleri*		*	*			
White-capped Mollymawk *D. cauta cauta*			*	*		
Salvin's Mollymawk *D. c. salvinii*			*	*		*
Chatham Is. Mollymawk *D. c. eremita*			*	*		
Light-mantled Sooty Albatross *Phoebetria palpebrata*		*	*			
Southern Giant Fulmar *Macronectes giganteus*		*	*			
Northern Giant Fulmar *Macronectes halli*			*	*		
Southern Fulmar *Fulmarus glacialoides*		*	*			
Cape Petrel *Daption capense*		*	*	*		
Antarctic Petrel *Thalassoica antarctica*	*	*				
Snow Petrel *Pagodroma nivea*	*					
Solander's Petrel *Pterodroma solandri*						*
Tahiti/White-throated Petrel *Pt. rostrata/alba*					*	*
Hawaiian Petrel *Pt. phaeopygia*					*	*
Gray-faced Petrel *Pt. macroptera*			*	*		*
Cook's Petrel *Pt. cookii*			*	*		*
Soft-plumaged Petrel *Pt. mollis*		*	*			
Mottled Petrel *Pt. inexpectata*		*	*			
White-headed Petrel *Pt. lessoni*		*	*			
Juan Fernandez Petrel *Pt. e. externa*				*	*	*

TABLE 3
CONTINUED

Species	Antarctic				Tropical	
					Salinity	
	Pack ice	Open water	Subantarctic	Subtropical	Low	High
White-necked Petrel						
Pt. e. cervicalis				*		*
Bonin/Black-winged Petrel						
Pt. hypoleuca/nigripennis				*		*
White-winged Petrel						
Pt. l. leucoptera						*
Gould's Petrel						
Pt. l. gouldi				*		*
Stejneger's Petrel						
Pt. longirostris				*		*
Herald Petrel						
Pt. arminjoniana				*		*
Kermadec Petrel						
Pt. neglecta				*		*
Shoemaker						
Procellaria aequinoctialis			*	*		
Westland Black Petrel						
Pr. westlandica			*	*		
Parkinson's Petrel						
Pr. parkinsoni				*		*
Gray Petrel						
Pr. cinerea			*	*		
Audubon's Shearwater						
Puffinus lherminieri					*	*
Wedge-tailed Shearwater						
P. pacificus					*	*
Buller's Shearwater						
P. bulleri			*	*		*
Hutton's Shearwater						
P. gavia huttoni				*		
Fluttering Shearwater						
P. g. gavia			*	*		*
Flesh-footed Shearwater						
P. carneipes				*		*
Pink-footed Shearwater						
P. creatopus			*	*		
Little Shearwater						
P. assimilis			*	*		*
Black-vented Shearwater						
P. opisthomelas				*		
Townsend's Shearwater						
P. auricularis				*	*	
Newell's Shearwater						
P. p. newelli					*	
Sooty Shearwater						
P. griseus		*	*	*		
Bulwer's Petrel						
Bulweria bulwerii						*
Antarctic Prion						
Pachyptila desolata		*	*			
Fairy Prion						
Pa. turtur			*	*		
Narrow-billed Prion						
Pa. belcheri		*	*			
Peruvian Diving Petrel						
Pelecanoides garnoti				*		
Diving Petrel spp.						
Pe. urinatrix/georgicus/magellani		*	*	*		

TABLE 3
CONTINUED

	Antarctic				Tropical	
					Salinity	
Species	Pack ice	Open water	Subantarctic	Subtropical	Low	High
Black-bellied Storm-Petrel *Fregetta tropica*		*	*			
White-throated Storm-Petrel *F. grallaria*				*		*
Galápagos Storm-Petrel *Oceanodroma tethys*				*		*
Harcourt's Storm-Petrel *O. casto*				*		*
Leach's Storm-Petrel *O. leucorhoa*				*		*
Markham's Storm-Petrel *O. markhami*				*		*
Black Storm-Petrel *O. melania*				*		*
White-faced Storm-Petrel *Pelagodroma marina*			*	*		*
Wilson's Storm-Petrel *Oceanites oceanicus*	*	*	*	*		
Elliot's Storm-Petrel *Oc. gracilis*				*		*
White-throated Storm-Petrel *Nesofregetta albigularis*						*
Red-footed Booby *Sula sula*					*	*
Peruvian Booby *S. variegata*				*		
Blue-faced Booby *S. dactylatra*				*	*	*
Magnificent Frigatebird *Fregata magnificens*					*	
Lesser Frigatebird *Fr. ariel*						*
Greater Frigatebird *Fr. minor*					*	*
White-tailed Tropicbird *Phaethon lepturus*						*
Red-tailed Tropicbird *Ph. rubricauda*				*		*
Red-billed Tropicbird *Ph. aethereus*				*	*	
South Polar Skua *Catharacta maccormicki*	*	*	*	*		
Parasitic Jaeger *Stercorarius parasiticus*				*	*	*
Pomarine Jaeger *St. pomarinus*				*	*	*
Scissor-tailed Gull *Creagrus furcatus*				*	*	*
Sooty Tern *Sterna fuscata*					*	*
Gray-backed Tern *Sterna lunata*						*
Arctic Tern *Sterna paradisaea*	*	*	*	*	*	
White Tern *Gygis alba*						*
Brown Noddy *Anous stolidus*						*

TABLE 3
CONTINUED

Species	Antarctic				Tropical	
					Salinity	
	Pack ice	Open water	Subantarctic	Subtropical	Low	High
Red Phalarope *Phalaropus fulicarius*			*	*	*	
Total	7	23	39	52	51	

further, we will continue the four-zone separation in the following analyses which attempt to delineate behavioral/morphological/ecological differences among the four avifaunas.

FEEDING METHODS

Ashmole (1971) emphasized the importance of feeding methods for characterizing seabird species; Ainley (1977) discussed how some oceanographic factors affect the use of various feeding methods in different regions. Ainley, however, considered only the breeding species in regional avifaunas. In some cases this was artificial because while certain feeding methods were not used by breeding species, nonbreeding species in surrounding waters employed them to great advantage. To simplify analysis, Ainley (1977) also assumed that each species used only its principal method of feeding. This is indeed a simplification (Table 1). Our cruises afforded us the opportunity to improve Ainley's analysis by gathering data to characterize the feeding methods within entire seabird communities, including both nonbreeding and breeding individuals and species. We calculated how the total avian community biomass was apportioned among eight different methods of feeding. Where the data were available (see Table 1), we divided a species' biomass among various feeding methods if that species employed more than one.

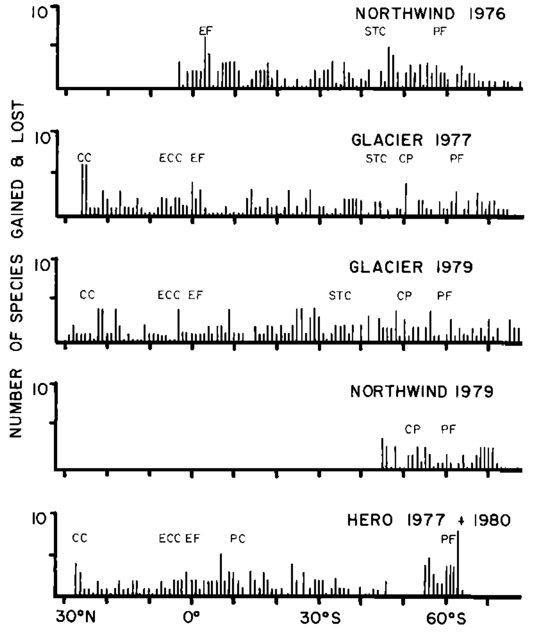

FIGURE 4. Change in species (species lost + species gained = species changed) with latitude along cruise tracks (compare with Figs. 2 and 3). See Figure 2 for definition of symbols.

Results confirmed Ainley's (1977) conclusions in regard to diving and plunging: moving from cold to warm, in subtropical waters diving disappeared and plunging appeared as a viable method of prey capture (Fig. 5). Trends that Ainley did not detect, however, were also evident. Dipping was a prominent method of prey capture in extremely cold water (≤2°C) as well as in warm waters (>13°C), and especially in waters warmer than 17°C. Pursuit plunging and shallow plunging were prominent in waters where dipping was not, i.e., 2 to 17°C. Aerial pursuit was evident only in tropical waters. Surface seizing was the method least related to sea surface temperature, but it was used less in the Antarctic pack ice and tropical communities than in others. Only diving, plunging and aerial pursuit were confined to distinct ranges of SST; the remaining methods were used to some degree in all regions.

On a relative scale, cold waters have much larger standing stocks of organisms, such as zooplankton (Foxton 1956, Reid 1962), than do warm waters, and thus in cold waters birds should find it easier to locate prey (e.g., Boersma 1978). Considering this general idea, Ainley (1977) reasoned that diving was adaptive only in cold waters where prey availability was relatively reliable because diving species have limited abilities to search for prey. Results obtained in the present study confirm this pattern. On a more local level Crawford and Shelton (1978) likewise noted that

TABLE 4
APPEARANCE AND DISAPPEARANCE OF SPECIES AND CHANGE IN SEA SURFACE TEMPERATURES AND SALINITIES WITH ONE DEGREE CHANGES IN LATITUDE (MEAN AND SD)

Cruise	Species change[a]	Temperature °C	Salinity PPT	Number of transects
Northwind 1976	1.8 ± 1.8	0.60 ± 0.56	0.17 ± 0.19	74
Northwind 1979	2.0 ± 1.6	0.57 ± 0.45	0.10 ± 0.15	30
Glacier 1977	1.8 ± 1.8	0.65 ± 0.76	0.10 ± 0.12	93
Glacier 1979	1.7 ± 1.5	0.56 ± 0.57	0.14 ± 0.14	83
Hero 1977 & 1980	2.1 ± 1.6	0.99 ± 1.14	0.15 ± 0.15	56
Total, $\bar{x}$	1.8 ± 1.7	0.67 ± 0.65	0.13 ± 0.15	336

[a] Species appearing plus those disappearing.

penguin (the ultimate family of divers) nesting colonies in South Africa occurred principally in conjunction with the optimal habitat for schooling fish, and not in peripheral habitat where suitable prey populations were more subject to fluctuation, and thus less reliable in availability. Continuing this line of reasoning, Ainley et al. (1983) hypothesized that Adélie Penguins (*Pygoscelis adeliae*) may feed on krill (*Euphausia* spp.) as heavily as they do perhaps not out of "specialization" but rather because such a prey type (surface swarming crustaceans) is the most reliable and abundant food source available to a bird which, compared to all other Antarctic birds, is relatively incapable of searching large areas for food.

Another reason why it is not adaptive for diving birds to occur in warmer waters may have to do with competition from similar creatures that can exploit resources in the tropics more efficiently. Coming most to mind are the porpoises, which as a group are largely tropical and

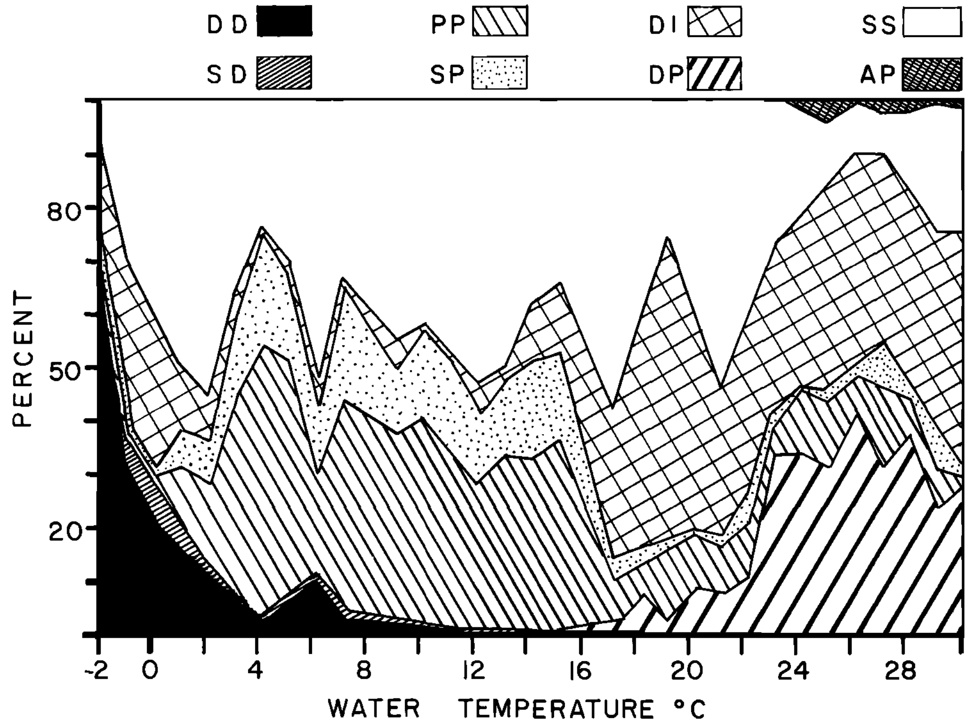

FIGURE 5. Proportion of avian biomass allocated to eight different feeding methods (see text p. 4) at different sea surface temperatures. All cruises combined; transects at similar water temperatures averaged.

subtropical in distribution (e.g., Gaskin 1982). The appearance of porpoises, from an evolutionary point of view, coincided with the disappearance of many flightless, diving birds (Simpson 1975, Olson and Hasegawa 1979), a pattern that may indicate competitive interaction between the two groups of animals.

In regard to deep plunging, which is used only among seabirds in warmer waters, Ainley (1977) reasoned that this feeding method is most effective in waters that are relatively clear. These waters have low concentrations of phytoplankton, a characteristic of subtropical and tropical waters (Forsbergh and Joseph 1964). Rather enigmatic is the Peru Current where rich blooms of phytoplankton cloud the water and where a plunging species, the Peruvian Booby (*Sula variegata*) is abundant. However, this species' usual prey, the Peruvian anchovy (*Engraulis ringens*), occurs in particularly dense schools right at the surface, a feature that may allow the Peruvian Booby, which feeds like its blue-water relatives, to occur in these waters. In addition, the aerial buoyancy of plunging species is second only to those species that feed by dipping (Ainley 1977) and thus plungers, with their efficient flight capabilities, are well adapted to search for prey under conditions where prey availability is relatively less reliable; i.e., warm waters which, as noted above, are generally considered to have more patchily distributed and lower standing stocks of prey than cold waters.

The bimodal prominence of dipping in the coldest and the warmest waters is interesting. In coldest waters, it seems that species are either capable of total immersion (penguins) or they avoid any contact with the water, and feed by dipping. Among several possible factors, this could be a function of thermal balance. Penguins can be large and have a thick insulating layer of fat because they do not have to fly in the air. Other species cannot possess these characteristics and still be able to fly, so they avoid contact with the cold water as much as possible. One way to do this is to feed by some form of dipping. Reduced contact with the sea in the tropics is manifested not only by the prominence of dipping, but also by aerial pursuit and even deep plunging (vs. actually swimming about after prey beneath the sea surface). The prominence of these methods in large part may be an artifact of a need for aerial buoyancy in waters where great mobility is advantageous (see above discussion on prey availability), but the high density of large predatory fish (e.g., sharks, tuna) in warm surface waters would also encourage adaptations for reduced contact with the sea. One has to observe only a few instances of tuna feeding at the surface to understand what advantage there is for tropical birds to restrict contact with the sea when feeding; if not eaten, certainly their chances of being bodily harmed would be high. Moreover, prey are often driven clear of the water by predatory fish. Being capable of catching these prey in mid-air, i.e., by aerial pursuit, would be of further advantage.

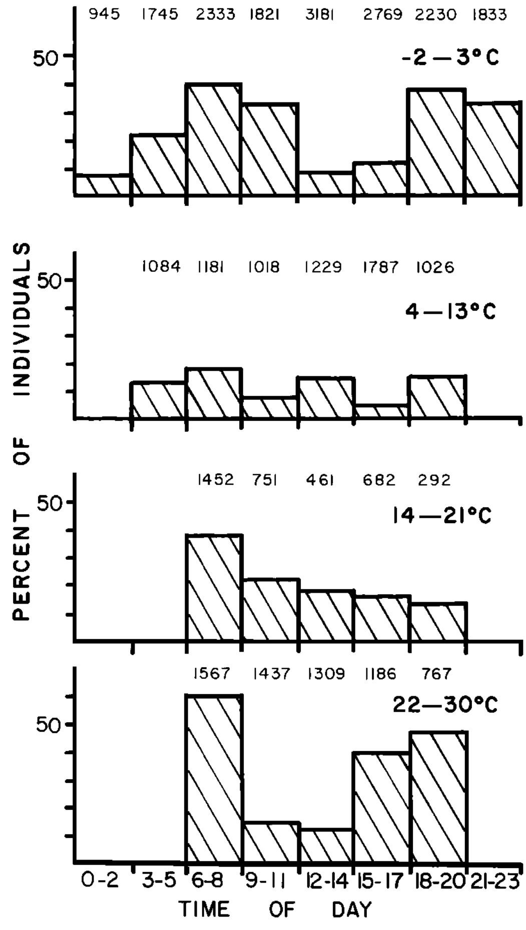

FIGURE 6. Percentage of individual birds observed feeding or in feeding flocks within three-hour periods of the day. All cruises combined; total number of birds observed in each period given at the top of each bar.

Temporal variations in feeding.—Also varying oceanographically to some degree (i.e., with SST) were the time of day when feeding occurred and the proportion of birds observed in feeding activity (Fig. 6). To study this, we grouped transects by three-hour intervals and established the following criteria for inclusion in the analysis: 1) farther than 75 km from land (to reduce the influence of shallow waters), and 2) winds less than

30 kts (because high winds increase sea surface turbulence and reduce prey visibility). Furthermore, we disregarded all penguins and diving petrels (which were difficult to distinguish as feeding or not feeding while we steamed by), and also Sooty Shearwaters (*Puffinus griseus*) and Mottled Petrels (*Pterodroma inexpectata*) (which were migrating in abundance through tropical waters but were never observed feeding there). The analysis indicates that feeding activity is dependent on time of day in all zones (*G*-test, $P <$ .01, Sokal and Rohlf 1969; *G* scores as follows: Antarctic, 1513.1, df = 7; subantarctic, 231.0, df = 5; subtropics, 171.5, df = 4; tropics, 1074.2, df = 4). In essence, seabirds in oceanic waters tend to feed during the morning and evening. This was expected because as a negative response to increased light intensity, many potential prey migrate to deeper waters during the day but return to the surface when daylight fades (e.g., Imber 1973). More interesting is the fact that feeding activity was also bimodal with respect to time of day in the Antarctic where daylight is continuous during summer. At 75°S latitude, light intensity nevertheless does become reduced at "night." As a response to the change in light intensity, prey such as euphausiids migrate vertically (Marr 1962). Bimodal feeding activity has also been observed in Antarctic seals (Gilbert and Erickson 1977).

We observed a higher proportion of birds feeding in Antarctic waters compared to subantarctic and subtropical waters, which is not surprising given our opportunity in high latitudes to observe birds round the clock under conditions of continuous light (Table 5). In subantarctic and subtropical waters, the predominance of squid-feeding species (i.e., albatrosses, large petrels and gadfly petrels), which feed mainly at night, probably contributed to the low proportion of birds observed feeding. On the other hand, the high proportion of birds observed feeding in tropical areas indicates that birds may tend to feed more during the day in those waters than elsewhere. This would be consistent with the hypothesis of Ashmole and Ashmole (1967) and others that many tropical seabirds often feed in association with predatory fish which force prey into surface waters. It must certainly be easier for birds to find feeding tuna/porpoise during daylight. The higher proportion of birds observed feeding in the tropics may also indicate that tropical seabirds need to spend more time feeding than seabirds in cooler, more productive waters. In addition to prey being more patchy and generally less abundant in the tropics, tropical seabirds may also have to feed more to make up for the lower amount of energy available to them in the form of wind to help sustain flight (see below).

TABLE 5
PROPORTION OF BIRDS OBSERVED FEEDING IN DIFFERENT OCEANOGRAPHIC ZONES[a]

Zones	Birds feeding	Birds observed	Percent feeding[b]
Antarctic	3994	12,451	32.1
Subantarctic	238	1742	13.7
Subtropical	335	2134	15.7
Tropical	1969	5802	33.9

[a] Includes only transects farther than 75 km from land having winds less than 30 knots; does not include penguins, diving petrels, Sooty Shearwaters or Mottled Petrels (see text).

[b] Figures for Antarctic and tropical waters are not statistically different, and neither are those for subantarctic and subtropical waters; figures for Antarctic and tropical waters are statistically different from those for the subantarctic and subtropics ($P < .05$; percentage test, Sokal and Rohlf 1969).

In still another feeding-related phenomenon, the tendency of birds to occur in mixed-species feeding associations also differed by oceanographic zone. In the Antarctic, we observed mixed species feeding assemblages in 10.0% of transects ($n = 338$ total transects where depth was ≥ 1000 m and wind was <30 knots), and the large majority of these transects where mixed flocks were observed were not in areas of pack ice. In the other three zones, the percentages of transects in which associations occurred were as follows: subantarctic 12.2% ($n = 205$), subtropics 12.4% ($n = 451$), and tropics 18.6% ($n = 693$). The percentage for the Antarctic is significantly less and that for the tropics is significantly greater than the others ($P < .05$; percentage test, Sokal and Rohlf 1969). In that prey are considered to be more patchy in occurrence in tropical waters compared to elsewhere (e.g., Boersma 1978), the above regional differences in the tendency for mixed species feeding flocks to occur may be an indirect measure of the relative degree of patchiness in seabird prey by region. More patchy prey may force seabirds to be more social in their feeding.

Regional differences in the tendency of birds to form mixed species feeding flocks are also apparent when the tendency of individual species to feed in association with others is compared (Tables 6–9). In Antarctic waters, all statistically significant "associations" were negative except those between Southern Fulmar (*Fulmarus glacialoides*) and Antarctic Prion (*Pachyptila vittata*) and between Sooty Shearwater and Mottled Petrel (Table 6). Compared to other zones, a much lower proportion of Antarctic species formed positive associations and a much higher proportion formed negative associations (Table 10). The positive associations in the Antarctic occurred among species that did not occur in waters covered by pack ice. In other words, pack ice species

TABLE 6

COLE'S COEFFICIENT OF ASSOCIATION AMONG SPECIES THAT OCCURRED IN AT LEAST THREE FEEDING FLOCKS WHERE SST WAS LESS THAN 4°C (UNDERLINING INDICATES SIGNIFICANCE AT $P < .01$).

Species[a]	Species 1	2	3	4	5	6	7
1. Southern Fulmar							
2. Antarctic Petrel	$\underline{-.40}$						
3. Cape Petrel	.14						
4. Snow Petrel		$\underline{-.56}$					
5. Antarctic Prion	$\underline{.24}$		.23				
6. Mottled Petrel							
7. South Polar Skua				$\underline{-.36}$			
8. Adélie Penguin	−.26						
9. Sooty Shearwater						$\underline{.50}$	
10. Wilson's St-Petrel	$\underline{-.62}$	.15	$\underline{-.46}$				−.15
11. Arctic Tern	−.12	.31					

[a] Numbers in this column correspond to those across top of table; species are in taxonomic order more or less except 8–11, placed at the end to reduce table width.

"avoided" one another, probably as an artifact of their marked preferences for different habitats which were defined largely by ice characteristics. In the case of the Snow Petrel (*Pagodroma nivea*) and skua (*Catharacta maccormicki*), it may well have been an active avoidance of the skua on the part of the petrel (Ainley et al. 1983). In spite of their different habitat preferences, Antarctic species have similar diets when they do feed in the same vicinity (Ainley et al. 1983).

In the subantarctic, none of the statistically significant feeding associations was negative (Table 7). Although nine different species were observed in feeding flocks with the Sooty Shearwater, only one of these associations, a positive one with the White-headed Petrel (*Pterodroma lessoni*), was significant. Compared to the Antarctic, a slightly higher proportion of species formed positive feeding associations. In the subtropics and tropics (Tables 8 and 9), there were also very few negative associations but the proportion of species forming significant positive associations was much higher than in the two cooler zones (Table 10). In the subtropics, 11 species associated positively with the Pink-footed Shearwater (*Puffinus creatopus*), 13 species with the Sooty Shearwater and 14 species with the Shoemaker (*Procellaria aequinoctialis*). Nine other species had negative associations with the Sooty. In the tropics, 11 species had positive associations with the Wedge-tailed Shearwater (*P. pacificus*), Sooty Tern, and Brown Noddy (*Anous stolidus*), and 13 with the Red-footed Booby (*Sula sula*). Three of the five significant negative associations in the subtropics and tropics involved the Juan Fernandez Petrel (*Pterodroma e. externa*); two of its negative associations were with species which, like it, use aerial pursuit as a means of capturing prey (Buller's Shearwater *Puffinus bulleri* and Sooty Tern). In general, from the Antarctic to the subantarctic and subtropics, shearwaters, and especially the Sooty Shearwater, were important components in mixed-species feeding flocks. In the tropics, species showing a high tendency to associate were more diverse taxonomically, but a shearwater was among these species as well. The numerous associations of shearwaters with other species argues for their role as "catalysts" to be much more significant than any role they may play as "suppressors" in seabird feeding flocks (see Hoffman et al. 1981).

FLIGHT CHARACTERISTICS

A factor to which marine ornithologists have not given much attention is the use by seabirds of wind as an energy source, and particularly the efficiency with which different species use it to their advantage. On the basis of morphology, Kuroda (1954) suggested that aquatic and aerial abilities among the shearwaters were inversely related, some species being more aquatic and less aerial than others. This idea was suggested also, and extended to all seabirds, by Ainley (1977) who demonstrated that feeding methods and aerial buoyancy (Hartman 1961) were interrelated. Harrington et al. (1972) showed that wind regimes interacting with the aerial buoyancy of the Magnificent Frigatebird (*Fregata magnificens*) affected the species behavior, occurrence and distribution. Considering these facts and that regional differences in wind patterns exist (see below), we thought it worthwhile to explore the possibility that wind conditions also may have an effect on structuring entire seabird communities.

TABLE 7

COLE'S COEFFICIENT OF ASSOCIATION AMONG SPECIES THAT OCCURRED IN AT LEAST THREE FEEDING FLOCKS WHERE SST WAS 3.0 TO 13.9°C (UNDERLINING INDICATES SIGNIFICANCE AT $P < .01$)

Species[a]	Species 1	2	3	4	5	6	7	8	9	10	11
1. Royal Albatross											
2. Black-browed Mollymawk	.16										
3. No. Giant Fulmar											
4. Cape Petrel	$\underline{.30}$	$\underline{.58}$									
5. Antarctic Prion		.16									
6. Mottled Petrel		.05									
7. Stejneger's Petrel											
8. White-headed Petrel		.05		$\underline{.31}$	$\underline{.41}$						
9. Shoemaker	.16	.24									
10. Sooty Shearwater		.05	−.08	.19	.02	.19	.19	$\underline{.70}$			
11. Wilson's St-Petrel		−.12					$\underline{.64}$			−.08	
12. Magellanic Penguin		−.05							.12		.03
13. Chatham I. Mollymawk	$\underline{.79}$								.17		
14. White-capped Mollymawk	$\underline{.37}$								.17	−.03	
15. Southern Fulmar			.10								
16. Fairy Prion						.29				−.04	
17. Black-bellied St-Petrel			−.06		−.08					−.05	

[a] Numbers in this column correspond to those across top of table; species are in taxonomic order, except 12–17 placed at the end to reduce table width.

The Antarctic and subantarctic are generally considered to be windier than the subtropics and tropics. This is supported by a comparison of average wind speeds relative to 1.0°C intervals of sea surface temperature along our cruise tracks (Fig. 7). Wind speeds were indeed lowest in the tropics: beginning at 14°C, winds averaged 6–12 kts after averaging approximately 10–20 kts where waters were colder. The standard deviations of the average wind speeds, however, were consistently similar from 0 to 30°C, indicating similar variation. Compared to their respective averages, this meant that the usual amount of negative deviation from the mean in Antarctic and subantarctic areas still allowed 8–15 kts of wind, but in the subtropics and tropics, the lower level of usual conditions meant that only two to six knots of wind were available. Thus it seems that flight could potentially be more energetically costly in the tropics than elsewhere.

We compared the proportion of birds employing various kinds of flight with wind speed. Transects were grouped in 1.0°C intervals of SST. The proportion of birds gliding was directly related ($r = .5111$, $n = 33$, $P < .01$) and the proportion in flapping flight was inversely related ($r = -.5687$, $n = 33$, $P < .01$) to average wind speed. Obviously we saw more birds in flapping flight in the tropics than elsewhere. In addition, only in tropical waters did we observe soaring birds, including not just frigatebirds but boobies and Sooty Terns as well. The most commonly observed method of flight, flapping interspersed with gliding, showed no relationship to wind speed ($r = .0674$).

Seabirds, and other species with long, thin wings, must fly faster to remain aloft in calm conditions than birds with short, broad wings (Greenewalt 1962). If wind is available, seabirds are able to fly more slowly and use relatively less energy in maintaining speed than they would when winds are calm. However, having more of a choice between fast and slow flight is an obvious advantage to seabirds, particularly when feeding and looking for food. In the tropics and subtropical zones, with less wind available, seabirds should have to be more efficient at using wind energy than in the cooler, windier regions. One type of evidence for this is the prevalence in the tropics of species with high degrees of aerial buoyancy, a characteristic typical of birds that feed by dipping, plunging and aerial pursuit (Table 1 in Ainley 1977). About 80% of birds (in terms of biomass) fed by these methods in the tropics, compared to about 50% in the subtropics and 30% or less in the subantarctic and Antarctic (Fig. 5). Another type of evidence is information on wing shapes and wing loadings. Such data are inadequate at present, but those presented by Warham (1977) certainly show that collecting more would prove to be fruitful. Warham (1977) collected and summarized information on 48 species of procellariiformes but unfortunately only a few were tropical. Among species of intermediate size, the three species having lower wing loading than average were gadfly petrels,

TABLE 8

COLE'S COEFFICIENT OF ASSOCIATION AMONG SPECIES THAT OCCURRED IN AT LEAST THREE FEEDING FLOCKS WHERE SST WAS 14.0 TO 21.9°C (UNDERLINING INDICATES SIGNIFICANCE AT $P < .01$).

	Species																				
Species[a]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. Salvin's Mollymawk																					
2. Waved Mollymawk	$\underline{1.0}$																				
3. Parkinson's Petrel																					
4. Shoemaker	.13	.31																			
5. Westland Petrel				.23																	
6. Fairy Prion				.13	$\underline{.31}$																
7. Bk-winged Petrel			$\underline{.31}$																		
8. Great-winged Petrel				−.09	$\underline{.31}$	$\underline{.22}$	.09														
9. Juan Fernand. Petrel				.09																	
10. Stejneger's Petrel				$\underline{.42}$				.05	.02												
11. Buller's Shearwater			.27	.11		−.05			$\underline{.41}$												
12. Pk-ft'd Shearwater	$\underline{.29}$	$\underline{.55}$		$\underline{.17}$					−.09	.15											
13. Sooty Shearwater	.05	−.06	$\underline{.58}$	−.08	.16	−.10	−.10	.21	$\underline{-.20}$	−.10	−.11	$\underline{.20}$									
14. Black St-Petrel												$\underline{.29}$	$\underline{.37}$								
15. Elliot's St-Petrel				−.10									.20								
16. Galapagos St-Petrel	$\underline{.41}$	$\underline{.76}$		−.10								−.04	$\underline{-.22}$		.01						
17. Harcourt's St-Petrel.	.07	$\underline{.18}$										.02				$\underline{.76}$					
18. Leach's St-Petrel													−.08	$\underline{.46}$							
19. Wh-bell'd St-Petrel									.16		$\underline{.46}$										
20. Wilson's St-Petrel									−.05	.06	.07	−.06	−.17		.11	.06			.19		
21. Peruvian Booby	$\underline{.47}$	$\underline{.57}$		.11								.21	.03		−.03	.02					
22. Brown Pelican				.13									.05								.10
23. Chilean Skua				.23					$\underline{1.0}$	$\underline{.31}$					.24						
24. Parasitic Jaeger			.31	.03		.13	.13	.13			.09		−.05								
25. Sc-tailed Gull	$\underline{.31}$	$\underline{.32}$									.27					.21	$\underline{.32}$				
26. Arctic Tern									.25		.27	$\underline{.62}$	$\underline{.58}$								
27. Royal Albatross				$\underline{.42}$	$\underline{.32}$	$\underline{.22}$		$\underline{.22}$					.05								
28. Bk-browed Mollymawk				$\underline{.62}$						$\underline{.31}$		.24	.21							$\underline{1.0}$	
29. Cook's Petrel												$\underline{.43}$	.16	$\underline{.31}$				$\underline{.28}$	$\underline{.23}$		
30. Diving Petrel									$\underline{.22}$					$\underline{1.0}$							
31. Markham's St-Petrel																	$\underline{.53}$	$\underline{.39}$			

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[a] Numbers in this column correspond to those across the top of the table; species are in alphabetic taxonomic groups which are in taxonomic order except for 27–31, placed at the end to reduce table width.

TABLE 9

COLE'S COEFFICIENT OF ASSOCIATION AMONG SPECIES THAT OCCURRED IN AT LEAST THREE FEEDING FLOCKS WHERE SST WAS >22.0°C (UNDERLINING INDICATES SIGNIFICANCE AT $P < .01$)

Species[a]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. Bk-wng'd Petrel																						
2. Great-wng'd Petrel																						
3. Tahiti Petrel																						
4. Wh-neck'd Petrel		$\underline{.32}$																				
5. Parkinson's Petrel	$\underline{.66}$			.31																		
6. Wedge-t'd Shearwater	.07	.36	−.03																			
7. Fl-foot'd Shearwater	$\underline{.30}$	$\underline{.22}$		$\underline{.30}$	$\underline{.30}$																	
8. Eliott's St-Petrel																						
9. Galapagos St-Petrel								$\underline{.70}$														
10. Harcourt's St-Petrel								$\underline{.71}$	$\underline{.49}$													
11. Leach's St-Petrel			.12						$\underline{.19}$	−.08												
12. Markham's St-Petrel								$\underline{.46}$	$\underline{.65}$	.58	−.04											
13. Wh.-bell'd St-Petrel										.22		.28										
14. Wh.-faced St-Petrel								$\underline{.46}$	.12	.19		.08	.28									
15. Masked Booby			.21			−.03				−.05		.03	$\underline{.30}$	.14								
16. Red-foot'd Booby	.12		.21			.23									.05							
17. Frigatebird, G & L			.24			$\underline{.57}$									$\underline{.51}$	$\underline{.30}$						
18. White Tern	.07					$\underline{.43}$										$\underline{.22}$	.26					
19. Gray-backed Tern						$\underline{.57}$										.30						
20. Sooty Tern			.35			$\underline{.51}$					$\underline{-.24}$				.09	.22	$\underline{1.0}$	−.11	$\underline{1.0}$			
21. Black Noddy	.13					.26										$\underline{.40}$		.11				
22. Brown Noddy	.07					$\underline{.46}$									−.04	$\underline{.22}$	.26	.04	.26	$\underline{.25}$	$\underline{.68}$	
23. Hawaiian Petrel			.21						.15	.18	.18	.13				.05				−.04		
24. Juan Fernan. Petrel						−.19				−.08	−.02	−.05	.22	.10	.06			−.04		$\underline{-.20}$		
25. Gould's Petrel	$\underline{.31}$												$\underline{.32}$									.26
26. Christmas Shearwater						$\underline{.49}$									.15	.15			.31	$\underline{.74}$		
27. Black St-Petrel			−.23							.23	.39	.13	.12									
28. Bulwer's Petrel			.32			$\underline{.57}$									$\underline{.30}$		$\underline{.49}$			$\underline{.57}$		
29. Wh.-t'd Tropicbird	$\underline{.17}$					.23										$\underline{.37}$		$\underline{.56}$		.22	$\underline{.17}$	$\underline{.33}$
30. Parasitic Jaeger	.13	$\underline{.22}$				$\underline{.45}$	$\underline{.25}$												.26	$\underline{.35}$	$\underline{.37}$	$\underline{.50}$

[a] Numbers in this column correspond to those at top of table; species are in alphabetic order within taxonomic groups which are in taxonomic order more or less, except 23–30 placed at the end to reduce table width.

TABLE 10
TENDENCIES OF SPECIES IN DIFFERENT ZONES TO FORM MIXED SPECIES FEEDING FLOCKS; DATA SUMMARIZED FROM TABLES 6–9

	A	B	C	D	E	F	G
Zone	No. species[a]	No. species in mixed flocks	B ÷ A	No. species in positive association[b]	D ÷ A	No. species in negative association[b]	F ÷ A
Antarctic	23	11	0.478	4	0.174	5	0.227
Subantarctic	39	17	0.436	9	0.231	0	0.000
Subtropical	52	31	0.596	29	0.558	3	0.055
Tropical	51	30	0.588	27	0.529	2	0.038

[a] From Table 2.

[b] Statistically significant associations in Tables 6–9.

and two of these were tropical and subtropical in occurrence, the Bonin Petrel (*Pterodroma hypoleuca*) and the Juan Fernandez Petrel. The latter often feeds by aerial pursuit. The one gadfly petrel that had atypically high wing loading was the Mottled Petrel, the main Antarctic representative of this group and the only gadfly petrel observed to dive into the sea somewhat like a shearwater. The unpublished data of Eric Knudtson (pers. comm.) are also encouraging. He calculated buoyancy indices for two tropical shearwaters, the Wedge-tailed and the Christmas Shearwater (*P. nativitatus*), to be 3.3 and 3.8, respectively, which indicates much more aerial efficiency than does the value of 2.7 for their cold-water relative, the Sooty Shearwater (cal-

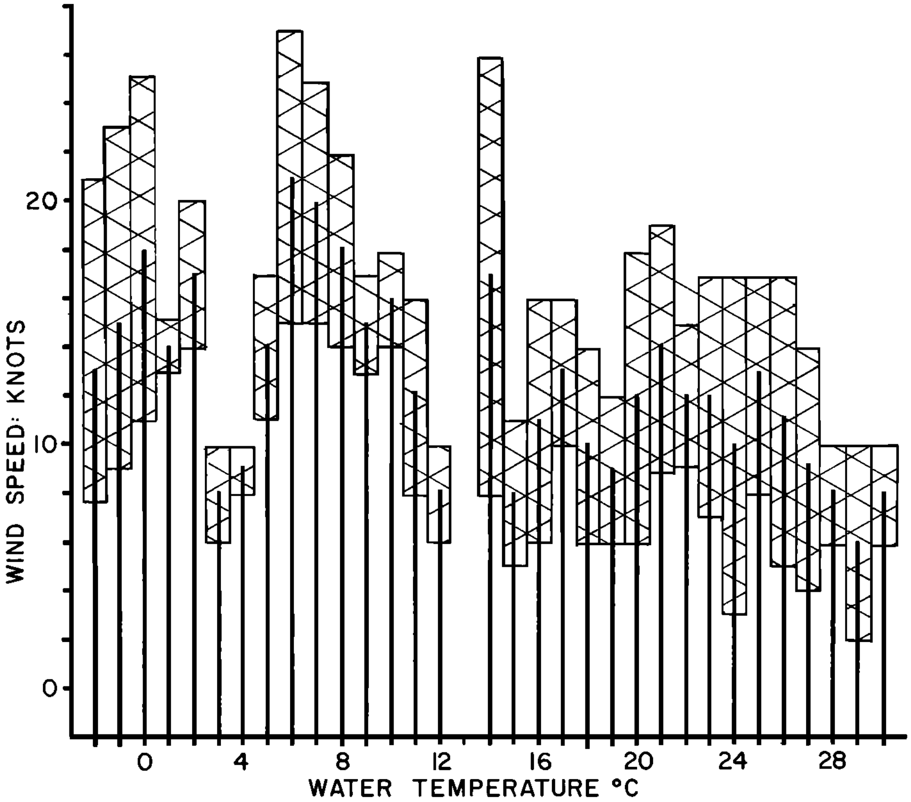

FIGURE 7. Mean wind speed (±SD, cross hatching) recorded on transects at 1.0 C° intervals of sea surface temperature; all cruises combined.

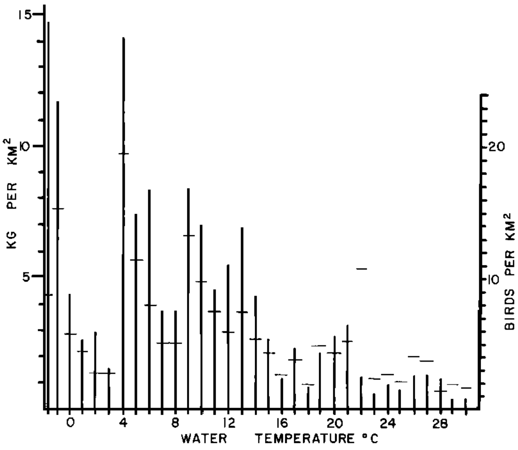

FIGURE 8. Mean density (vertical bars) and biomass (horizontal lines) of seabirds at 1.0 C° intervals of sea surface temperature; all cruises combined.

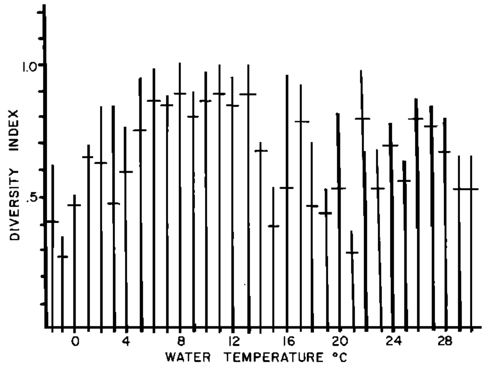

FIGURE 9. Mean indices of species diversity based on density (vertical bars) and biomass (horizontal lines) at 1.0 C° intervals of sea surface temperature; all cruises combined.

culated by using Warham's 1977 data). Kuroda (1954), based on morphology, also suggested that the flight capabilities of the Wedge-tailed and Christmas Shearwater differed from the Sooty, but he did not really consider that climatic differences could be an underlying factor; rather, he ascribed the differences mainly to the more aquatic abilities of the Sooty. Much more comparative work is needed on the flight morphology of seabirds.

COMMUNITY BIOMASS AND SPECIES DIVERSITY

Density and biomass varied as one would expect in relation to the productivity of surface waters: they were highest in the Antarctic, declined with increasing temperatures, and were lowest in the tropics (Fig. 8, Table 11). Densities in the Antarctic and subantarctic were not significantly different. Penguins comprise a relatively high proportion of individuals in Antarctic communities and storm-petrels comprise a relatively high proportion of individuals in the tropics. This, and the fact that penguins are large and storm-petrels are small, would explain in part the greater discrepancy between Antarctic and tropical avifaunas in biomass (11-fold difference) compared to density (three-fold difference).

Trends in species diversity were not clearly evident (Fig. 9, Table 11). The mean diversity index for each of the four climatic zones was statistically significant from figures for each of the other zones. The lack of trend in species diversity is in contrast to the number of species in each zone: 23 in the Antarctic, 39 in the subantarctic, and 52 and 51 in the subtropics and tropics, respectively (Table 3). This tends to support our earlier suggestion that the number of species may prove to be a function of the range

TABLE 11

DENSITY, BIOMASS AND SPECIES DIVERSITY OF SEABIRDS IN FOUR BROAD ECOLOGICAL ZONES: MEAN (±SD) VALUES FOR TRANSECTS FARTHER THAN 50 KM FROM LAND

	Number of Transects	Density[a] Birds/km²	Biomass[b] kg/km²	Species Diversity[c]			
				Density		Biomass	
Antarctic	573	9.5 ± 7.4	10.2 ± 5.4	−.5386	.1826	−.3362	.1642
Subantarctic	276	9.0 ± 4.5	6.7 ± 3.0	−.8788	.0940	−.7258	.1686
Subtropical	392	4.2 ± 1.2	2.7 ± 1.1	−.6642	.2038	−.4698	.1725
Tropical	654	3.4 ± 2.9	0.9 ± 0.4	−.7534	.1204	−.5926	.1217
Total	1895	6.2 ± 4.1	4.9 ± 2.4	−.6891	.1526	−.5091	.1519

[a] Figures for Antarctic and subantarctic are not significantly different, but all other figures in the column are (*t*-test, $P < .01$).

[b] All figures are statistically significant (*t*-test, $P < .01$).

[c] All figures within each column, not including "Total," are significantly different from each other (*t*-test, $P < .01$).

in the temperatures and especially salinities in a region; a wider range means more habitats or water-types which in turn allows the presence of more species.

DISCUSSION

In general, the steepness of horizontal temperature and salinity gradients in surface waters seemed to determine the amount of avifaunal change that we encountered as we steamed across the ocean. Like Pocklington (1979) we found that the transition between subtropical and semitropical/tropical waters (i.e., approximately the 23°C isotherm) was a major avifaunal "barrier" in warmer oceanic waters. In the South Pacific, this isotherm is at the cooler edge of the Equatorial Front, which with its strong gradient in SST, may prove to be the actual barrier. Another major avifaunal barrier in oceanic waters was the pack ice edge. The Antarctic and Subtropical Convergences were relatively less effective as avian zoogeographic boundaries.

The tropical marine avifauna was rather distinctive in several ways.

(1) Tropical waters shared first place with subtropical waters in having the highest number of species.

(2) The proportion of species confined to tropical waters, however, was much higher than the proportion of subtropical species confined to subtropical and subantarctic species confined to subantarctic waters.

(3) In the tropical avifauna there existed the strongest tendency for species to associate in multispecies feeding flocks.

(4) Tropical species fed more by dipping, plunging and aerial pursuit than did species in other avifaunas, and correspondingly, they apparently had much higher degrees of aerial buoyancy (and in general, probably lower wing loading). Greater aerial buoyancy was adaptive because wind speeds were generally lowest in the tropics.

(5) The density and biomass of the tropical avifauna was much lower than elsewhere.

The other distinctive avifauna was that of the Antarctic pack ice. Many of this avifauna's characteristics were similar in nature to those of the tropical avifaunas but were different in extreme (usually opposite).

(1) Antarctic pack ice had the lowest number of species, but

(2) had the second highest proportion of species confined only to it. Ice-free waters of the Antarctic, and waters of the subantarctic and subtropics, had very few species confined to any one of the three zones.

(3) The low number of species in the Antarctic corresponded to that zone's narrow range in sea surface salinities; that narrow range plus the uniqueness of pack ice, corresponded to a distinct group of species associated with the pack ice (Ainley et al. 1983).

(4) Species in the pack ice showed a markedly strong negative tendency to associate in mixed species foraging flocks, i.e., they avoided one another.

(5) Antarctic pack ice species, more than other avifaunas, fed by deep diving; like birds in the tropics, they fed to a great extent by dipping.

(6) The density and biomass of birds in Antarctic waters were the highest.

Based on inferences from data on breeding biology, marine ornithologists generally agree on the hypothesis that tropical seabirds experience food that is relatively less abundant and, mainly, more patchy in occurrence than avifaunas of other regions, and that the opposite is true of Antarctic seabirds. Many of the characteristics listed above could be explained by that hypothesis, but would also be consistent with the hypothesis that seabirds are strongly tied by morphological/behavioral adaptations to specific water-types or marine habitats (habitats which move about somewhat seasonally and interannually) and that in the tropics more habitats are available for exploitation. This is a complicated hypothesis which seems to be supported by Pocklington's (1979) study of avifaunal association to water-types in the Indian Ocean, and an hypothesis about which we will soon have more to say when we analyze the T/S regimes of individual species and species groups in our own data for the Pacific.

The differences in species diversity among tropical, subtropical, subantarctic and Antarctic avifaunas indicated that it may have been the number of habitats or T/S water-types that determined the number of species in an area, assuming that the number of water-types is a function of the range in temperature and salinity. If the Indian Ocean system studied by Pocklington is typical of the Pacific, this assumption should be a safe one. The widest and narrowest ranges in the salinity of oceanic waters of the Pacific occurred in the tropical and Antarctic zones, respectively. These zones had similar species diversity but, also respectively, had the highest and lowest number of species. Such patterns also point to the need to understand better the association of species to water-types and to the number of water-types per region.

The species diversity estimates we present here are comparable to those calculated for grassland avifaunas by Willson (1974), and also for seabirds near Hawaii by Gould (1971). Since species diversity is a function of habitat complexity in terrestrial ecosystems, we conclude that oceanic marine habitats rank among the least complex for birds. Bird habitats in oceanic waters are largely two dimensional, although depth does add a third dimension. Compared to waters of the continental shelf, however, depth is less important in oceanic waters. If a greater degree of variation in depth penetration were possible by birds in oceanic waters, depth might be more important and we might expect higher estimates of bird species diversity. At first glance, it would appear that depth is a more significant factor in Antarctic and subantarctic avifaunas because they contain diving species. Tropical and subtropical avifaunas are compensated, however, because prey that would otherwise remain deep are forced to the surface by porpoise, tuna, and other predatory fish. While the importance of tuna to tropical seabirds has often been intimated, and is agreed upon by seabird biologists, we lack direct observations on the interaction of seabird flocks with tuna schools. The mobility of tuna may be another factor, along with wind conditions and prey availability, that places a premium on flight efficiency for tropical seabirds. A detailed study of the interaction between seabirds and tuna schools is long overdue (see Au et al. 1979).

Rather low species diversity also argues against there being many different foraging guilds (see Willson 1974) in oceanic habitats. The guilds would be definable in oceanic waters mainly by feeding behavior. Unlike terrestrial habitats and even shallow water habitats (see Ainley et al. 1981), foraging substrate is everywhere rather similar, and, because seabirds are rather opportunistic in their feeding, little diet specialization exists (e.g., Ashmole and Ashmole 1967, Ainley and Sanger 1979, Croxall and Prince 1980, Ainley et al. 1983, Harrison et al., 1983; also, compare Brown et al. 1981, Ogi, In press, and Chu, In press). Increasing our knowledge about the habitats and water-types preferred by seabirds may eventually help to integrate our rather checkerboard concept of seabird diet. For instance, we may be better able to explain the dramatic differences in diet between species nesting in both the Northwestern Hawaiian Islands (Harrison et al., 1983) and at Christmas Island (Ashmole and Ashmole 1967; Schreiber and Hensley 1976), which geographically are relatively close together, or between species frequenting both the Ross Sea (Ainley et al. 1983) and Scotia Sea (Croxall and Prince 1980), which are geographically far apart. More research on the biology of seabirds at sea is obviously needed.

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FEEDING OVERLAP IN SOME TROPICAL AND TEMPERATE SEABIRD COMMUNITIES

A. W. DIAMOND[1]

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 coexisting 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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[1] Edward Grey Institute of Field Ornithology, South Parks Road, Oxford OX1 3PS, England. *Current Address:* Canadian Wildlife Service, Ottawa, Ontario K1A 0E7, Canada.

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.

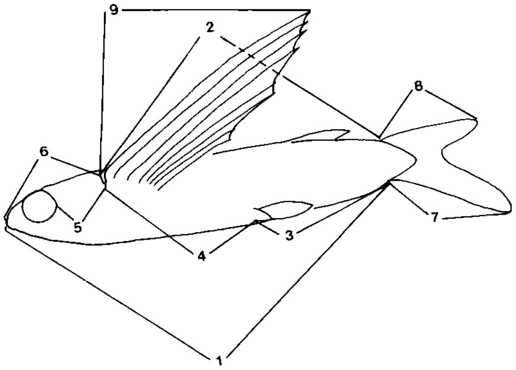

FIGURE 1. Measurements taken on fish specimens: 1: standard length, 2: base of pectoral fin to base of upper caudal fin, 3: base of pelvic fin to base of lower caudal fin, 4: base of pectoral fin to base of pelvic fin, 5: shortest length between eye and base of pectoral fin, 6: tip of nose to base of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

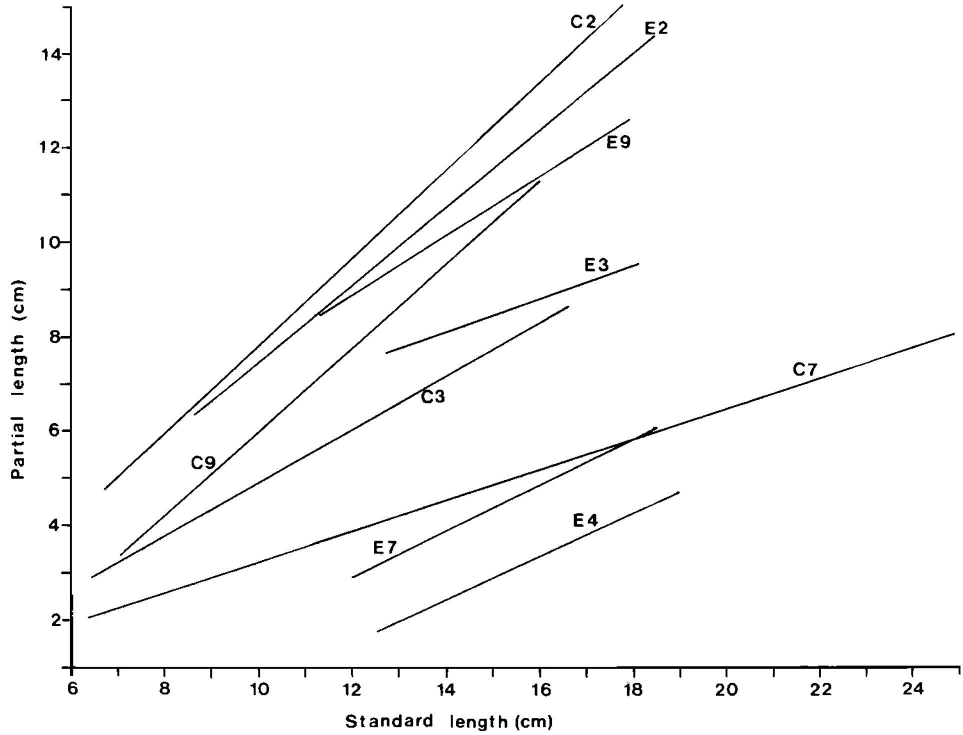

FIGURE 2. Relationships between selected partial measurements and standard length of flying fish in food samples. (Numbers as in Figure 1. E = *Exocoetus volitans,* C = *Cypselurus furcatus.*)

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.

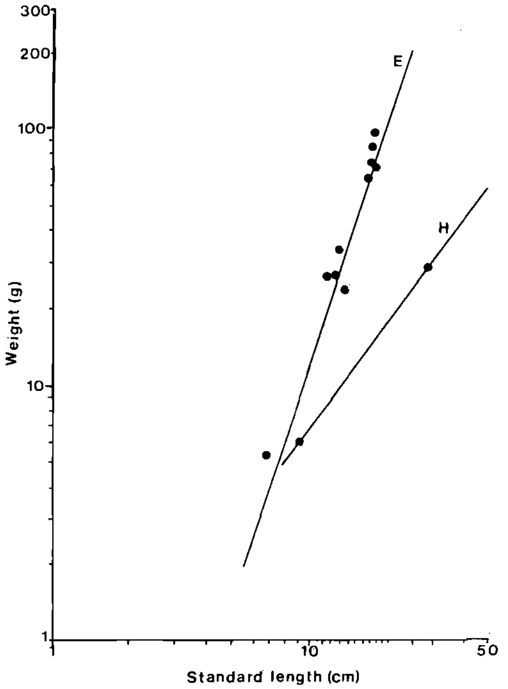

FIGURE 3. Weight/length relationships of Exocoetidae (E) and Hemirhamphidae (H) in food samples.

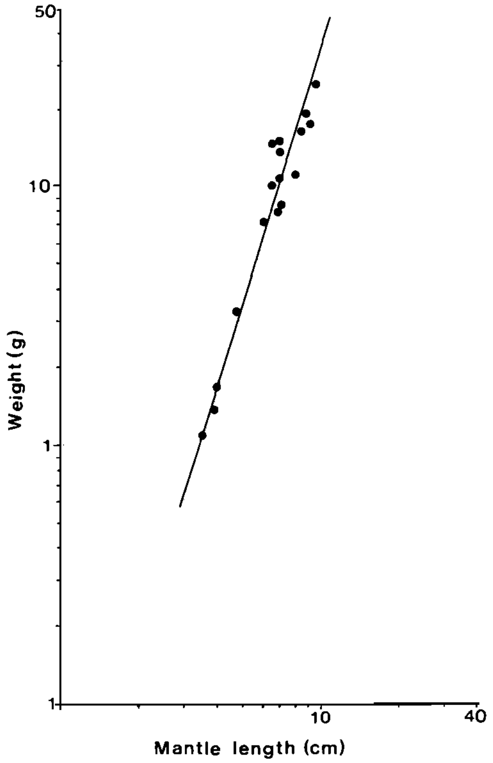

FIGURE 4. Weight/mantle length relationship in squid (Ommastrephidae) in food samples.

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.

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-

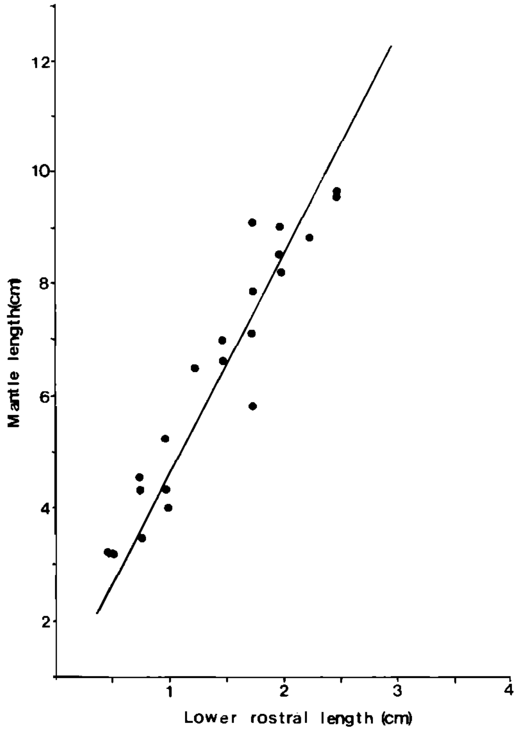

FIGURE 5. Mantle length/beak length relationship in squid (Ommastrephidae) in food samples.

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.

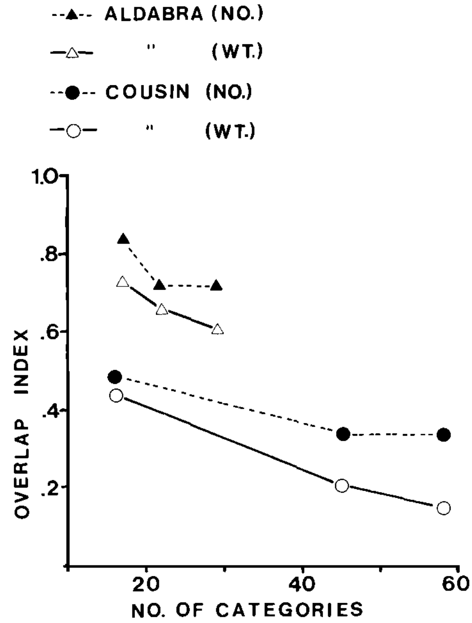

FIGURE 6. Inverse relation between Index of Overlap and number of categories used in comparison (see text for calculation of index).

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-

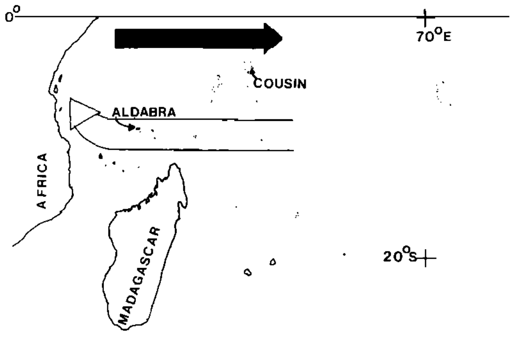

FIGURE 7. Location of Aldabra Atoll and Cousin Island in relation to South Equatorial Current (open arrow) and Equatorial Counter-current (solid black arrow).

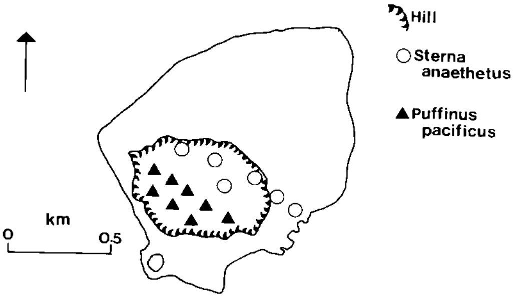

FIGURE 8. Distribution of breeding colonies of Bridled Tern (*Sterna anaethetus*) and Wedge-tailed Shearwater (*Puffinus pacificus*) on Cousin Island. Other seabirds breed in scattered pairs or colonies throughout the island.

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

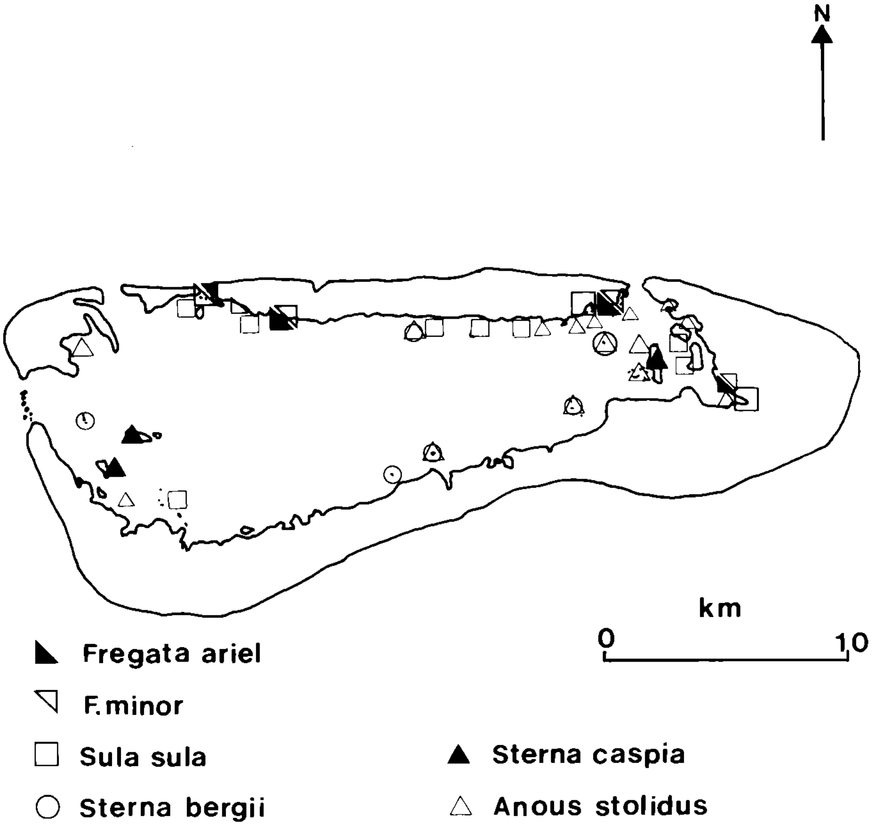

FIGURE 9. Distribution of breeding colonies of seabirds on Aldabra Atoll. Symbol sizes indicate relative sizes of colonies within each species. Locations shown have been used at one time between 1967 and 1976 but not necessarily in same season. Tropicbirds (*Phaethon* spp.) and Audubon's Shearwater (*Puffinus 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

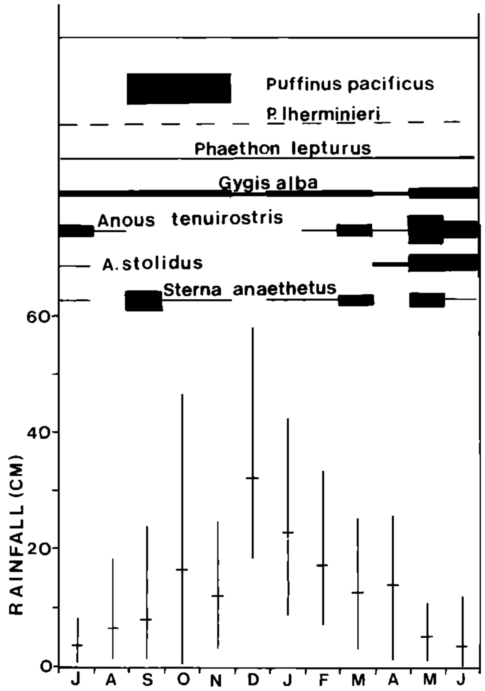

FIGURE 10. Seabird laying seasons in relation to rainfall on Cousin Island. Rainfall data from Prŷs-Jones and Diamond (In press). Depth of solid line indicates degree of restriction to months shown.

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-

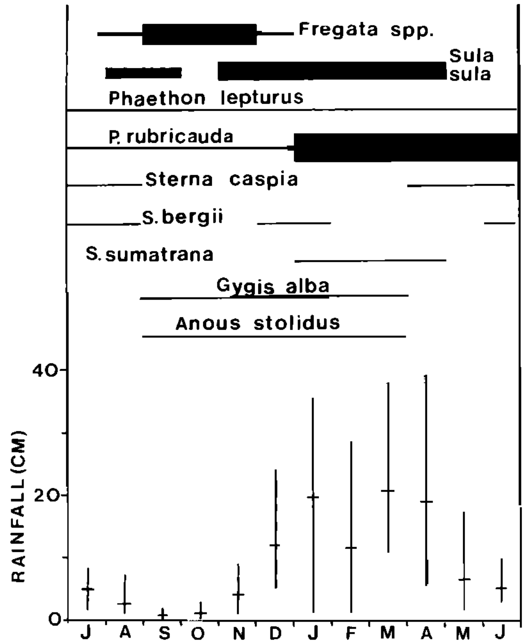

FIGURE 11. Seabird laying seasons in relation to rainfall on Aldabra Atoll. Rainfall data from Prŷs-Jones and Diamond (In press). Depth of solid line indicates degree of restriction to months shown.

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	

[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*		*Fregata minor*		*Sula sula*		*Phaethon rubricauda*		*Phaethon lepturus*		*Anous stolidus*
		No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	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).

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.

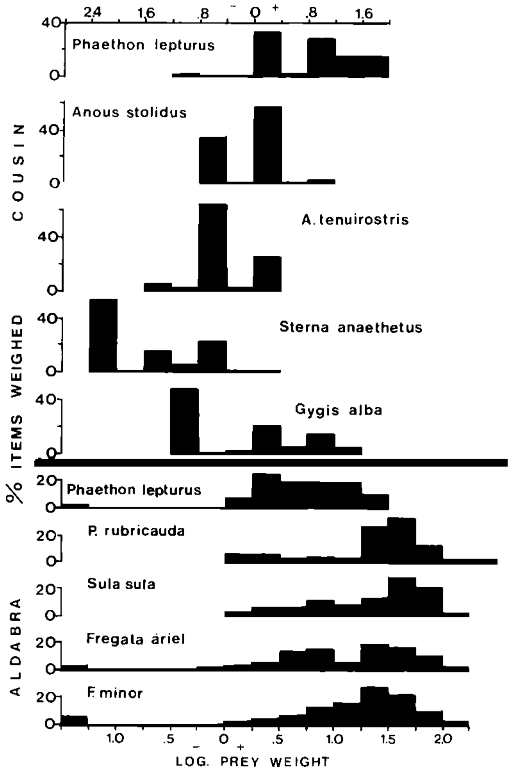

FIGURE 12. Number of prey items in each Log weight-class of Aldabra and Cousin seabirds.

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					

[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

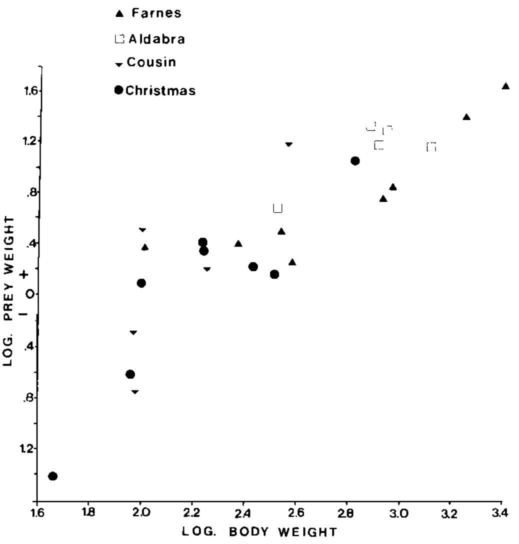

FIGURE 13. Relationship between body weight of seabirds and mean weight of their prey in four communities. Data from Ashmole and Ashmole (1967), Pearson (1968) and this study.

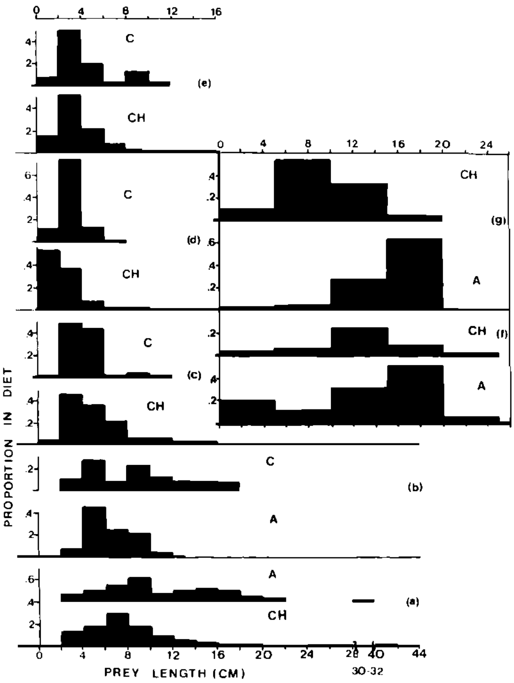

FIGURE 14. Lengths of prey taken by seven species of seabird in each of two different localities. (a) *Phaethon rubricauda* (b) *P. lepturus* (c) *Anous stolidus* (d) *A. tenuirostris* (e) *Gygis alba* (f) *Fregata minor* (g) *Sula sula.* A = Aldabra, C = Cousin, CH = Christmas Island (Pacific). Data 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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PHYSIOLOGICAL ECOLOGY OF INCUBATION IN TROPICAL SEABIRDS

G. C. WHITTOW[1]

ABSTRACT.—Loss of water vapor and carbon dioxide from the egg, uptake of oxygen, and transfer of heat to the egg were compared in tropical seabirds and seabirds breeding in higher latitudes. In the smaller Procellariiformes (petrels, shearwaters) the rate of gas transfer (water vapor, carbon dioxide and oxygen) across the eggshell was relatively low, regardless of geographical distribution. Gas transfer was also comparatively low in tropical charadriiform and pelecaniform seabirds that have been studied. To a large extent, these low rates of gas transfer could be attributed to prolonged incubation which is a feature of the smaller Procellariiformes and of tropical seabirds in general. Gas transfer between eggs and their environment is greatly influenced by the sequence of events during pipping. In many tropical seabirds a relatively large percentage of total water loss from, and oxygen uptake by, the egg, occurs during the pipping phase. Heat transfer between parent bird and the egg is poorly understood in seabirds and there is a need to standardize the measurement of egg temperature so that valid comparisons may be made between species.

Physiological ecology deals with the exchange of materials and energy between an organism and its natural environment. In the specific instance of the seabird's egg, the only such exchanges that occur are the loss of water vapor and carbon dioxide from the egg to the environment, the uptake of oxygen by the egg, and the transfer of heat from the incubating adult to the egg. These exchanges are determined partly by the size and structure of the egg, partly by the physiological activity and growth of the embryo, and partly by ecological factors. Many of these factors are interrelated. The purpose of this paper is to summarize what is known about the factors that affect gas and heat transfer between the egg and its microclimate. Special attention is given to differences between tropical seabirds and seabirds of higher latitudes.

There is no satisfactory definition of a "tropical seabird." For the present review, Ashmole's (1971) definition of the tropic zone was adopted—"comprising all areas where the sea-surface temperature remains above 23°C throughout the year. This approximates the area enclosed by the 23° isotherms for February and August in the Northern and Southern hemispheres, respectively." Thus, all seabirds nesting within a geographical area confined by the 23°C isotherms have been designated tropical seabirds. Seabirds nesting outside this zone were considered to be from "higher latitudes." This definition is less arbitrary than the rigid exclusion of species nesting outside the Tropics of Cancer and Capricorn, and considerably less confining than the use of the tropical convergence (where warm and cool ocean currents meet) to delineate boundaries.

In some instances, insufficient data were available to allow comparisons between tropical seabirds and those that breed in higher latitudes. For the same reason little attempt has been made to distinguish between different families of seabirds.

WATER LOSS FROM THE EGGS

DAILY RATE OF WATER LOSS ($\dot{M}_{H_2O}$)

The mass of the avian egg decreases continuously throughout incubation. This is largely due to loss of water from the egg (Drent 1973, Rahn and Ar 1974). For birds in general, the daily water loss from the egg ($\dot{M}_{H_2O}$) may be predicted from the mass of the freshly-laid egg by means of the following relationship:

$$\underset{(\text{mg/day})}{\dot{M}_{H_2O}} = 13.243\,\underset{(\text{g})}{W^{0.754}} \qquad \text{(Ar and Rahn 1980)}$$

in which $\dot{M}_{H_2O}$ = daily mass loss in mg/day, W = mass of the freshly laid egg in g. This relationship is represented in Figures 1 and 2 by the solid line. All Procellariiformes were below the line, indicating that the water loss from their eggs was less than expected, on the basis of fresh-egg mass (Fig. 1). Insufficient data were available to permit comparisons between tropical seabirds and other seabirds within the order Procellariiformes. The magnitude of the deviation from predicted values, based on egg mass, seemed to be greater for the smaller species. However, the lowest values were for the Fork-tailed Storm-Petrel, *Oceanodroma furcata*, a species which deserts its egg for part of the time, a circumstance which would result in a reduced water loss from the egg. The smallest deviation from predicted values was recorded from the Dark-rumped Petrel, *Pterodroma phaeopygia*, which nests at 3000 m in Haleakala Crater on Maui in the Hawaiian Islands. At this altitude enhanced water loss from the egg is a serious problem because of the reduced barometric pressure (Carey 1980).

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[1] Department of Physiology, John A. Burns School of Medicine, University of Hawaii, Honolulu, Hawaii 96822.

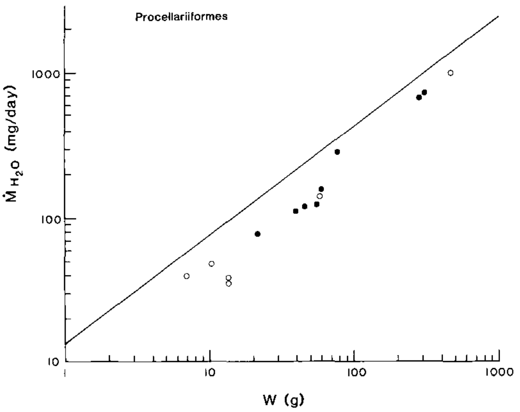

FIGURE 1. Relationship between daily rate of water loss from eggs ($\dot{M}_{H_2O}$) and fresh-egg mass (W) in the Procellariiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $\dot{M}_{H_2O} = 13.243\ W^{0.754}$ (Ar and Rahn 1980). Data from Harris (1966), Tickell (1968), Scott (1970), Boersma and Wheelwright (1979), Grant et al. (1982a, b), Whittow et al. (1982), Rahn and Huntington, pers. comm.; Grant, Whittow and Pettit, unpubl. data, Simons and Whittow, unpubl. data, Whittow, Garnett and Teebaki, unpubl. data, Whittow and Pettit, unpubl. data.

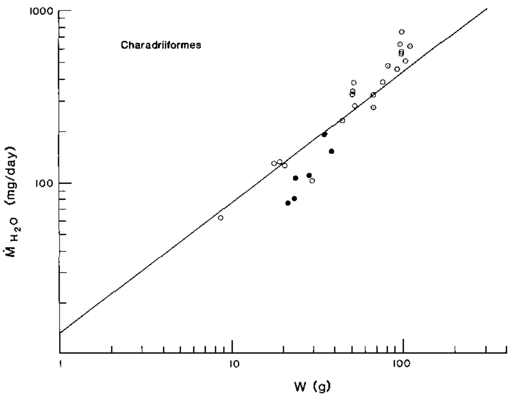

FIGURE 2. Relationship between daily rate of water loss from eggs ($\dot{M}_{H_2O}$) and fresh-egg mass (W) in the Charadriiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $\dot{M}_{H_2O} = 13.243\ W^{0.754}$ (Ar and Rahn 1980). Data from Drent (1970), Rahn et al. (1976), Rahn et al. (1977), Morgan et al. (1978), Rahn and Dawson (1979), Roudybush et al. (1980), Pettit et al. (1981), Vleck, Vleck, Rahn and Paganelli, pers. comm., Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

Among the Charadriiformes also, the water loss from the eggs of the tropical species (terns and noddies) was less than predicted values based on fresh-egg mass (Fig. 2). The daily water loss from the eggs of species from higher latitudes, on the other hand, was close to, or higher than, predicted values. There were two exceptions to this generalization: the water loss from the eggs of the Sooty Tern, *Sterna fuscata,* a tropical species, was very close to the expected value, while that from the Cassin's Auklet's, *Ptychoramphus aleuticus,* egg was considerably lower than predicted.

Insufficient data were available for the water loss from eggs of Pelecaniformes breeding in higher latitudes to permit comparisons with tropical species. However, Table 1 reveals that the values for $\dot{M}_{H_2O}$ in four tropical species were all below the values predicted on the basis of the fresh-egg mass.

Water-vapor conductance of the shell (G_{H_2O})

The rate of water loss from the egg is determined by the water-vapor conductance of the shell (G_{H_2O}) on the one hand, and the difference in water-vapor pressure across the shell (ΔP_{H_2O}), on the other:

TABLE 1
WATER LOSS ($\dot{M}_{H_2O}$) FROM THE EGGS OF FOUR TROPICAL PELECANIFORMES

Species	W (g)[a]	$\dot{M}_{H_2O}$ (mg/day) Measured	Predicted[b]	Reference
White-tailed Tropicbird (*Phaethon lepturus*)	40.7	170.0	216.6	Stonehouse 1962, 1963
Red-footed Booby (*Sula sula*)	58.3	167.1	284.0	Whittow and Pettit, unpubl. data.
Red-tailed Tropicbird (*Phaethon rubricauda*)	71.6	199.2	331.6	Whittow, Grant and Pettit, unpubl. data
Great Frigatebird (*Fregata minor*)	89.1	194.3	391.0	Grant, Whittow and Pettit, unpubl. data

[a] W = Fresh-egg mass.
[b] $\dot{M}_{H_2O} = 13.243\ W^{0.754}$ (Ar and Rahn 1980).

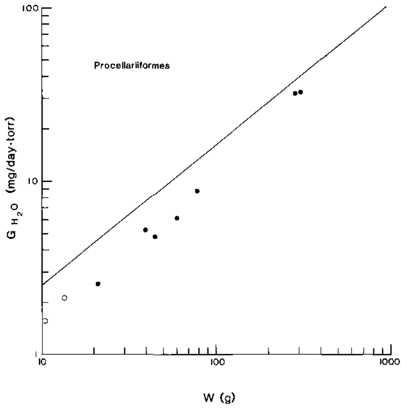

FIGURE 3. Relationship between water-vapor conductance of egg shells and shell membranes (G_{H_2O}) and the fresh-egg mass (W) in Procellariiformes. ● = tropical species; ○ = species breeding in higher latitudes. The solid line represents the relationship $G_{H_2O} = 0.384\ W^{0.814}$ (Ar and Rahn 1978). Data from Vleck and Kenagy (1980), Grant et al. 1982a, b, Whittow et al. 1982, Rahn and Huntington, pers. comm., Grant, Whittow and Pettit, unpubl. data, Pettit and Whittow, unpubl. data, Whittow and Simons, unpubl. data.

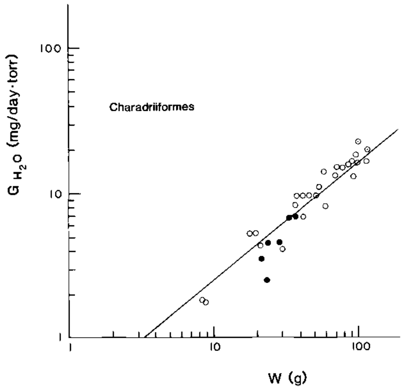

FIGURE 4. Relationship between water-vapor conductance of egg shells and shell membranes (G_{H_2O}) and fresh-egg mass (W) in Charadriiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $G_{H_2O} = 0.384\ W^{0.814}$ (Ar and Rahn 1980). Data from Ar et al. (1974), Rahn et al. (1976), Ar and Rahn (1978), Morgan et al. (1978), Rahn and Dawson (1979), Roudybush et al. (1980), Pettit et al. (1981), Grant, Whittow and Pettit, unpubl. data, Vleck, Vleck, Rahn and Paganelli, pers. comm.

$$\underset{\text{(mg/day)}}{\dot{M}_{H_2O}} = \underset{\text{(mg/day torr)}}{G_{H_2O}} \cdot \underset{\text{(torr)}}{\Delta P_{H_2O}}$$

(Rahn and Ar 1974)

The water-vapor conductance is a measure of the rate at which water vapor may diffuse through the shell and shell membranes. The water-vapor conductance is related to egg mass as follows:

$$\underset{\text{(g/day torr)}}{G_{H_2O}} = 0.384\, \underset{\text{(g)}}{W^{0.814}}$$

(Ar and Rahn 1978)

represented by the solid line in Figures 3 and 4. The water-vapor conductance of the eggs of Procellariiformes was lower than predicted values based on egg mass, but it was not possible to distinguish between tropical and non-tropical species (Fig. 3). As was true for water loss from eggs (Fig. 1), values for the two largest species were closer to the expected values than were values for smaller eggs. As far as Charadriiformes are concerned, species from higher latitudes were well represented by predictions based on their egg mass (Fig. 4); Cassin's Auklet presented the greatest deviation. Among tropical species the deviation was least in the Sooty Tern and greatest in the White Tern, *Gygis alba*. The available data on water-vapor conductance of eggs of Pelecaniformes are presented in Table 2. All measured values were lower than expected in tropical species. They were lower in the two species from higher latitudes also, but clearly more information is needed on non-tropical species, particularly in view of the discrepancy between the two sets of values for the Double-crested Cormorant, *Phalacrocorax auritus*.

Shell thickness (L).—One factor determining the water-vapor conductance of the shell is the shell thickness, because thickness largely prescribes the length of the pathway along which water vapor must diffuse. Shell thickness (L) may also be predicted from mass (W) of the freshly laid egg:

$$\underset{\text{(mm)}}{L} = 5.126 \cdot 10^{-2}\, \underset{\text{(g)}}{W^{0.456}}$$

(Ar et al. 1974)

This relationship is represented by the solid line in Figure 5, which presents data for shell thickness of Procellariiformes. All procellariiform shells were thinner than expected but there seemed to be little difference between the tropical species and other seabirds in this connection. Therefore, low water-vapor conductance of the shell (Fig. 3) was not the consequence of a thicker shell. The shells of charadriiform seabirds were also thinner than for birds in general (Fig. 6) but there seemed to be little difference between tropical and non-tropical species (Fig. 6). What little information exists on the Pelecaniformes suggests that species with obviously chalky shell surfaces (cormorants, boobies) have thicker shells than might be expected on the basis of their fresh-

TABLE 2

WATER-VAPOR CONDUCTANCE (G_{H_2O}) OF THE EGGSHELL AND SHELL MEMBRANES OF PELECANIFORM SEABIRDS

Species	W (g)[a]	G_{H_2O} (mg/day torr)		Reference
		Measured	Predicted[b]	
Tropical species				
Red-footed Booby (*Sula sula*)	58.3	5.80	10.51	Whittow, Pettit, Ackerman and Paganelli, unpubl. data
Red-tailed Tropicbird (*Phaethon rubricauda*)	67.7	9.56	11.88	Ar and Rahn 1978
	71.6	8.98	12.42	Grant, Whittow and Pettit, unpubl. data
Brown Booby (*Sula leucogaster*)	67.8	7.64	11.88	Ar and Rahn 1978
Great Frigatebird (*Fregata minor*)	89.1	7.50	14.84	Grant, Whittow and Pettit, unpubl. data
Species breeding in higher latitudes				
	39.3	6.78	7.62	Ar and Rahn 1978
Pelagic Cormorant (*Phalacrocorax pelagicus*)	49.9	5.56	9.26	Ar and Rahn 1974
Double-crested Cormorant (*Phalacrocorax auritus*)	57.7	8.36	10.42	Ar and Rahn 1978

[a] W = Fresh-egg mass.

[b] $G_{H_2O} = 0.384\ W^{0.814}$ (Ar and Rahn 1978).

egg mass (Table 3). This must be considered as contributory to the low values for G_{H_2O} included in Table 2. The Great Frigatebird, *Fregata minor,* and Red-tailed Tropicbird, *Phaethon rubricauda,* on the other hand, had relatively thin egg shells (Table 3).

Total functional pore area (A_p).—Water vapor diffuses through pores in the shell. The total functional pore area provides an indication of the pore area available for diffusion. Based, in theory, on Fick's Law of Diffusion (Ar et al. 1974), the total functional pore area may be calculated from the measured values of shell thickness (L) and water-vapor conductance (G_{H_2O}):

$$\underset{(\mathrm{mm}^2)}{A_p} = 0.447 \cdot \underset{(\mathrm{mg/torr \cdot day})}{G_{H_2O}} \cdot \underset{(\mathrm{mm})}{L}$$

(Rahn et al. 1976)

The functional pore area so calculated is related to the mass of the freshly laid egg, in most birds, as follows:

$$\underset{(\mathrm{mm}^2)}{A_p} = 9.2 \cdot 10^{-3} \cdot \underset{(\mathrm{g})}{W^{1.236}} \qquad \text{(Ar et al. 1974)}$$

Figure 7 reveals that the functional pore area in Procellariiformes was lower than the value predicted by the above equation, represented in Figure 7, by the solid line. There is no indication from the limited data in Figure 7 that tropical species differed from other seabirds in this respect. In temperate Charadriiformes (Fig. 8) calculated values for A_p were distributed about the line representing predicted values. Tropical species were all below the line but only the White Tern's egg had a functional pore area significantly below predictions. The two cormorants that made up the sample of Pelecaniformes from higher latitudes both had functional pore areas greater than the predicted value (Table 4). All four tropical species had lower values, that for the Great Frigatebird was particularly low—only 52% of predicted.

Number of pores in the eggshell (N).—A low functional pore area means that there are fewer pores in the shell, pores are of smaller diameter, or both. The number of pores (N) in an egg is related to the mass of the freshly laid egg in the following way:

$$\underset{(\mathrm{pores/egg})}{N} = 1449 \cdot \underset{(\mathrm{g})}{W^{0.42}}$$

(Tullet and Board 1977)

This relationship holds for a large number of birds and it is represented by the solid line in Figure 9. The seabirds included in Figure 9 all had fewer pores in their eggshells than might be expected, on the basis of egg mass, with the exception of the two albatross, the largest species included in Figure 9. The pore count for Abbott's Booby, *Sula abbotti,* was also close to the value predicted by the line. Abbott's Booby has the largest egg of any booby and also the longest incubation period in relation to egg mass. Since the pore count included in Figure 9 was performed on a fragment of shell it would seem important to corroborate this datum point on additional specimens of shell.

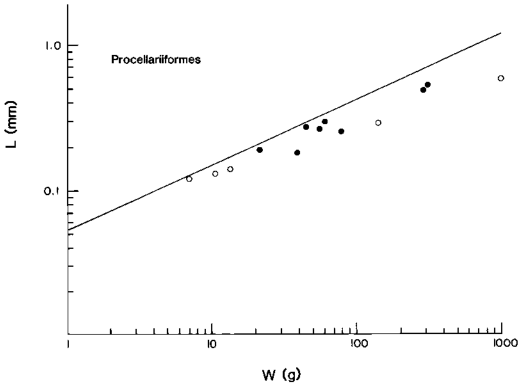

FIGURE 5. Relationship between eggshell thickness (L) and fresh-egg mass (W) in Procellariiformes. ● = tropical species; ○ = breeding in higher latitudes. The line represents the relationship $L = 5.126 \cdot 10^{-2} \cdot W^{0.456}$ (Ar et al. 1974). Data from Harris (1966), Tickell (1968), Scott (1970), Vleck and Kenagy (1980), Grant et al. (1982a, b), Whittow et al. (1982), Rahn and Huntington, pers. comm.; Whittow, Garnett, and Teebaki, unpubl. data, Whittow, Grant, Pettit and Naughton, unpublished data, Whittow, Pettit and Naughton, unpubl. data, Whittow and Simons, unpubl. data.

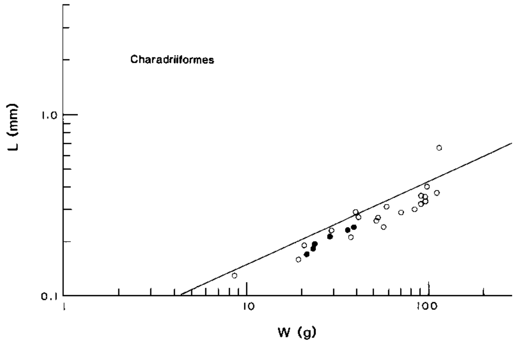

FIGURE 6. Relationship between eggshell thickness (L) and fresh-egg mass (W) in Charadriiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $L = 5.126 \cdot 10^{-2} \cdot W^{0.456}$ (Ar et al. 1974). Data from Rahn et al. (1976), Ar and Rahn (1978), Morgan et al. (1978), Rahn and Dawson (1979), Roudybush et al. (1980), Pettit et al. (1981), Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

In fact, Figure 9 presents evidence that there is a difference in the relationship between pore numbers and fresh-egg mass in seabirds and in the birds represented by the line, rather than between tropical seabirds and other seabirds. The relationship for seabirds is as follows:

$$N = 278.6 \cdot W^{0.704}$$

Pore geometry.—Functional pore area A_p may be divided by number of pores to obtain the average area for each pore (P_A). The radius (P_r) of a single average pore may then be derived from the relationship:

TABLE 3
EGGSHELL THICKNESS (L) OF PELECANIFORM SEABIRDS

Species	W (g)[a]	L (mm) Measured	L (mm) Predicted[b]	Reference
Tropical species				
Red-footed Booby (*Sula sula*)	58.3	0.40	0.33	Whittow, Pettit, Ackerman and Paganelli, unpubl. data
Red-tailed Tropicbird (*Phaethon rubricauda*)	67.7	0.36	0.35	Ar and Rahn 1978
	71.6	0.34	0.36	Whittow, Grant and Pettit, unpubl. data
Brown Booby (*Sula leucogaster*)	67.8	0.39	0.35	Ar and Rahn 1978
Great Frigatebird (*Fregata minor*)	89.1	0.37	0.40	Whittow, Grant and Pettit, unpubl. data
Abbott's Booby (*Sula abbotti*)	112.0	0.48	0.44	Whittow, Rahn and Powell, unpubl. data; Nelson, 1971
Species breeding in higher latitudes				
Pelagic Cormorant (*Phalacrocorax pelagicus*)	39.3	0.35	0.27	Ar and Rahn, 1978
Double-crested Cormorant (*Phalacrocorax auritus*)	57.7	0.39	0.33	Ar and Rahn, 1978

[a] W = Fresh-egg mass.
[b] $L = 5.126 \cdot 10^{-2} \cdot W^{0.456}$ (Ar et al. 1974).

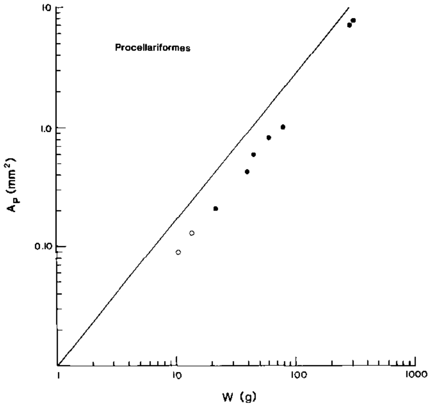

FIGURE 7. Relationship between functional pore area (A_p) of eggshell and fresh-egg mass (W) in Procellariiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $A_p = 9.2 \cdot 10^{-3} \cdot W^{1.236}$ (Ar et al. 1974). Data from Vleck and Kenagy (1980), Grant et al. (1982a, b), Whittow et al. (1982), Rahn and Huntington, pers. comm., Grant, Whittow, Pettit and Naughton, unpubl. data, Whittow and Simons, unpubl. data.

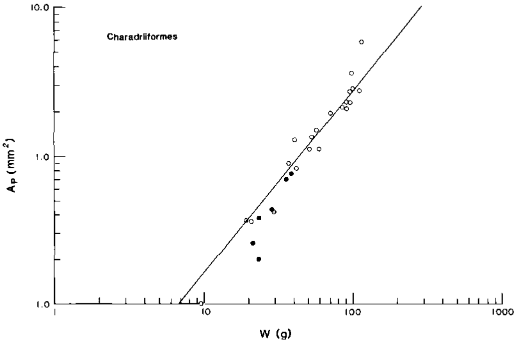

FIGURE 8. Relationship between functional pore area (A_p) of eggshell and fresh-egg mass (W) in Charadriiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $A_p = 9.2 \cdot 10^{-3} \cdot W^{1.236}$ (Ar et al. 1974). Data from Rahn et al. (1976), Ar and Rahn (1978), Morgan et al. (1978), Rahn and Dawson (1979), Roudybush et al. (1980), Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

$$P_r = \sqrt{P_A/\pi} \qquad \text{(Rahn 1980)}$$

Allometric relationships have not been established for pore area and radius. In Figures 10 and 11 available data for P_A and P_r are plotted against mass of the fresh egg, for tropical and non-tropical seabirds. There was a linear relationship between both P_A and P_r on one hand, and W on the other (Figs. 10, 11) and little evidence of any difference between tropical seabirds and other birds.

Water-vapor pressure difference (ΔP_{H_2O})

As indicated above, daily rate of water loss from the egg is determined by two factors: water-vapor conductance of the shell (G_{H_2O}) and the difference in water-vapor pressure (ΔP_{H_2O}) between contents of the egg and the microclimate of the incubated egg. Preceding sections have shown that water-vapor conductance of shells of many seabird eggs, particularly those of tropical

TABLE 4
FUNCTIONAL PORE AREA (Ap) OF THE EGGSHELL OF PELECANIFORM SEABIRDS

Species	W (g)[a]	Ap (mm²) Calculated[b]	Predicted[c]	Reference
		Tropical species		
Red-footed Booby (*Sula sula*)	58.3	1.04	1.40	Whittow, Pettit, Ackerman and Paganelli, unpubl. data
Red-tailed Tropicbird (*Phaethon rubricauda*)	67.7	1.54	1.68	Ar and Rahn 1978
	71.6	1.36	1.80	Whittow, Grant and Pettit, unpubl. data
Brown Booby (*Sula leucogaster*)	67.8	1.33	1.69	Ar and Rahn 1978
Great Frigatebird (*Fregata minor*)	89.1	1.24	2.37	Whittow, Grant and Pettit, unpubl. data
		Species breeding in higher latitudes		
Pelagic Cormorant (*Phalacrocorax pelagicus*)	39.3	1.06	0.86	Ar and Rahn 1978
Double-crested Cormorant (*Phalacrocorax auritus*)	57.7	1.46	1.38	Ar and Rahn 1978

[a] W = Fresh-egg mass.
[b] $Ap = 0.447 \cdot G_{H_2O} \cdot L$. (Rahn et al. 1976).
[c] $Ap = 9.2 \cdot 10^{-3} \cdot W^{1.236}$ (Ar et al. 1974).

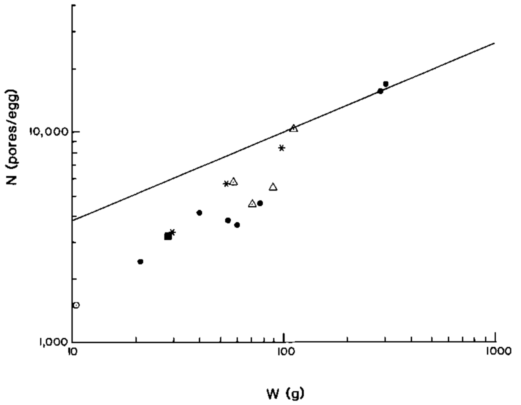

FIGURE 9. Relationship between number of pores (N) in eggshells of sea birds and fresh-egg mass (W). ● = tropical Procellariiformes; ○ = Procellariiformes breeding in higher latitudes; ■ = tropical Charadriiformes; * = Charadriiformes breeding in higher latitudes; Δ = tropical Pelecaniformes. The line represents the relationship $N = 1449 \cdot W^{0.42}$ (Tullet and Board 1977). Data from Nelson (1971), Rahn and Dawson (1979), Roudybush et al. (1980), Grant et al. (1982a, b), Whittow et al (1982), Rahn and Huntington, pers. comm. Whittow and Pettit, unpubl. data, Whittow, Garnett, Teebaki and Pettit, unpubl. data, Whittow, Grant and Pettit, unpubl. data, Whittow, Pettit and Naughton, unpubl. data, Whittow, Simons, and Pettit, unpubl. data, Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

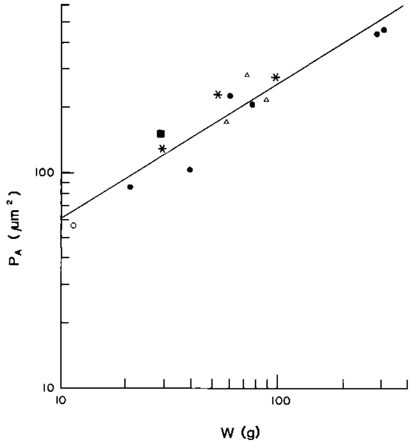

FIGURE 10. Relationship between mean area of a pore (P_A) and fresh-egg mass (W). ● = tropical Procellariiformes; ○ = Procellariiformes breeding in higher latitudes; ■ = tropical Charadriiformes; * = Charadriiformes breeding in higher latitudes; Δ = tropical Pelecaniformes. The line represents the relationship $P_A = 14.44\ W^{0.627}$, $r = 0.954$ (correlation coefficient), calculated as linear regression of logarithms of data. Data from Rahn and Dawson (1979), Roudybush et al. (1980), Grant et al. (1982a, b), Whittow et al. (1982), Rahn and Huntington, pers. comm., Whittow and Pettit, unpubl. data, Whittow, Garnett, Teebaki and Pettit, unpubl. data, Whittow, Grant and Pettit, unpubl. data, Whittow, Simons and Pettit, unpubl. data, Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

seabirds, is lower than expected. Is there a comparable reduction in ΔP_{H_2O}? Values for ΔP_{H_2O} may be calculated if $\dot{M}_{H_2O}$ and G_{H_2O} are known. Data for ΔP_{H_2O}, so calculated, are shown in Table 5. Data for Fork-tailed Storm-Petrels are no more than an approximation because of the variable degree of egg neglect in this species. Ar and Rahn (1980) reported an average value of 34 torr for ΔP_{H_2O} in a large number of birds. Table 5 reveals that average values for three orders of seabirds were below this figure. Average values for species breeding more distant from the equator were higher than those of tropical species, but adequate data for statistical comparisons were available only for Charadriiformes. That comparison did not reveal a significant difference between tropical and non-tropical species. Little evidence exists at present that a lower value for ΔP_{H_2O} in tropical seabirds contributes to their relatively low $\dot{M}_{H_2O}$.

Water-vapor pressure of egg contents ($P_{H_2O,egg}$).— Water-vapor pressure difference ΔP_{H_2O} is the difference between water-vapor pressure of contents of the egg ($P_{H_2O,egg}$) and that of the microclimate of the egg ($P_{H_2O,nest}$). Assuming that contents of the egg are saturated with water vapor, water-vapor pressure may be calculated if egg temperature is known. Mean central egg temperatures (T_{egg}) of seabirds are included in Table 5 together with egg water-vapor

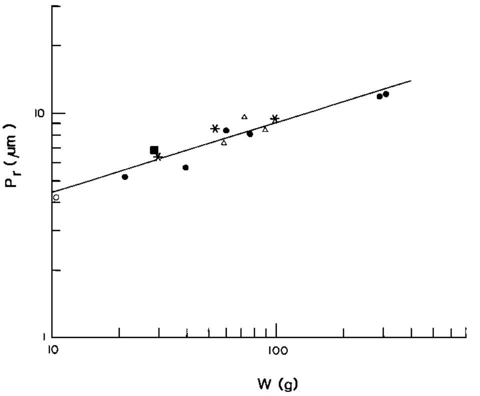

FIGURE 11. Relationship between pore radius (P_r) and fresh-egg mass (W). The symbols and sources of data are the same as in Figure 10. The line represents the relationship $P_r = 2.17\ W^{0.31}$, $r = 0.947$ (correlation coefficient), calculated as linear regression of logarithms of data.

pressures ($P_{H_2O,egg}$) derived from them. Variations in water-vapor pressure of the egg reflect variations in egg temperature. Mean egg temperature of twenty-seven species of birds was reported to be 35.6°C by Drent (1975). The average values for the seabirds included in Table 5 were close to, or above, 35.6°C. Procellariiform eggs tended to be incubated at a relatively low temperature; the egg temperature of the Fork-tailed Storm-Petrel's egg is particularly low. In some seabirds (e.g., the Laysan Albatross, *Diomedea immutabilis*) it is known that the central egg temperature changes during incubation. A single value for egg temperature may therefore be quite misleading. It would be valuable, for future reference, if egg temperatures were measured at comparable stages in development of the embryo. The time immediately prior to the initial event in the pipping process would be a useful reference point for comparisons between species, and it would also be in accord with measurements of embryonic oxygen consumption and other physiological variables (see below).

The technique of measuring egg temperature is also a source of variation. Insertion of a rapidly responding, fine needle thermistor probe immediately after removal of the egg from under the bird is the method of choice. Indwelling thermistors invariably result in death of the embryo, abolition of embryonic heat production, and a change in egg temperature (Grant et al. 1982b). The position of the tip of the thermistor is also important. From the standpoint of embryonic development and metabolism, the thermistor tip should be placed close to the embryo, which changes position during incubation. If egg temperature is taken immediately prior to the initial event during pipping, as suggested above, the center of the egg would be an appropriate position for the thermistor tip. Central egg temperature would also be the best *single* position for the measurement of egg temperature for calculations of heat transfer between the egg and its surroundings and also for computation of the water-vapor pressure inside the egg.

Water-vapor pressure of the nest ($P_{H_2O,nest}$).—Subtraction of the water-vapor pressure difference (ΔP_{H_2O}) from water-vapor pressure of the contents of the incubated egg ($P_{H_2O,egg}$), yields water-vapor pressure of the micro-climate of the incubated egg ($P_{H_2O,nest}$). This value may also be measured directly, by the technique of egg hygrometry (Rahn et al. 1977). The information in Table 5 was derived from both computed and measured values. Ar and Rahn (1978) reported that the average water-vapor pressure of the egg's micro-climate was 19 torr, for 23 species. Average values for tropical species of seabirds, given in Table 5, were close to this figure (19). However, mean values do not reveal some interesting divergences from the mean. Thus, among tropical Procellariiformes, the $P_{H_2O,\ nest}$ for two burrowing species, Bonin Petrel, *Pterodroma hypoleuca,* (Grant et al. 1982a) and Wedge-tailed Shearwater, *Puffinus pacificus* (Whittow et al. 1982), are not notably different from those for the surface nesting Laysan and Black-footed albatross, *Diomedea nigripes* (Grant et al. 1982b), and the Christmas Shearwater, *Puffinus nativitatus* (Whittow, Grant and Pettit, unpub. data). In tropical Pelecaniformes, information was available on only three species. The lowest value (15.8 torr) was recorded in the Red-footed Booby, *Sula sula* (Whittow and Pettit, unpubl. data), a tree-nesting species, and the highest figure occurred in the Red-tailed Tropicbird (Whittow, Grant and Pettit, unpub. data), which lays its egg directly on the moist soil. The two petrels from higher latitudes had especially low values for $P_{H_2O,nest}$; the Fork-tailed Storm-Petrel (Boersma and Wheelwright 1979, Vleck and Kenagy 1980), neglects its egg for a variable amount of time and, during this time, the microclimate of the egg is that of ambient air, i.e., the $P_{H_2O,nest}$ is correspondingly low. However, the low egg temperature of the continuously incubated egg (Table 5) would, other things being equal, lead to a low calculated value for $P_{H_2O,nest}$ in this species. The low water-vapor pressure of the cooler air may also be a factor in determining the low $P_{H_2O,nest}$ in the Fork-tailed and Leach's Storm-Petrel, *Oceanodroma leucorhoa,* (Rahn and Huntington, pers. comm.). The diversity of values among Charadriiformes is considerable.

NEST VENTILATION ($\dot{V}_{nest}$)

Water that diffuses out of the egg into the microclimate of the egg is ultimately lost to ambient air. Water loss from the incubated egg's microclimate to the surrounding air occurs by a combination of diffusion and convection. Convection is probably the major pathway for water loss, especially if there is air movement around the incubating bird. Moreover, convective water loss is susceptible to modification by the incubating bird itself. Thus, each time the bird stands up, turns its egg or leaves the egg unattended, there must be an increased convective water loss from the vicinity of the egg. Rahn et al. (1976) presented an equation to describe this convective water loss in terms of the amount of ventilation ("nest ventilation") required to remove water lost from the egg:

$$\underset{\text{(l/day)}}{\dot{V}_{nest}} = \underset{\text{(mg/day)}}{\dot{M}_{H_2O}} \ / \ \underset{\text{(mg/l)}}{(C_{nest} - C_{air})}$$

(Rahn et al. 1976)

where $\dot{V}_{nest}$ = nest ventilation; $\dot{M}_{H_2O}$ = daily water

TABLE 5

Water-vapor Pressure Difference (ΔP_{H_2O}) Between the Egg and the Nest Microclimate, Central Egg Temperature (T_{egg}), Water-vapor Pressure Inside the Egg ($P_{H_2O,egg}$) and in the Nest Microclimate ($P_{H_2O,nest}$). Data are from References Cited in Figures 1–4 and Tables 1–2 Unless Otherwise Indicated

Order Breeding latitude Species	ΔP_{H_2O} (torr)	T_{egg} (°C)	$P_{H_2O,egg}$ (torr)	$P_{H_2O,nest}$ (torr)
Procellariiformes				
Tropical				
Bulwer's Petrel (*Bulweria bulwerii*)	30.3	—	—	—
Bonin Petrel (*Pterodroma hypoleuca*)	21.3	33.8	39.5	18.1[d]
Christmas Shearwater (*Puffinus nativitatis*)	24.8	35.3	42.9	18.1
Wedge-tailed Shearwater (*Puffinus pacificus*)	22.6	35.0	42.2	19.6[d]
Dark-rumped Petrel (*Pterodroma phaeopygia*)	21.9	34.9	41.9	20.0
Laysan Albatross (*Diomedea immutabilis*)	25.0	35.8	44.1	19.1[d]
Black-footed Albatross (*Diomedea nigripes*)	24.9	35.0	42.2	17.3[d]
	24.4	35.0	42.1	18.7
Higher latitudes				
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	30.7	33.4	38.6	7.9
Fork-tailed Storm-Petrel (*Oceanodroma furcata*)	16.6	29.7[a]	31.3	14.7
	23.7	31.6	34.9	11.3
Charadriiformes				
Tropical				
White Tern (*Gygis alba*)	21.3	35.4	43.1	22.0
	26.8	35.3	42.9	14.6[d]
	23.5	37.4	48.1	24.5
Black Noddy (*Anous tenuirostris*)	—	34.9	41.9	—
Sooty Tern (*Sterna fuscata*)	28.1	35.7[b]	43.8	15.7
Brown Noddy (*Anous stolidus*)	25.3	35.6	43.6	18.3
Gray-backed Tern (*Sterna lunata*)	23.6	36.5	45.8	22.2
	24.8	35.9	44.2	19.4
Higher latitudes				
Least Tern (*Sterna albifrons*)	35.2	—	—	—
Arctic Tern (*Sterna paradisaea*)	25.1	—	—	—
Common Tern (*Sterna hirundo*)	29.3	—	—	—
Forster's Tern (*Sterna fosteri*)	21.3	34.8	41.7	20.4[d,e]
Cassin's Auklet (*Ptychoramphus aleuticus*)	24.8	—	—	—
Sandwich Tern (*Sterna sandvicensis*)	22.0	—	—	—
Laughing Gull (*Larus atricilla*)	23.0	—	—	—
Black-legged Kittiwake (*Rissa tridactyla*)	33.2	37.4	48.1	15.0
Heermann's Gull (*Larus heermanni*)	27.8	36.8	46.6	18.4[d]
Common Puffin (*Fratercula arctica*)	33.8	—	—	—
Royal Tern (*Sterna maxima*)	24.0	37.8	49.2	25.2
Lesser Black-backed Gull (*Larus fuscus*)	23.7	—	—	—
Herring Gull (*Larus argentatus*)	27.4	38.3	50.5	23.0
Glaucous-winged Gull (*Larus glaucescens*)	24.6	36.0	44.6	20.0
Western Gull (*Larus occidentalis livens*)	35.6	33.8[c]	39.5	26.1[d]
South Polar Skua (*Catharacta maccormicki*)	35.5	36.0	44.6	9.0
Great Black-backed Gull (*Larus marinus*)	29.9	—	—	—
	28.0	36.4	45.6	19.6
Pelecaniformes				
Tropical				
Red-footed Booby (*Sula sula*)	28.8	36.0	44.6	15.8
Red-tailed Tropicbird (*Phaethon rubricauda*)	22.2	36.0	44.6	22.4
Great Frigatebird (*Fregata minor*)	25.9	36.8	46.6	20.7
	25.6	36.3	45.3	19.6

[a] Boersma et al. 1980.
[b] Howell and Bartholomew 1962.
[c] Bennett et al. 1981.
[d] Measured directly by egg hygrometry (Rahn et al. 1977).
[e] Grant 1982.

TABLE 6

FRESH-EGG MASS (W), NEST VENTILATION ($\dot{V}_{nest}$), WATER-VAPOR PRESSURE IN THE NEST ($P_{H_2O,nest}$) AND AMBIENT WATER-VAPOR PRESSURE ($P_{H_2O,air}$) FOR SEVEN SPECIES OF SEABIRDS

Order Species	W (g)	$\dot{V}_{nest}$ (l/day)	$P_{H_2O,nest}$ (torr)	$P_{H_2O,air}$ (torr)	$P_{H_2O,nest} - P_{H_2O,air}$ (torr)	Reference
Procellariiformes						
Bonin Petrel (*Pterodroma hypoleuca*)	39.5	36.5	18.1	14.9	3.2	Grant et al. 1982a
Wedge-tailed Shearwater (*Puffinus pacificus*)	60.0	70.9	19.6	17.3	2.3	Whittow et al. 1982
Laysan Albatross (*Diomedea immutabilis*)	285.0	133.0	19.1	13.7	5.4	Grant et al. 1982b
Black-footed Albatross (*Diomedea nigripes*)	305.0	209.0	17.3	13.7	3.6	Grant et al. 1982b
Charadriiformes						
Black-legged Kittiwake (*Rissa tridactyla*)[a]	51.5	39.7	15.0	6.4	8.6	Morgan et al. 1978
Heermann's Gull (*Larus heermanni*)[a]	53.4	81.0	18.4	14.4	4.0	Rahn and Dawson, 1979
Glaucous-winged Gull (*Larus glaucescens*)[a]	98.2	44.0	20.0	6.4	13.6	Morgan et al. 1978

[a] Breeding outside the tropics.

loss from the egg = water lost from the nest; C_{nest} and C_{air} = water-vapor content of air in the nest microclimate and ambient air, respectively. Water loss from the egg may be measured directly and so may water-vapor content of ambient air, if air temperature and either air relative humidity or its water-vapor pressure are measured. The value for C_{nest} may be calculated if the mean temperature of the nest microclimate is taken to be 34°C (Drent 1975) and the nest microclimate water-vapor pressure has been measured by egg hygrometry or calculated as described above.

Morgan et al. (1978) calculated nest ventilation for two Alaskan gulls sharing the same ambient conditions (Table 6). The egg of the Glaucous-winged Gull (*Larus glaucescens*) was almost twice as large as that of the Black-legged Kittiwake (*Rissa tridactyla*). Other things being equal, one might expect the larger egg, with its greater water loss, to require a considerably greater ventilation of its nest. However, nest ventilation of the gull was only 10.8% greater. This might be attributed to higher nest water-vapor pressure (20 torr) for the gull than for kittiwake (15 torr), with a correspondingly greater difference in water-vapor pressure between nest and ambient air. Thus, the kittiwake's nest might require relatively more ventilation because of a smaller difference in $P_{H_2O,nest} - P_{H_2O,air}$. These data invite comparison with calculated nest ventilation for Heermann's Gulls (*Larus heermanni*) breeding under warm conditions off the Mexican coast (Rahn and Dawson 1979). The size of the egg is similar in the Black-legged Kittiwake and Heermann's Gull. However, ambient water-vapor pressure is higher in Heermann's Gulls with a correspondingly lower difference in ($P_{H_2O,nest} - P_{H_2O,air}$) and a greater requirement for nest ventilation (Table 6). Considerations of nest ventilation in the gulls is complicated by differences in clutch size. Bonin Petrels, *Pterodroma hypoleuca* and Wedge-tailed Shearwaters are two Procellariiforms that lay a single egg in a burrow in the ground. Of the seven species included in Table 6, these two species have lowest values for $P_{H_2O,nest} - P_{H_2O,air}$. Nest ventilation of Bonin Petrels is not much less than that for the larger egg of Black-legged Kittiwakes. Nest ventilation for Wedge-tailed Shearwaters is well above that for the larger egg of Glaucous-winged Gulls, *Larus glaucescens*. In two species of albatross investigated by Grant et al. (1982b), a single egg is laid, and the eggs are similar size. Nevertheless, nest ventilation required by Black-footed Albatross was 57% greater than that for Laysan Albatross, reflecting the lower water-vapor pressure in the Black-footed Albatross' nest and the smaller difference in water-vapor pressure between its nest and surroundings. However, direct observations of birds revealed a greater frequency of nest ventilating behavior by Laysan Albatrosses! In fact, Walsberg (1980) calculated that, in general, changes in nest ventilation would be relatively ineffective in regulating water loss from the egg. He subsequently produced evidence that two species of terrestrial birds did not actively regulate nest humidity (Walsberg 1983).

Calculation of nest ventilation is subject to three errors. In the first place, the computation does not include water loss from the incubation patch. Therefore total water loss must exceed water loss from the egg by an unknown amount. Nevertheless, nest ventilation as computed does

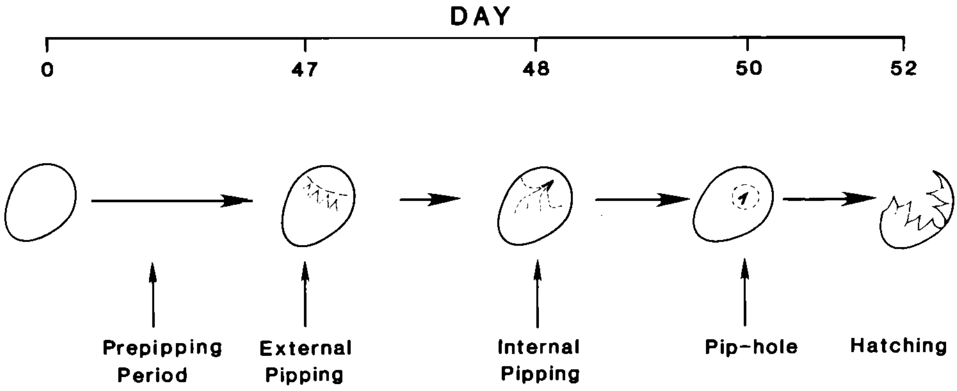

FIGURE 12. Sequence of events during pipping in Wedge-tailed Shearwaters (Pettit and Whittow 1982b).

represent the minimal ventilation necessary to dissipate water lost from the egg itself. Another error arises from the assumption that nest temperature is 34°C. Nest temperature has never been measured satisfactorily; it is a heterogeneous temperature and its exact measurement would require measurement of area and temperature of the interface between egg and feathers, and egg and nest material. Nest temperatures should then be a weighted mean of these measurements. The concept of nest ventilation is potentially useful, because it assigns quantitative values to behavioral phenomena. I hope that future applications of the equation for nest ventilation will employ measurements of water loss from the skin of the incubating bird together with measured values of nest temperature. A third error arises from the use of daily rate of water loss from unpipped eggs. While this would be appropriate before the egg is pipped, it would underestimate nest ventilation from pipped eggs, from which water loss is very much greater (see following section).

Water Loss from Pipped Eggs

In many species of tropical seabirds, the initial event in the pipping process is a series of star fractures in the shell. This may occur up to a week before emergence of the hatchling. The implications of star fracturing of the shell, for water loss from the egg, are considerable. Prior to star fracturing, which has been referred to as "external pipping" by the present author and his colleagues, water loss from the egg can occur only by diffusion through pores in the shell. Shell fracture, however, effectively establishes a leak through the shell, and then water loss through the shell is, not surprizingly, higher.

In shearwaters and petrels, and also in the terns that have been studied, the next event in the pipping process is penetration of the air cell by the beak of the embryo (Fig. 12). This event ("internal pipping") has little effect on water loss from the egg, although it marks the beginning of embryonic pulmonary ventilation, the embryo rebreathing gas in the air cell. However, establishment of a distinct hole ("pip-hole"—some investigators have termed this phenomenon "external pipping") in the shell, provides further opportunities for increased water loss, including from the respiratory tract of the embryo. The duration of the pipping phase (from star fracture to hatching) is short in relation to total duration of incubation. However, the augmented water loss during this period means that total water loss from the pipped egg is a significant fraction of cumulative water loss from the egg during the entire incubation period (Table 7). In the six species included in Table 7, water loss between star fracture and hatching was as high as 42% of cumulative water loss over the entire incubation period. In the two species of albatross the water loss from pipped eggs amounted to only 9–11% of total water loss from the egg. The pipping sequence in albatross differs from that in petrels, shearwaters and terns. In the albatross, internal pipping is the initial event, followed by star fracture. The interval between star fracture and hatching is correspondingly shorter in the albatross (Table 7). Therefore, in four Procellariiformes and two Charadriiformes, total water loss from star fractured eggs, expressed as a percentage of cumulative water loss from the egg, parallels the duration of the interval between star fracture and hatching. It is noteworthy that, in this small series of tropical procellariiform seabirds, in which egg size varied by a factor of more than seven, there was a change in sequence of pipping with increasing egg size, and also a definite change in both relative duration of the interval between star fracture and hatching, and the fraction of total water loss that is lost during this interval. It may also be pertinent that the incubation period of smaller eggs is relatively longer than those of the larger albatross eggs (see Discussion). Thus, there may be a correlation between sequence of pipping, size of the egg, duration of its pipping phase, and fractional water loss from pipped eggs. A corollary to these observations is that total water loss during the pre-pipping period is relatively large in bigger eggs (Table 7).

Total Water Loss from the Egg

In contrast to the different way in which water loss is partitioned between the pre-pipping period and the pip-to-hatch interval (Table 7), cumulative water loss over the entire incubation period, expressed as a fraction of the fresh-egg mass, did not vary greatly in six species (Table 7). These observations, although limited in scope, are compatible with the belief that total water loss from the egg is a closely regulated fraction of fresh-egg mass. This belief conforms also with evidence presented by Ar and Rahn (1980) that water content of the freshly laid egg and of the hatchling, are very similar. Thus, in six charadriiform seabirds, mean water content of freshly laid egg and hatchling was 77.2 and 78.2%, respectively.

OXYGEN UPTAKE BY THE EGG

Daily Rate of Embryonic Oxygen Consumption ($\dot{V}_{O_2}$,$\dot{M}_{O_2}$)

The rate of oxygen transfer into the egg through the shell is equal to the rate of oxygen consumption by the embryo. Unlike the rate of water loss from the egg, which is constant over a large part of the incubation period, oxygen uptake by the egg increases as the embryo grows (e.g., Ackerman et al. 1980). The pattern of increase in oxygen consumption with time, for two tropical Procellariiformes, is illustrated in Figure 13. A similar pattern has been reported for Leach's Storm-Petrel (Rahn and Huntington, pers. comm.) and the Fork-tailed Storm-Petrel (Vleck and Kenagy 1980), two species from higher latitudes. As the mode of development of all four species is similar, a similar pattern of increase in oxygen consumption is expected (Vleck et al. 1980), but does not necessarily follow. Pettit et al. (1981, 1982a, b) considered a logistic equation to best describe the data.

Rahn and Ar (1974), Hoyt et al. (1978) and Hoyt and Rahn (1980) established a relationship between oxygen uptake immediately prior to internal pipping, and fresh-egg mass. In those eggs in which internal pipping is the initial event in the pipping process, this is a valid point of ref-

TABLE 7

Time Interval and Water Loss Between (a) the Laying of the Egg and Star Fracture of the Shell (Pre-pipping), (b) Star-fracture of the Shell and Hatching (Pip-hatch) and the Total Water Loss from the Egg in Six Species of Tropical Seabirds

Order Species	W^a (g)	I^b (days)	Total water loss (g)	Total water loss (% of W)	Pre-pipping period (% of I)	Pre-pipping water loss (% of total water loss)	Pip-hatch interval (% of I)	Pip-hatch water loss (% of total)	Reference
Procellariiformes									
Bonin Petrel (*Pterodroma hypoleuca*)	39.2	48.7	7.3	18.6	87.7	65.1	12.1	34.9	Grant et al. 1982a
Wedge-tailed Shearwater (*Puffinus pacificus*)	60.0	52.0	10.7	17.2	90.8	71.0	9.2	29.0	Whittow et al. 1982, Pettit and Whittow 1982b
Laysan Albatross (*Diomedea immutabilis*)	284.8	65.0	45.7	16.0	95.1	91.2	4.9	8.8	Grant et al. 1982b
Black-footed Albatross (*Diomedea nigripes*)	304.9	66.0	49.2	16.1	94.4	88.9	5.6	11.1	Grant et al. 1982b
Charadriiformes									
White Tern (*Gygis alba*)	23.3	35.5	4.1	17.6	85.4	58.0	14.6	42.2	Pettit et al. 1981
Gray-backed Tern (*Sterna lunata*)	28.7	30.3	4.1	14.3	86.5	68.3	13.5	31.7	Whittow, Grant, Flint and Pettit, unpubl. data

[a] Fresh-egg mass.
[b] Incubation period.

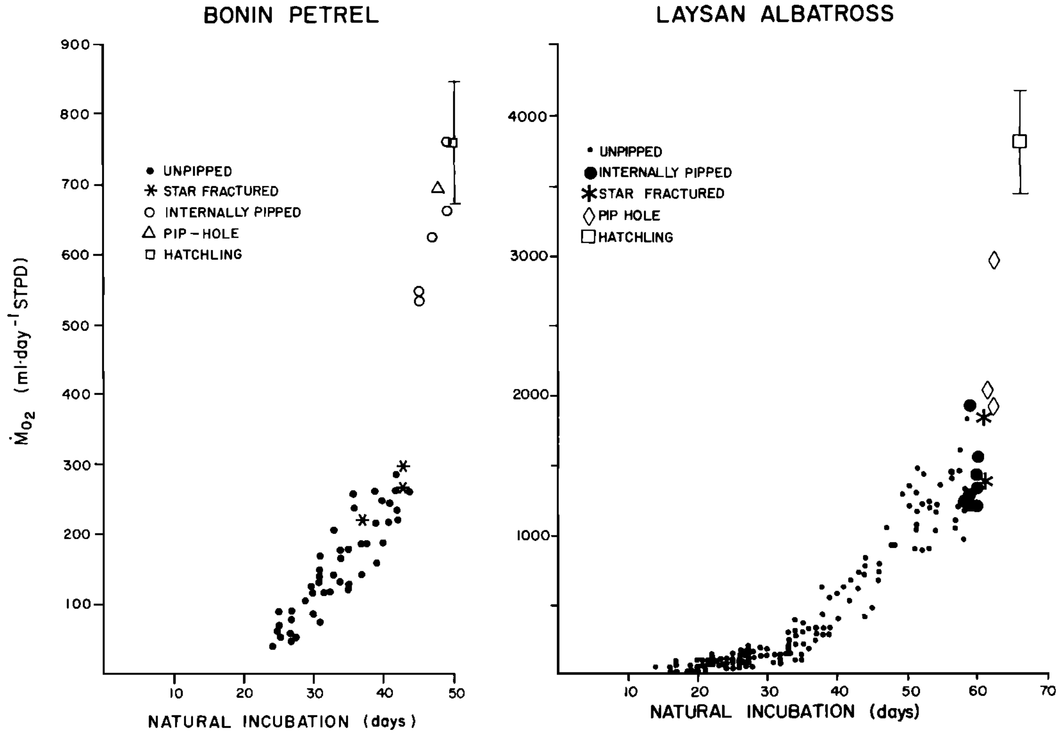

FIGURE 13. Embryonic oxygen consumption ($\dot{M}_{O_2}$) during natural incubation in Bonin Petrel, *Pterodroma hypoleuca*, and Laysan Albatross, *Diomedea immutabilis*, After Pettit et al. (1982a, b).

erence for comparisons between species. Prior to internal pipping oxygen can diffuse into the egg only through pores in the eggshell and it does so under influence of a difference in partial pressure of oxygen between gas inside the egg (air cell) and that in the microclimate of the egg (see below). Once internal pipping has occurred, partial pressure of oxygen in the air cell diminishes because the embryo rebreathes gas in the air cell. The increased difference in oxygen partial pressure (ΔP_{O_2}) results in an increased rate of diffusion of oxygen into the egg. The extent of this increase depends on the degree to which the embryo rebreathes the air in the air cell. In eggs in which star fracture is the initial pipping event, an increase in oxygen uptake occurs because fractures in the shell establish a "leak." The magnitude of the increase depends on the degree to which the shell is fractured (Pettit et al. 1982a). Since this happens before internal pipping occurs, oxygen uptake subsequent to star fracture, but prior to internal pipping, is likely to be variable. Consequently, the pre-internal pipping point in time is not a good reference point for comparative purposes. In such eggs, oxygen uptake immediately prior to star fracture is a valid time for reference purposes. At that time, the shell has not been fractured and the air cell has not been penetrated. If comparisons are to be made between species in which the pipping sequence differs, then the reference point should be immediately before the initial event in the pipping process, be it star fracture or internal pipping (Pettit and Whittow 1982a). Pettit and Whittow (1982a) showed that air-cell partial pressures of oxygen and carbon dioxide are very similar prior to the initial event in the pipping process, irrespective of whether this event is star fracture or internal pipping. Both star-fracture and internal pipping result in an increase in oxygen consumption by the embryo. Therefore, the time of incubation immediately prior to the initial event in the pipping process, regardless of whether this is star-fracture or internal pipping, represents a period in which air-cell gas tensions appear to be similar in all or most eggs, and the integrity of the shell and shell membranes has not been violated. Oxygen uptake of the egg at this point is determined by pore geometry of the eggshell and the difference in oxygen partial pressure between the air cell and the air surrounding the egg. As the latter difference is similar in all eggs, oxy-

TABLE 8

OXYGEN CONSUMPTION ($\dot{V}_{O_2}$) OF THE EMBRYO IMMEDIATELY PRIOR TO THE INITIAL EVENT IN THE PIPPING PROCESS, TOGETHER WITH THE OXYGEN CONSUMPTION OF THE NEWLY-HATCHED CHICK, IN SEVEN SPECIES OF TROPICAL SEABIRDS

Order Species	W^a (g)	Embryonic pre-pipping $\dot{V}_{O_2}$ (ml·O_2/day)	Hatchling $\dot{V}_{O_2}$ (ml·O_2/day)	Embryonic pre-pipping $\dot{V}_{O_2}$ (% of hatchling $\dot{V}_{O_2}$)	Reference
Procellariiformes					
Bonin Petrel (*Pterodroma hypoleuca*)	39.2	246	757	32.5	Pettit et al. 1982b
Wedge-tailed Shearwater (*Puffinus pacificus*)	60.0	304	840	36.2	Ackerman et al. 1980
Laysan Albatross (*Diomedea immutabilis*)	284.8	1250	3820	32.7	Pettit et al. 1982a
Black-footed Albatross (*Diomedea nigripes*)	304.9	1225	3680	33.3	Pettit et al. 1982a
Charadriiformes					
White Tern (*Gygis alba*)	23.3	159	470	33.8	Pettit et al. 1981
Black Noddy (*Anous tenuirostris*)	24.8	184	524	35.1	Pettit and Whittow, unpubl. data
Brown Noddy (*Anous stolidus*)	40.1	283	690	41.0	Pettit and Whittow, unpubl. data

[a] W = Fresh-egg mass.

gen uptake is determined largely by pore geometry of the shell and intrinsic metabolic machinery of the embryo. At this stage the functional pore area of the shell is potentially a limiting factor in oxygen uptake. In Table 8 oxygen uptake of eggs of seven tropical seabirds, just prior to the initial pipping event, is expressed as a percentage of oxygen consumption of the newly-hatched chick, which represents the end product of incubation. The pre-pipping rate of oxygen consumption varied from 32.5 to 41.0% of hatchling rate. Within the Procellariiformes included in Table 8, there was little evidence of any trend, but in the three tropical Charadriiformes, the pre-pipping embryonic oxygen consumption was relatively lowest in the White Tern and highest in the Brown Noddy. The White Tern has the longest incubation period relative to its egg mass. The significance of this is indicated in the discussion.

It is difficult to compare the tropical species in Table 8 with species from higher latitudes, because of uncertainty regarding pipping sequence in the latter species, and because embryonic oxygen consumption was measured after star fracture had occurred. Thus, in data presented by Vleck and Kenagy (1980) for the Fork-tailed Storm-Petrel, "pre-pipping" oxygen consumption was 61.4% of that of the hatchling. The eggs were reported to have hatched "within 1 or 2 days of pipping" but it is uncertain whether "pipping" refers to star fracture, internal pipping or formation of a pip hole. If oxygen consumption was measured three days prior to hatching, the value would be expected to be high, by comparison with other Procellariiformes, because star fracture would have already occurred. With regard to "the chicken," it is possible to be more exact: pre-internal pipping embryonic oxygen consumption represented 49.0% of that of the hatchling (Freeman and Vince 1974). In "the chicken," internal pipping is the initial event in the pipping process. Hoyt and Rahn's (1980) relationship between pre-internal pipping oxygen consumption and fresh-egg mass was derived from 27 species of birds. Unfortunately, in some species, internal pipping was not the initial pipping event so oxygen consumption of these species was presumably elevated as a result of star fracture. This would have the effect of elevating oxygen consumption predicted on the basis of fresh-egg mass. With this reservation in mind, the values shown in Table 8 were all lower than predictions based on fresh-egg mass (W), using Hoyt and Rahn's (1980) equation:

$$\underset{(\text{ml/day})}{\dot{V}_{O_2}} = 28.9\,\underset{(\text{g})}{W^{0.714}}$$

The measured values ranged from 56.5% of predictions for the Wedge-tailed Shearwater to 76.5% for the Laysan Albatross. However, in the Common Tern (Rahn et al. 1974) and the Royal Tern (Vleck, Vleck, Rahn and Paganelli, pers. comm.), two terns nesting outside the tropics, pre-internal pipping $\dot{V}_{O_2}$ was also lower than predictions. In

TABLE 9

OXYGEN CONDUCTANCE OF THE SHELL (G_{O_2}), PARTIAL PRESSURE OF OXYGEN IN THE AIR CELL ($P_{O_2,egg}$) AND IN THE AIR SURROUNDING THE NEST ($P_{O_2,air}$), TOGETHER WITH THE DIFFERENCE BETWEEN $P_{O_2,egg}$ AND $P_{O_2,air}$ (ΔP_{O_2}), IN SEVEN SPECIES OF TROPICAL SEABIRDS

Order Species	G_{O_2} (measured)[a] (ml/day torr)	G_{O_2} (calculated)[b] (ml/day torr)	$P_{O_2,egg}$ (torr)	$P_{O_2,air}$ (torr)	ΔP_{O_2} (torr)	Reference
Procellariiformes						
Bonin Petrel (*Pterodroma hypoleuca*)	4.9	5.6	100.6	150.5	49.9	Pettit et al. 1982b
Wedge-tailed Shearwater (*Puffinus pacificus*)	7.6	6.6	100.8	149.3	48.5	Ackerman et al. 1980
Laysan Albatross (*Diomedea immutabilis*)	30.5	34.7	106.0	156.3	50.3	Pettit et al. 1982a
Black-footed Albatross (*Diomedea nigripes*)	29.5	34.2	106.0	156.3	50.3	Pettit et al. 1982a
Charadriiformes						
White Tern (*Gygis alba*)	3.0	2.7	100.3	153.6	53.3	Pettit et al. 1981
Black Noddy (*Anous tenuirostris*)	3.7	4.9	98.5	153.6	54.1	Pettit and Whittow, unpubl. data
Brown Noddy (*Anous stolidus*)	4.4	7.5	92.1	153.6	61.5	Pettit and Whittow, unpubl. data

[a] Rahn et al (1974); $G_{O_2} = \dot{V}_{O_2}/\Delta P_{O_2}$.

[b] Hoyt et al. (1979); $G_{O_2}^{38°C} = 1.08\ G_{H_2O}^{25°C}$

the Herring Gull (another non-tropical species), on the other hand, oxygen consumption immediately prior to internal pipping was 116% of the expected value based on fresh-egg mass (Rahn et al. 1974). It is difficult to draw conclusions from these figures particularly in view of the uncertainty regarding the precise point in the pipping sequence that measurements of $\dot{V}_{O_2}$ were made.

This discussion should not end without drawing attention to the fact that immediately prior to the initial event in the pipping process, the embryonic mass will not necessarily be the same even in eggs of similar fresh-egg mass. In future work, it would seem important to measure oxygen consumption immediately prior to the initial pipping event and to relate oxygen consumption to yolk-free mass of the embryo. Once such a relationship between yolk-free embryonic mass and oxygen consumption has been established, comparisons will be possible between different species with different shell gas conductances, incubation times and other factors.

OXYGEN CONDUCTANCE OF THE SHELL (G_{O_2})

As far as can be ascertained from the preceding analysis, the rate of embryonic oxygen consumption immediately before the initial pipping event is relatively low in tropical seabirds. Oxygen consumption is determined by oxygen conductance of the shell and shell membranes on one hand, and the difference in partial pressure of oxygen across the shell (ΔP_{O_2}) on the other:

$$\underset{\text{(ml/day)}}{\dot{V}_{O_2}} = \underset{\text{(ml/day·torr)}}{G_{O_2}} \cdot \underset{\text{(torr)}}{\Delta P_{O_2}}$$

(Rahn et al. 1974)

The low value for water-vapor conductance of the shell of many tropical seabirds, as described previously, implies that oxygen conductance of the shell is also low, because water vapor and oxygen diffuse through the same pores. Conductance to water vapor and oxygen is in fact proportional to their respective diffusion coefficients (Paganelli et al. 1978). Consequently, if the value for G_{H_2O} is known, the G_{O_2} may be calculated:

$$\underset{\text{(ml/day·torr)}}{G_{O_2}^{38°C}} = \underset{\text{(mg/day torr)}}{1.08\ G_{H_2O}^{25°C}}$$

(Hoyt et al. 1979)

If the $\dot{V}_{O_2}$ is measured, together with the partial pressure of oxygen in the air cell and air surrounding the egg, a value for G_{O_2} may be calculated. In Table 9 values for G_{O_2} computed from the G_{H_2O}, and from the $\dot{V}_{O_2}$ and ΔP_{O_2}, are presented for a small number of tropical species. There is some disparity in the data but, in general, they lead to the conclusion that oxygen conductance, like water-vapor conductance, is relatively low in the tropical species that have been studied.

OXYGEN PARTIAL PRESSURE DIFFERENCE (ΔP_{O_2})

Attention was drawn in a preceding section to the fact that the oxygen partial pressure in the

TABLE 10

PARTITION OF THE TOTAL AMOUNT OF OXYGEN CONSUMED DURING INCUBATION BETWEEN THE PRE-PIPPING PERIOD AND THE PERIOD FROM THE INITIATION OF PIPPING TO HATCHING, IN 12 SPECIES OF SEABIRDS

	Total oxygen consumption		Pre-pipping[a] oxygen consumption		Pip[a]-to-hatch oxygen consumption		
Order Species	ml	ml/g·fresh-egg mass	ml	% of total	ml	% of total	Reference
Procellariiformes[b]							
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)[c]	1870	179.0	—	—	—	—	Rahn and Huntington, pers. comm.
Fork-tailed Storm-Petrel (*Oceanodroma furcata*)[c]	2830	207.9	—	—	—	—	Vleck and Kenagy 1980
Bonin Petrel (*Pterodroma hypoleuca*)	5610	143.1	2790	50.0	2820	50.0	Pettit et al. 1982b
Wedge-tailed Shearwater (*Puffinus pacificus*)	7776	132.5	4574	57.6	3202	42.4	Ackerman et al. 1980; Pettit et al. 1982b
Laysan Albatross (*Diomedea immutabilis*)	29,671	104.2	17,271	58.2	12,400	41.8	Pettit et al. 1982a
Black-footed Albatross (*Diomedea nigripes*)	30,246	99.2	17,500	58.1	12,746	41.9	Pettit et al. 1982a
Charadriiformes[b]							
Common Tern (*Sterna hirundo*)[c]	1599	78.0	—	—	—	—	Rahn et al. 1974
White Tern (*Gygis alba*)	2565	110.0	1490	58.1	1075	41.9	Pettit et al. 1981
Black Noddy (*Anous tenuirostris*)	3180	128.2	1532	48.2	1648	51.8	Pettit and Whittow, unpubl. data
Brown Noddy (*Anous stolidus*)	4780	119.2	2400	50.2	2380	49.8	Pettit and Whittow, unpubl. data
Royal Tern (*Sterna maxima*)[c]	5236	77.0	—	—	—	—	Vleck et al. 1980
Herring Gull (*Larus argentatus*)[c]	9669	110.0	—	—	—	—	Rahn et al. 1974

[a] "Pip" and "pipping" refers to the initial event in the pipping process.
[b] In both Procellariiformes and Charadriiformes the species are arranged in order of increasing egg mass.
[c] Breeding outside the tropics.

air-cell gas, immediately prior to initiation of pipping is very similar in different species (Table 9). In two species of seabirds from higher latitudes, Common Tern (*Sterna hirundo*) and Herring Gull (*Larus argentatus*), oxygen partial pressure in the air cell was 108.7 and 99.7 torr, respectively (Rahn et al. 1974), close to values reported for tropical seabirds (Table 9). There is some uncertainty as to whether the shells of the tern and gull had star fractured, which is known to increase the P_{O_2} in the air cell (Pettit and Whittow 1982). The partial pressure of oxygen in the air surrounding the nest was rather lower in burrowing species (petrel and shearwater), as might be expected. However, the difference in oxygen pressure across the eggshell was similar in all seven species (Table 9) except for the Brown Noddy, a surface nesting species. The greater ΔP_{O_2} for the Brown Noddy was due to a relatively low $P_{O_2,egg}$ (Table 9).

TOTAL OXYGEN CONSUMED DURING INCUBATION

The total amount of oxygen consumed by the embryo, over the entire incubation period, for several species, is presented in Table 10. Hoyt and Rahn (1980) claimed that the total amount of oxygen consumed during incubation averaged 102 ml/g fresh-egg mass. This figure was based on data from 27 species, individual species ranged from 61 to 141 ml/g. It is clear from Table 10 that several procellariiform seabirds, particularly the smaller petrels, lie outside this range and well above the mean value of 102 ml/g. It is also apparent from Table 10 that the two petrels from higher latitudes (Fork-tailed Storm-Petrel and Leach's Storm-Petrel) had the highest total oxygen cost of incubation. However, these two species also had the smallest eggs listed in Table 10. Consequently, the greater oxygen cost of incubation in these two species may reflect size of their eggs rather than the geographical situation of their breeding colony. Among Charadriiformes, the Black Noddy had the highest total oxygen consumption; there was little evidence of a relationship between the total amount of oxygen consumed and the fresh-egg mass in this order.

Although the period between first indication

TABLE 11

CARBON DIOXIDE PARTIAL PRESSURE IN THE AIR CELL OF THE EGG ($P_{CO_2,egg}$) AND IN THE AIR SURROUNDING THE NEST ($P_{CO_2,air}$) FOR PROCELLARIIFORM AND CHARADRIIFORM SEABIRDS

Order Species	$P_{CO_2,egg}$ (torr)	$P_{CO_2,air}$ (torr)	ΔP_{CO_2} ($P_{CO_2,egg} - P_{CO_2,air}$) (torr)	Reference
Procellariiformes				
Bonin Petrel (*Pterodroma hypoleuca*)	45.5	5.0	40.5	Pettit et al. 1982b
Wedge-tailed Shearwater (*Puffinus pacificus*)	41.8	0.5	41.3	Ackerman et al. 1980
Laysan Albatross (*Diomedea immutabilis*)	40.0	0.3	39.7	Pettit et al. 1982a
Black-footed Albatross (*Diomedea nigripes*)	40.0	0.3	39.7	Pettit et al. 1982a
Charadriiformes				
Common Tern (*Sterna hirundo*)[a]	32.8	0.3	32.5	Rahn et al. 1974
White Tern (*Gygis alba*)	48.5	0.3	48.2	Pettit et al. 1981
Black Noddy (*Anous tenuirostris*)	42.3	0.3	42.0	Pettit and Whittow, unpubl. data
Brown Noddy (*Anous stolidus*)	46.6	0.3	46.3	Pettit and Whittow, unpubl. data
Herring Gull (*Larus argentatus*)[a]	36.2	0.3	35.9	Rahn et al. 1974

[a] Breeding outside the tropics.

of pipping and hatching of the chick is short in relation to total length of incubation, it is clear that a substantial fraction of total oxygen consumption of the embryo occurs during this interval. In the Bonin Petrel and Black Noddy more than half of total oxygen consumption took place in the last 12.1% and 15.0%, respectively, of the total incubation period. Unfortunately, it is not possible to compare tropical species with seabirds from higher latitudes, in this regard, because no data for the latter exist.

CARBON DIOXIDE PRODUCTION BY THE EMBRYO

Few measurements of carbon dioxide production by the embryo have been made in seabirds. Partial pressure of carbon dioxide in the air-cell gas immediately prior to initiation of pipping has, however, been recorded in a number of species (Table 11). Values are rather lower for the two species breeding outside the tropics (Common Tern and Herring Gull) but as there is uncertainty regarding the exact point during the pipping process that air-cell gas was sampled in these two species, it is premature to draw any conclusions. Partial pressure of carbon dioxide in deep burrows of Bonin Petrels was 5.0 torr (Pettit et al. 1982b), considerably above that of fresh air. The P_{CO_2} in air-cell gas in this species was 45.5 torr, resulting in a value for ΔP_{CO_2} of 40.5, very similar to that for other seabirds and for birds in general (Rahn et al. 1974).

HEAT TRANSFER BETWEEN PARENT BIRD AND THE EGG

Direct measurements of heat transfer between parent bird and the egg have not been made in any seabird. Incubation patch temperatures have been measured in some species, and, in conjunction with central egg temperatures, provide a measure of the difference in temperature responsible for heat flow from bird to egg (Table 12). The smallest difference between incubation patch temperature and egg temperature was recorded in the Bonin Petrel, a tropical, burrow-nesting species. The greatest difference was for another petrel, Fork-tailed Storm-Petrel, which breeds in cold conditions. However, the magnitude of the difference ($T_{ip} - T_{egg}$) for the latter species partly reflects the very low egg temperature. Data presented in Table 12 must be considered in the perspective that both incubation patch and egg temperatures have been measured by a variety of procedures, and at different stages of incubation.

Although heat transfer to the egg has not been measured directly, it may be estimated from attempts to determine the energy cost to the parent of incubating the egg. Such attempts have been made for petrels and penguins by Croxall (1982). Estimates were based on weight loss of incubating birds: daily energy expenditure was 1.3–1.4 times basal metabolic rates. Thus, an albatross or shearwater, with basal metabolic rates of 443 kcal/day or 22 kcal/day, respectively, would expend an additional 70 or 13 kcal/day in order to incubate the single egg. Direct measurements of oxygen consumption of incubating Laysan Albatross and Bonin Petrels led Grant and Whittow (1983) to conclude that metabolic rates of incubating birds were below or equal to basal metabolic rates, separately measured. These results imply that the Laysan Albatross and Bonin Petrel did not need to generate additional heat in order to incubate their egg. It implies also, and this is an important point, that the thermal conduc-

TABLE 12
INCUBATION PATCH (T_{ip}) AND CENTRAL EGG (T_{egg}) TEMPERATURES IN SEABIRDS

Order Species	T_{ip} (°C)	T_{egg}[b] (°C)	$T_{ip} - T_{egg}$ (°C)	Reference
Procellariiformes				
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)[a]	35.8	33.4	2.4	Rahn and Huntington, pers. comm.
Fork-tailed Storm-Petrel (*Oceanodroma furcata*)[a]	37.6	29.7	7.9	Wheelwright and Boersma 1979
Bonin Petrel (*Pterodroma hypoleuca*)	34.9	33.8	1.1	Grant, Pettit, Whittow, Rahn and Paganelli, unpubl. data
Wedge-tailed Shearwater (*Puffinus pacificus*)	37.6	35.0	2.6	Whittow et al. 1982
Laysan Albatross (*Diomedea immutabilis*)	38.7	35.8	2.9	Grant, Pettit, Whittow, Rahn and Paganelli, unpubl. data
Black-footed Albatross (*Diomedea nigripes*)	38.3	35.0	3.3	Grant, Pettit, Whittow, Rahn and Paganelli, unpubl. data
Charadriiformes				
White Tern (*Gygis alba*)	36.7	35.3	1.4	Pettit et al. 1981
Sooty Tern (*Sterna fuscata*)	39.6	35.7	3.9	Howell and Bartholomew 1962
Black-legged Kittiwake (*Rissa tridactyla*)[a]	38.9	37.4	1.5	Barrett 1980
Herring Gull (*Larus argentatus*)[a]	40.5	38.3	2.2	Drent 1970
Great Skua (*Catharacta skua*)[a]	39.3	35.6	3.7	Drent 1970
South Polar Skua (*Catharacta maccormicki*)[a]	39.0	36.0	3.0	Spellerberger 1969

[a] Breeding outside the tropics.
[b] Taken from Table 5.

tance of the egg is similar to that of the feathers dropped when birds develop their incubation patch.

DISCUSSION

The foregoing analysis has brought to light a number of apparent differences between tropical seabirds and their counterparts in higher latitudes. In a previous review of incubation in seabirds (Whittow 1980) it was recognized that prolonged incubation was a common feature of tropical seabirds. In Figure 14, the line represents the relationship between incubation period (I) and fresh-egg mass (W), for birds in general:

$$\underset{\text{(days)}}{I} = 12.03\,\underset{\text{(g)}}{W^{0.217}} \qquad \text{(Rahn and Ar 1974)}$$

As far as Procellariiformes are concerned, all species included in Fig. 14 had longer incubation periods than the expected values based on egg mass. The limited data suggest there was no difference between tropical and non-tropical species in this respect. The tropical Charadriiformes also had long incubation periods and so also did three alcids breeding outside the tropics. However, incubation periods of most Charadriiformes from higher latitudes were close to or below predicted values (Fig. 14). The limited information on Pelecaniformes indicates that all tropical species have relatively long incubation periods. These conclusions conform with those made previously (Whittow 1980).

To what extent can the differences between tropical and non-tropical sea birds be attributed to longer incubation times of the former? An attempt can be made to answer this question for daily rate of water loss from the egg. Thus, Ar and Rahn (1980) have shown that for birds in general, daily rate of water loss ($\dot{M}_{H_2O}$) may be related to the fresh-egg mass (W) and to incubation period (I) in the following way:

$$\underset{\text{(mg/day)}}{\dot{M}_{H_2O}} = 130.4\,\frac{W^{0.977}}{I^{0.937}} \qquad \text{(Ar and Rahn 1980)}$$
$$\text{(g/day)}$$

This equation essentially provides a predicted value for $\dot{M}_{H_2O}$, based on fresh-egg mass *and* incubation time. In Table 13 daily rates of water loss, expressed in this way, are presented for tropical members of the three orders of seabirds. In tropical Procellariiformes, measured daily rate of water loss was considerably lower than the value predicted solely on the basis of fresh-egg

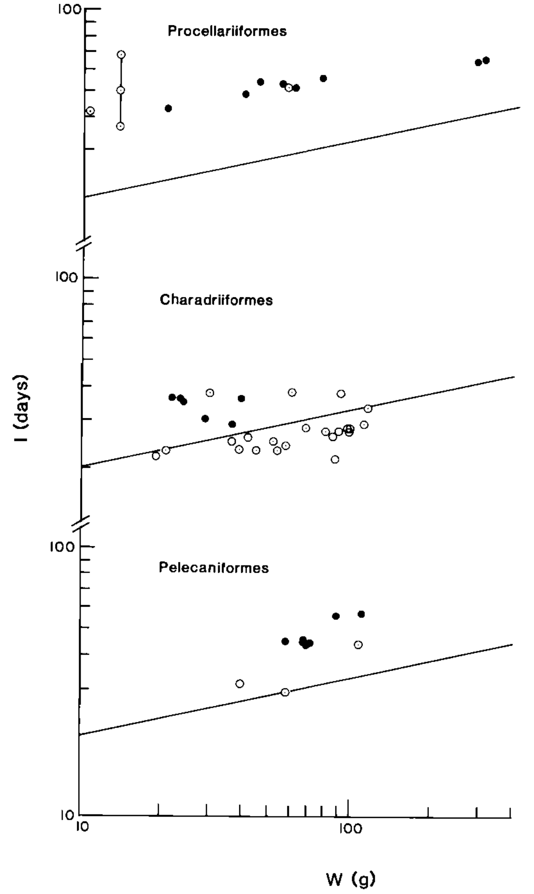

FIGURE 14. Relationship between incubation period (I) and fresh-egg mass (W) in seabirds for which data on other aspects of their incubation physiology are available. ● = tropical species; ○ = species from higher latitudes. The three points connected by a vertical line are incubation periods for Fork-tailed Storm-Petrels, which vary with degree of egg neglect (Boersma and Wheelwright 1979). The line represents the relationship $I = 12.03W^{0.217}$ (Rahn and Ar, 1974). Data from Rice and Kenyon 1962, Fordham 1964a, b, Harris, 1966, Ashmole and Ashmole 1967, Lack, 1968, Kepler 1969, Nelson 1969, 1971, Fisher 1971, Shallenberger 1973, Fleet 1974, Rahn et al. 1976, Ar and Rahn 1978, Morgan et al. 1978, Rahn and Dawson 1979, Ricklefs and Montevecchi 1979, Hoyt and Rahn, 1980, Roudybush et al. 1980, Vleck and Kenagy 1980, Pettit et al. 1981, Pettit et al. 1982a, Rahn and Huntington, pers. comm., Simons, pers. comm., Vleck, Vleck, Rahn and Paganelli, pers. comm., Flint and Whittow, unpubl. data, Grant, Whittow and Pettit, unpubl. data, Pettit and Whittow, unpubl. data, Whittow, Garnett and Teebaki, unpubl. data, Whittow, Pettit, Ackerman and Paganelli, unpubl. data.

mass. However, when incubation time was taken into account, predicted values (right-hand column of Table 13) were much closer to measured water loss. Accurate measurements of water loss were available only for two species nesting outside the tropics, Fork-tailed Storm-Petrel and Leach's Storm-Petrel. In both species, the predicted value based on fresh-egg mass and incubation time was again closer to measured rate than was the prediction based on fresh-egg mass alone. Similar conclusions may be made with regard to tropical Charadriiformes (Table 13). In Sooty Terns, there was little difference between measured values and either predicted value. However, in this species, incubation was not prolonged (Fig. 14). In Cassin's Auklets and the Common Puffins, two alcids breeding in higher latitudes, which had relatively long incubation periods (Fig. 14), the measured daily water loss from eggs was lower than predicted values but it was most closely approximated by predictions incorporating incubation period. In tropical Pelecaniformes also, the discrepancy between measured values and values predicted were attenuated by making allowance for incubation period (Table 13). In general, then, the divergence of measured rates of water loss for tropical seabirds from the value for birds in general can be attributed to prolonged incubation. However, there are sufficient discrepancies in the data (e.g., Wedge-tailed Shearwater, Great Frigatebird) to suggest that other factors may be involved in some instances.

The departure of water-vapor conductance of the eggshell of tropical seabirds from predictions based on fresh-egg mass may also be examined in terms of the contribution of prolonged incubation to this departure. Thus, Hoyt (1980) reported a relationship between incubation time (I), fresh-egg mass (W) and shell water-vapor conductance ($G_{\mathrm{H_2O}}$):

$$\underset{(\mathrm{mg/day\cdot torr})}{G_{\mathrm{H_2O}}} = 2.32\frac{W^{0.976}}{\underset{(\mathrm{g/day})}{I^{0.73}}}$$

Data in Table 14 make it clear that, on the whole, measured water-vapor conductance of tropical Procellariiformes could be predicted with greater precision if incubation period was taken into account. This is also true for Fork-tailed Storm-Petrels and Leach's Storm-Petrels, two species nesting outside the tropics. A similar conclusion may be made with regard to tropical Charadriiformes (Table 14), and also for three alcids which breed in higher latitudes and which have long incubation periods (Fig. 14). In the four species of tropical Pelecaniformes included in Table 14, measured values of $G_{\mathrm{H_2O}}$ were closer to predic-

TABLE 13

COMPARISON OF THE MEASURED DAILY RATE OF WATER LOSS FROM THE EGG ($\dot{M}_{H_2O}$) WITH PREDICTED VALUES BASED ON THE MASS OF THE FRESHLY LAID EGG AND ON BOTH FRESH-EGG MASS (W) AND INCUBATION TIME (I), IN TROPICAL SEABIRDS

Order Species	Measured	$\dot{M}_{H_2O}$ (mg/day) Predicted: $\dot{M}_{H_2O} =$ $13.243\ W^{0.754}$[a]	$\dot{M}_{H_2O} =$ $130.4\ (W^{0.977}/I^{0.937})$[a]
Procellariiformes			
Bulwer's Petrel (*Bulweria bulwerii*)	77	132	76
Bonin Petrel (*Pterodroma hypoleuca*)	110	212	124
Christmas Shearwater (*Puffinus nativitatis*)	119	233	128
Phoenix Petrel (*Pterodroma alba*)	123	271	158
Wedge-tailed Shearwater (*Puffinus pacificus*)	155	290	198
Dark-rumped Petrel (*Pterodroma phaeopygia*)	286	351	213
Laysan Albatross (*Diomedea immutabilis*)	674	939	651
Black-footed Albatross (*Diomedea nigripes*)	707	989	688
Charadriiformes			
White Tern (*Gygis alba*)	74	133	91
	79	142	100
Black Noddy (*Anous tenuirostris*)	106	144	103
Gray-backed Tern (*Sterna lunata*)	107	166	142
Sooty Tern (*Sterna fuscata*)	190	196	185
Brown Noddy (*Anous stolidus*)	150	209	162
Pelecaniformes			
Red-footed Booby (*Sula sula*)	167	284	196
Red-tailed Tropicbird (*Phaethon rubricauda*)	199	332	245
Great Frigatebird (*Fregata minor*)	194	391	245

[a] Ar and Rahn 1980. References for data on fresh-egg mass, incubation time, and water loss are given in the legends for Figures 1, 2, and 14, and Table 1.

tions based on fresh-egg mass and incubation than to values predicted solely on the basis of the fresh-egg mass alone.

The analysis performed in the preceding sections, for $\dot{M}_{H_2O}$ and G_{H_2O}, may be extended to the functional pore area, A_p, and the number of pores, N. Thus Ar and Rahn (1978) established the following relationship between A_p, incubation time (I), fresh-egg mass (W), and shell thickness (L):

$$\underset{(\mathrm{mm}^2)}{A_p} = \frac{(2.2\,WL)}{\underset{(\mathrm{g \cdot mm/day})}{I}}$$

In tropical Procellariiformes, and also in the two species from higher latitudes, predictions that took into account incubation time were a closer approximation to calculated values than were those based on fresh-egg mass alone (Table 15), again with the exception of the two larger species, the albatross. With regard to the tropical Charadriiformes remarks similar to those made above are applicable, viz. that predictions incorporating incubation period were not *consistently* superior to those that did not (Table 15). The functional pore area of tropical Pelecaniformes was best approximated by the equation of Ar and Rahn (1978) in all four cases (Table 15).

It is apparent from Figure 9 that the number of pores in eggshells of all species included, with the exception of the two albatross, is less than predicted by Tullett and Board (1977) on basis of fresh-egg mass. Rahn and Ar's (1980) predictive equation (Table 16), incorporating incubation period, provided a better approximation of measured values for Procellariiformes, including Leach's Storm-Petrel, the only species from higher latitudes for which data are available. The combined use of incubation time and fresh-egg mass also provided a better estimate of the number of pores in shells of three tropical Pelecaniformes, than did fresh-egg mass alone (Table 16). In the Gray-backed Tern, a tropical species, the measured number of pores was closely approximated by the predicted value based on both fresh-egg mass and incubation. In Cassin's Auklet, from higher latitudes, a much closer approximation to measured values was furnished when incubation time was taken into account.

Hoyt and Rahn (1980) presented equations relating embryonic oxygen consumption prior to internal pipping to fresh-egg mass and also to

TABLE 14

COMPARISON OF THE MEASURED WATER-VAPOR CONDUCTANCE OF THE EGGSHELL (G_{H_2O}) IN TROPICAL SEABIRDS, WITH PREDICTED VALUES

Order Species	Measured	G_{H_2O} (mg/torr·day) Predicted $G_{H_2O} = 0.384W^{0.814}$[a,b,e]	 $G_{H_2O} = 2.32(W^{0.976}/I^{0.73})$[b,c,d,e]
Procellariiformes			
Bulwer's Petrel (*Bulweria bulwerii*)	2.5	4.6	2.9
Bonin Petrel (*Pterodroma hypoleuca*)	5.2	7.7	4.9
Christmas Shearwater (*Puffinus nativitatis*)	4.8	8.5	5.2
Wedge-tailed Shearwater (*Puffinus pacificus*)	6.1	10.8	7.1
Dark-rumped Petrel (*Pterodroma phaeopygia*)	8.8	13.2	8.6
Laysan Albatross (*Diomedea immutabilis*)	32.0	38.2	27.4
Black-footed Albatross (*Diomedea nigripes*)	32.5	40.4	29.0
Charadriiformes			
White Tern (*Gygis alba*)	3.5	4.7	3.4
	2.5	5.0	3.7
Black Noddy (*Anous tenuirostris*)	4.5	5.1	3.8
Gray-backed Tern (*Sterna lunata*)	4.5	5.9	5.1
Sooty Tern (*Sterna fuscata*)	6.8	7.1	6.6
Brown Noddy (*Anous stolidus*)	7.0	7.6	6.0
Pelecaniformes			
Red-footed Booby (*Sula sula*)	5.8	10.5	7.6
Red-tailed Tropicbird (*Phaethon rubricauda*)	9.0	12.4	9.5
Brown Booby (*Sula leucogaster*)	7.6	11.9	8.8
Great Frigatebird (*Fregata minor*)	7.5	14.8	10.0

[a] Ar and Rahn 1978.
[b] W = fresh-egg mass.
[c] Hoyt 1980.
[d] I = incubation period.
[e] References for data on W, I and G_{H_2O} are given in Table 2 and Figures 3 and 4.

both fresh-egg mass and incubation time. Reservations were expressed in an earlier section regarding these equations because the equations were based on eggs in which the sequence of events during pipping varied. With these reservations in mind, values have been collected together in Table 17 to allow comparisons between the measured values for pre-internal pipping $\dot{V}_{O_2}$ and predictions based on fresh-egg mass and incubation time. The purpose of this exercise was to test the conclusion, made earlier, that prepipping embryonic oxygen consumption of tropical seabirds was relatively low and, further, to determine whether this could be attributed to their prolonged incubation. In four tropical Procellariiformes, measured $\dot{V}_{O_2}$ could be predicted with greater precision by the equation:

$$\underset{(\text{ml/day})}{\dot{V}_{O_2}} = 139\,\underset{(\text{g/day})}{\frac{W^{0.85}}{I^{0.65}}}$$

This was not the case for two petrels (Fork-tailed Storm-Petrel and Leach's Storm-Petrel) from higher latitudes. However, there are uncertainties regarding both incubation period (because of egg neglect) and the precise point in incubation at which $\dot{V}_{O_2}$ was measured in the Fork-tailed Storm-Petrel. In three tropical terns the predicted $\dot{V}_{O_2}$ was considerably closer to the measured value when corrected for incubation time (Table 17).

Hoyt and Rahn (1980) assembled evidence to show that the total amount of oxygen required by the embryo over the entire incubation period averaged 102 ml/g egg. They claimed this value was independent of incubation time. In Table 18 a number of seabirds are ranked according to the degree to which their incubation times exceed predictions based on fresh-egg mass. In Procellariiformes it was clear that the amount of oxygen consumed per gram of fresh-egg mass greatly exceeded Hoyt and Rahn's (1980) prediction, particularly in smaller species with relatively long incubation periods. This trend was not apparent in Charadriiformes. A similar conclusion was made by Vleck et al. (1980) with regard to Procellariiformes. Ackerman (1981) presented a predictive equation for total oxygen consumed by an avian egg, predicated on the belief that an increase in either egg mass or incubation time incurs an increase in oxygen requirements. In

TABLE 15

COMPARISON OF THE FUNCTIONAL PORE AREA OF THE SHELL (A_p), CALCULATED FROM THE WATER-VAPOR CONDUCTANCE (G_{H_2O}) AND SHELL THICKNESS (L), WITH PREDICTED VALUES BASED ON THE MASS OF THE FRESHLY-LAID EGG (W) AND INCUBATION PERIOD (I), IN TROPICAL SEABIRDS[a]

Order Species	Calculated[b]	A_p (mm^2) Predicted $A_p = 9.2 \cdot 10^{-3} \cdot W^{1.236}$[c]	A_p (mm^2) Predicted $A_p = 2.2WL/I$[d]
Procellariiformes			
Bulwer's Petrel (*Bulweria bulwerii*)	0.21	0.40	0.21
Bonin Petrel (*Pterodroma hypoleuca*)	0.42	0.87	0.32
Christmas Shearwater (*Puffinus nativitatis*)	0.55	1.01	0.49
Wedge-tailed Shearwater (*Puffinus pacificus*)	0.71	1.45	0.69
Dark-rumped Petrel (*Pterodroma phaeopygia*)	0.95	1.98	0.78
Laysan Albatross (*Diomedea immutabilis*)	7.02	9.94	4.72
Black-footed Albatross (*Diomedea nigripes*)	7.73	10.82	5.39
Charadriiformes			
White Tern (*Gygis alba*)	0.26	0.41	0.22
	0.20	0.45	0.26
Black Noddy (*Anous tenuirostris*)	0.38	0.46	0.28
Gray-backed Tern (*Sterna lunata*)	0.48	0.58	0.44
Sooty Tern (*Sterna fuscata*)	0.69	0.76	0.63
Brown Noddy (*Anous stolidus*)	0.72	0.85	0.55
Pelecaniformes			
Red-footed Booby (*Sula sula*)	0.99	1.40	1.14
Red-tailed Tropicbird (*Phaethon rubricauda*)	1.30	1.80	1.22
Brown Booby (*Sula leucogaster*)	1.33	1.68	1.29
Great Frigatebird (*Fregata minor*)	1.18	2.36	1.31

[a] References for data on W, I and A_p are given in Table 4 and Figures 7 and 8.
[b] Rahn et al. 1976.
[c] Ar et al. 1974.
[d] Ar and Rahn 1978.

TABLE 16

COMPARISON OF THE MEASURED NUMBER OF PORES IN THE EGGSHELLS (N) OF TROPICAL SEABIRDS WITH PREDICTED VALUES[a]

Order Species	N (pores/egg) Measured	N (pores/egg) Predicted $N = 1449W^{0.42}$[b]	N (pores/egg) Predicted $N = 3390(W/I)^{0.96}$[c]
Procellariiformes			
Bulwer's Petrel (*Bulweria bulwerii*)	2439	5215	1712
Bonin Petrel (*Pterodroma hypoleuca*)	4159	6786	2773
Phoenix Petrel (*Pterodroma alba*)	3798	7795	3509
White-tailed Shearwater (*Puffinus pacificus*)	3587	8089	3889
Dark-rumped Petrel (*Pterodroma phaeopygia*)	4553	8992	4694
Laysan Albatross (*Diomedea immutabilis*)	15,753	15,563	14,011
Black-footed Albatross (*Diomedea nigripes*)	16,700	16,013	14,736
Charadriiformes			
Gray-backed Tern (*Sterna lunata*)	3165	5934	3217
Pelecaniformes			
Red-footed Booby (*Sula sula*)	5778	7992	4347
Red-tailed Tropicbird (*Phaethon rubricauda*)	4536	8712	5434
Great Frigatebird (*Fregata minor*)	5368	9548	5385

[a] W = fresh-egg mass; I = incubation period.
[b] Tullett and Board 1977.
[c] Rahn and Ar 1980.

TABLE 17

COMPARISON OF THE EMBRYONIC OXYGEN CONSUMPTION ($\dot{V}_{O_2}$), MEASURED IMMEDIATELY PRIOR TO THE INITIAL EVENT DURING PIPPING, WITH PREDICTED VALUES[a]

Order Species	$\dot{V}_{O_2}$ (ml/day) Measured	Predicted $\dot{V}_{O_2} = 28.9W^{0.714}$[b]	 $\dot{V}_{O_2} = 139(W^{0.85}/I^{0.65})$[b]
Procellariiformes			
Bonin Petrel (*Pterodroma hypoleuca*)	246	399	253
Wedge-tailed Shearwater (*Puffinus pacificus*)	305	538	346
Laysan Albatross (*Diomedea immutabilis*)	1250	1636	1125
Black-footed Albatross (*Diomedea nigripes*)	1225	1717	1182
Charadriiformes			
White Tern (*Gygis alba*)	159	274	198
Black Noddy (*Anous tenuirostris*)	184	344	211
Brown Noddy (*Anous stolidus*)	283	403	312

[a] W = fresh-egg mass; I = incubation period. References for data on W, I and $\dot{V}_{O_2}$ are given in Table 8.

[b] Hoyt and Rahn 1980.

Table 19 the measured total volume of oxygen is compared with Ackerman's prediction derived from fresh-egg mass and incubation time. Allowing for variation in incubation time of the Fork-tailed Storm-Petrel, the small number of experimental observations on which oxygen consumption is based in some instances, and on other sources of variation and error, Ackerman's equation provides a reasonably good estimate of oxygen consumption of the embryo.

The overall conclusion to be drawn from this discussion is that many of the differences between tropical seabirds and seabirds from higher latitudes, with regard to gas transfer between the egg and its environment, may be attributed to the prolonged incubation prevalent in tropical

TABLE 18

TOTAL VOLUME OF OXYGEN ($V_{O_2,tot}$, ml) CONSUMED BY THE EMBRYO (PER GRAM OF FRESH-EGG MASS) IN SEABIRDS RANKED ACCORDING TO THE DEGREE TO WHICH INCUBATION IS PROLONGED

Order Species	I_m/I_p[a]	$V_{O_2,tot/g\ egg}$	Reference
Procellariiformes			
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	2.1	179	Rahn and Huntington, pers. comm.
Fork-tailed Storm-Petrel (*Oceanodroma furcata*)	1.9	208	Vleck and Kenagy 1980
Bonin Petrel (*Pterodroma hypoleuca*)	1.8	143	Pettit et al. 1982b
Wedge-tailed Shearwater (*Puffinus pacificus*)	1.8	133	Ackerman et al. 1980
Laysan Albatross (*Diomedea immutabilis*)	1.6	104	Pettit et al. 1982a
Black-footed Albatross (*Diomedea nigripes*)	1.6	99	Pettit et al. 1982a
Charadriiformes			
White Tern (*Gygis alba*)	1.5	110	Pettit et al. 1981
Black Noddy (*Anous tenuirostris*)	1.4	128	Pettit and Whittow, unpubl. data
Brown Noddy (*Anous stolidus*)	1.4	119	Pettit and Whittow, unpubl. data
Common Tern (*Sterna hirundo*)	1.0	78	Rahn et al. 1974
Herring Gull (*Larus argentatus*)	0.8	110	Rahn et al. 1974
		129	Drent 1970

[a] I_m = measured incubation time; I_p = incubation time predicted by Rahn and Ar 1974 ($I = 12.03W^{.217}$).

TABLE 19
TOTAL VOLUME OF OXYGEN ($V_{O_2,tot}$) CONSUMED BY THE EMBRYOS OF SEABIRDS[a]

Order Species	$V_{O_2,tot}$ (ml) Measured	Predicted[b]	Measured/predicted
Procellariiformes			
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	1881	1472	1.3
Fork-tailed Storm-Petrel (*Oceanodroma furcata*)	2831	2018[c]	1.4
Bonin Petrel (*Pterodroma hypoleuca*)	5606	4890	1.1
Wedge-tailed Shearwater (*Puffinus pacificus*)	7980	7281	1.1
Laysan Albatross (*Diomedea immutabilis*)	29,619	30,930	1.0
Black-footed Albatross (*Diomedea nigripes*)	30,185	33,060	0.9
Charadriiformes			
White Tern (*Gygis alba*)	2563	2641	1.0
Black Noddy (*Anous tenuirostris*)	3174	3910	0.8
Brown Noddy (*Anous stolidus*)	4772	4196	1.1
Common Tern (*Sterna hirundo*)	1599	1865	0.9
Herring Gull (*Larus argentatus*)	9933	7186	1.4

[a] For sources of information see Table 18.
[b] Ackerman 1981.
[c] For "average" incubation time of 50 days.

seabirds. Differences within the tropical seabird community are also explicable, to some extent, in terms of duration of incubation. Furthermore, in Procellariiformes, which have the longest incubation periods, quantitative differences between eggs of different species seem to be more closely related to the degree to which their incubation is prolonged rather than to their geographical distribution.

Prolonged incubation has clearly necessitated substantial adaptive changes in the physiology of eggs and embyros. Nevertheless, it is equally true to conclude that other factors have played a part in shaping incubation characteristics of tropical seabirds. Ironically, we shall have a better understanding of these factors when we know more about incubation physiology of seabirds breeding outside the tropics.

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GROWTH STRATEGIES IN MARINE TERNS

N. P. LANGHAM[1]

ABSTRACT.—Clutch size, brood size, and growth rates of chicks of *Sterna sandvicensis, S. hirundo, S. dougallii,* and *S. paradisea* were studied on Coquet Island, Northumberland, England (a temperate regime) and compared to *S. sumatrana, S. bergii, S. anaethetus,* and *Anous tenuirostris* on One Tree Island, Great Barrier Reef, Australia (a tropical regime). Species and regime-specific differences in these features are related to the general biology of the species, and especially to the role of courtship feeding, inshore or offshore feeding behavior, presence of predators, mobility of young, and the necessity of chicks to withstand periodic food shortage.

Marine terns are specialised larids primarily feeding on shoaling fish or squid, usually nesting colonially in areas free of ground predators. Despite their morphological similarity, they exhibit a number of different strategies when breeding. Tern chicks are semi-nidifugous and at hatching their legs are well-formed and the bodies are down-covered for mobility and thermo-regulation, respectively. Although they show precocial development resembling Galliformes and Anseriformes, they are altricial in that they continue to be fed by their parents up till and beyond fledging. The breeding adults are monogamous and share incubation and feeding duties. Some species nest in trees or cliffs whilst others nest on the ground amongst vegetation or on bare shingle, sand or rock. Various nest densities are adopted, with some species nesting in dispersed colonies with nest, eggs and chicks having cryptic coloration, whilst others nest in dense groups where although the eggs and chicks may appear cryptic amongst the droppings (Croze 1970) the area itself is conspicuous. Cullen (1960) has described the adaptations associated with such nesting with respect to north-temperate species and similar patterns are shown by subtropical and tropical species.

Besides nesting densities, marine terns exhibit variations in clutch size, subsequent brood size and growth rate of nestlings. It has been suggested that brood size is influenced by the food supply which is less abundant in the tropics and liable to fluctuations in offshore- or pelagic-feeding species and as a result these tend to have smaller broods and slower growth rates (Lack 1968). Most tropical and subtropical species have single egg clutches whether offshore or inshore feeders, whereas north-temperate species have larger clutches, with two or three egg clutches frequent in most inshore feeders. Brood size and growth of nestlings are interrelated, and theoretically a species could increase its brood size at the expense of growth and adopt a slower rate, or alternatively reduce its brood size and grow faster. In the tropical and subtropical species, it would appear that single chicks are growing at the maximum rate, determined by the available food and the adult's ability to collect it.

In recent years, there has been an increased focus on the growth rate of birds (see Ricklefs 1967, 1968, 1979a, 1979b; O'Connor 1978), with particular emphasis on the energetic constraints imposed by particular modes of reproduction. Ricklefs (1968) improved the method of measuring growth rate, by considering growth as a percentage of the asymptote, instead of considering a chick's growth from the time of hatching to fledging as used by Lack (1968). Also, it was no longer necessary to interpret chick growth as simply a compromise between chick mortality and the availability of food. Instead, growth rates could be related to adult weight, nestling period, food availability and brood size. Ricklefs (1979b) compared the growth rate of the Common Tern, *Sterna hirundo* with two other non-larid species, one precocial which grew slower and one altricial which grew faster. In the present study the growth rates of several different tern species are examined and the different strategies adopted by temperate and tropical species are compared.

STUDY AREAS

The study areas were confined to two islands: 1) *Coquet Island,* Northumberland, England (55°38'N, 1°37'W) has been described by Langham (1974) and is a breeding site for four species of terns in a north-temperate regime. It is about 2 km from the coast and on the continental shelf in water less than 50 m depth and surrounded by water of not more than 100 m deep. 2) *One Tree Island* (23°31'S, 152°06'E) situated at the southern end of the Great Barrier Reef, Australia, in the Capricorn-Bunker group. It is a coral rubble island with the southern edge consisting of a shelving reef, and the remainder of the island surrounded by a shallow lagoon. The island is close to waters exceeding 180 m. A full description of the island and its vegetation is given by Hulsman (1979) and Heatwole et al. (1981). The island has at least four, and sometimes six, species of terns nesting during the southern summer in a subtropical regime. Although in the subtropics, its period of productivity is spread over eight to nine months of the year (Hulsman 1980) and will be referred to as tropical in the following account as the tern species considered are all found breeding in tropical waters.

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[1] School of Natural Resources, The University of the South Pacific, P.O. Box 1168, Suva, Fiji. *Current Address*: Ecology Division, D.S.I.R., Goddards Lane, Havelock North, New Zealand.

TABLE 1
CLUTCH SIZE AND HATCHING SUCCESS

Species	Clutch size[a]	Hatching success (%)
Temperate		
Arctic Tern	1.82 ± 0.28	77.1
Common Tern	2.45 ± 0.29	75.5
Roseate Tern	1.49 ± 0.17	91.4
Sandwich Tern	1.23 ± 0.04	85.5[b]
Tropical		
Black-naped Tern	1.78 ± 0.39	31.4
Crested Tern	1.01 ± 0.01	69.4
Bridled Tern	1.00	91.2
White-capped Noddy	1.00	46.2

[a] ±1.96 standard error of $\bar{x}$.

[b] Unweighted mean: 73.9%.

TABLE 2
HATCHING AND FLEDGING SUCCESS IN RELATION TO CLUTCH SIZE AND BROOD SIZE

Species	Clutch size	Hatching success (%)	Brood size	Fledging success (%)
Arctic Tern	1	52	1	93
	2	74	2	76
	3	83	3	0
Common Tern	1	41	1	69
	2	67	2	74
	3	76	3	67
Roseate Tern	1	86	1	99
	2	92	2	90
Sandwich Tern	1	57	1	90
	2	70	2	77
Black-naped Tern	1	16	1	25
	2	34	2	67
Crested Tern	1	99	1	85
	2	<1	2	0

METHODS

In both areas, chicks being studied were weighed close to hatching and marked with monel bands soon after so that individual growth rates could be be measured. In this study, growth was measured by weight to the nearest gram using either a pesola spring balance or a torsion pan balance placed in a blind to avoid disturbance by wind. Wing growth was measured after the primaries had sprouted, using a wing-stop rule to measure the longest primary from the carpal joint to the nearest mm. The bill length was measured from the base of the cere to the tip, using vernier calipers to the nearest 0.1 mm. Only growth by weight is considered in this paper.

In those species that nested in a dispersed manner, the nests were marked and the chicks either collected in a partitioned box for weighing and measuring, or weighed on the spot, before returning them to their individual refuges. In dense nesting species, enclosures were sometimes set up to enable the same individuals to be weighed and measured regularly. In some cases, enclosures led to injury or deformity of the bill and these measurements were discounted. Enclosures were removed prior to fledging or during adverse weather conditions so as not to influence chick mortality.

RESULTS

The terns nesting on Coquet Island include the Common Tern, Sandwich Tern, *Sterna sandvicensis,* Roseate Tern, *S. dougallii* and Arctic Tern, *S. paradisaea.* Their general breeding biology in this area with reference to clutch size variation and breeding success has been described (Langham 1974). The growth and survival in Common Tern chicks of different brood sizes have been compared (Langham 1972) and detailed development of this species has been monitored (Ricklefs 1979b). In the following results, the information from Coquet Island is based on three years, whilst the tropical species described: Black-naped Tern, *S. sumatrana,* Crested Tern, *S. bergii,* Bridled Tern, *S. anaethetus,* and the White-capped Noddy, *Anous tenuirostris* are mainly based on one year's results. Only the last species has been the subject of a detailed study of its breeding biology in the tropical Atlantic (Ashmole 1962).

CLUTCH SIZE

Clutch size and hatching success in the different species are given in Table 1. Apart from the Black-naped Tern, most tropical species have a single egg clutch. In temperate species, the clutch sizes are larger, particularly in the Common Tern, with a declining average clutch size in the order Arctic Tern, Roseate Tern, Sandwich Tern. Other tropical species [the Sooty Tern, *Sterna fuscata* (Ashmole 1963a, Robertson 1964), Brown Noddy, *Anous stolidus* (Woodward 1972) and Fairy Tern, *Gygis alba* (Dorward 1963)] lay single eggs. The small clutch of tropical species may be viewed as a result of competition around the colony during the breeding season where there is no marked seasonal fluctuation in food in tropical waters (Ashmole 1963b). The lack of fluctuation in productivity made it possible for adults loosing their eggs early in incubation to re-lay in less than annual periods, either nine months on Ascension (Ashmole 1963a) or six months on Christmas Island, Pacific Ocean (Schreiber and Ashmole 1970).

BROOD SIZE

All species experienced a relatively high hatching success, apart from the Black-naped Tern whose loose colonies along the foreshore were

TABLE 3
GROWTH RATE, WEIGHT, AND BROOD SIZE

Species	K (growth constant)	Asymptotic weight (g)	Adult weight (g)	Brood size
Arctic Tern	0.302	115	110	1/2
Common Tern B/1	0.311	126	126	1
B/2	0.270	124	126	2
B/3	0.226 to 0.449[a]	119	126	3
Roseate Tern	0.263	105	124	1/2
Sandwich Tern	0.232	189	230	1/2
Black-naped Tern	0.288	100	110	1/2
Crested Tern (a)	0.107	279	350	1
(b)	0.094	318	350	1
Bridled Tern	0.114	128.5	130	1
White-capped Noddy	0.152[b]	117	115	1
Brown Noddy[c]	0.153	160	159	1
Sooty Tern[d]	0.073	205	175	1

[a] $\bar{x} = 0.279$.
[b] Gompertz a = 1979/80, b = 1981/82.
[c] Dry Tortugas (Ricklefs 1978).
[d] Kure Atoll (Woodward 1972).

relatively vulnerable to predation by Silver Gulls, *Larus novaehollandae* or wading birds, despite camouflage. In 1979/80, most of the Black-naped Tern clutches were lost through high spring tides associated with strong winds. The Black-naped Tern was the only tropical species to have a number of broods of two chicks (Table 2). It is possible that single eggs in this species had a higher hatching success as some single eggs may represent deserted clutches before a complete clutch had been laid. Only chicks ringed at birth and subsequently seen weighing more than 50 g were deemed to have survived. Although a few Crested Terns hatched two chicks, there was no evidence to suggest they raised two.

Temperate species had brood sizes ranging from one to three (Table 2). The lower hatching success of single egg clutches was probably due to desertion before the clutch was complete, otherwise hatching success was relatively high. The subsequent brood sizes were in a similar proportion except that in the Arctic Tern broods of three were very rare and unsuccessful.

GROWTH RATE

The details of growth are shown in Table 3. Except for the White-capped Noddy, a logistic equation fitted the growth curves of each species. Values were derived from the asymptote adopting the method described by Ricklefs (1967). The growth curves based on these asymptotes were fitted to a logistic or Gompertz curve. Comparison of the t_{50} (or the time it takes to reach half the asymptotic weight) shows a close similarity between the temperate species and the Black-naped Tern (Table 4). It takes longer in the White-capped Noddy and Bridled Tern and longest in the Crested Tern. A similar resemblance is shown in the time taken to reach t_{90} between the Crested Tern and Bridled Tern. Although the Bridled Tern and Noddy reach 90% of their asymptotic weight at about 38 and 29 days, respectively, they do not fledge until about 58–60 and 51–53 days, respectively. In contrast, the Crested Tern, which takes about 38–40 days to reach 90% of its asymptotic weight, fledges at about the same time as it reaches its asymptotic weight. Earlier hatched chicks appeared to complete their growth quicker and were flying at about 35 days. The growth constants of the White-capped Noddy and the Brown Noddy, *Anous stolidus,* are almost identical, although the former had a closer fit to a Gompertz equation.

In the Common Tern there was sufficient information to compare the growth rates in different brood sizes (Table 5). Single chicks and chicks in broods of two showed similar growth rates although the growth constant was slightly lower in broods of two chicks (Table 3). Examination of the growth rates in broods of three chicks showed that the growth rates were similar in the first chick ($K = 0.256$) and the second chick ($K = 0.239$), but that third chicks showed a marked change in growth rate after 10 days (Fig. 1). The first part of the fitted curve gives a very low constant ($K = 0.145$) which indicates that the third chick experiences a shortage in food during that period. However, the second part of the fitted curve follows a different slope, giving a growth constant ($K = 0.312$) that is as high as single chick broods. Although the data on third chicks in broods of three were based on relatively few chicks (see Langham 1972), it suggests that if chicks survived the first 10 days they would attain a similar growth constant ($K = 0.250$) as that shown by first and second chicks over the whole period. However, these third chicks still appeared to fledge at a lower weight than first (83%) and second (95%) chicks which may be critical in post-fledging survival

DISCUSSION

Lack (1968) has said that the clutch size of birds corresponds to the maximum number of young that the parents can raise on average. Although terns are semi-nidifugous, acquiring mobility and the ability to thermo-regulate early in life, they are still fed by their parents as are altricial species. The variation in average clutch size between marine tern species nesting in the same locality presumably evolved to be the most productive. Pelagic species have reduced their clutch size to the minimum possible, one egg,

TABLE 4
SUMMARY OF TERN CHICK GROWTH STATISTICS

Species	Arctic	Common	Roseate	Sandwich	Black-naped	Crested[a]	Bridled	White-capped Noddy	Sooty
Clutch size	1.82	2.45	1.49	1.23	1.78	1.01	1.00	1.00	1.00
Incubation (days)	22	23	24	23	21	28–30	28–30	35	30
Fledging (days)	19	22	22	25+	24	35–41	58–60	51–53	60
Asymptotic weight (g)	115	128	105	189	100	279–318	128.5	117*	205
Adult weight (g)	110	126	124	230	110	350	130	115	175
Feeding zone	inshore	inshore	inshore	inshore	inshore	inshore	offshore	offshore	offshore
t_{10}–t_{90}	14.5	14.1	16.7	26.6	15.3	38–40	38.4	28.9[b]	—
t_{50}	7.5	7.6	7.3	7.8	8.2	16.4–19.6	14.8	10.6[b]	—

[a] 1979/80 and 1981/82 asymptotes, respectively.
[b] Gompertz.

TABLE 5
PERIOD TO ASYMPTOTE AND FLEDGING IN THE COMMON TERN

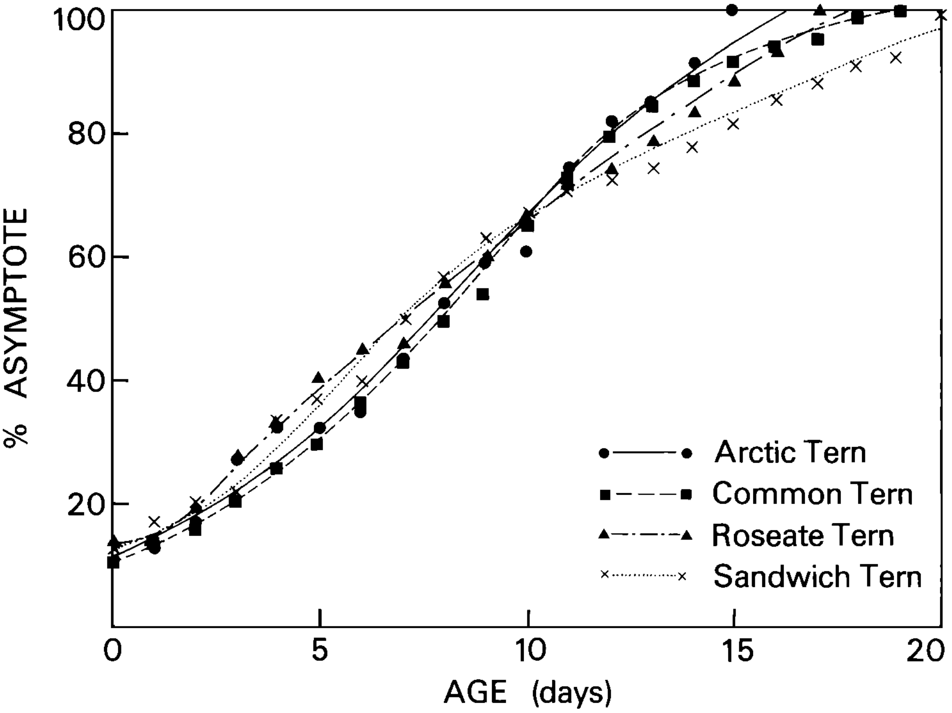
Brood size	Chick order	t_{10}/t_{90} (days)	Asymptotic period (days)	Fledging period (days)
1	1	14.1	19	19
2	1	17.1	20	24
	2	18.4	20	24
3	1	19.7	23	23
	2	16.9	17	24
	3	30.3/14.6[a]	18	24

[a] First 10 days/after 10 days.

where there is little variation in food abundance through the year. Inshore-feeders have an average clutch size which varies from one to three according to species. It is unlikely that egg production in the inshore feeders is limited by food, although early pair bonding and courtship feeding may be an important influence as demonstrated for the Common Tern (Nisbet 1973, 1977). In marine terns, eggs are normally between 15–20% of adult body weight (Table 6), and food required for egg production will depend on clutch size. In temperate species, and also in the Black-naped Tern and Crested Tern, fish are presented to females prior to egg-laying. In the Bridled Tern and White-capped Noddy, fish and other food items are carried in the crop (pelagic foraging making it uneconomical to return with one or few items carried in the bill), but courtship feeding by regurgitation has been observed in the Bridled Tern (Hulsman and Langham, in prep.).

Clutch size tends to be smaller in those inshore feeders that nest in dense groups: Sandwich Tern, Crested Tern, and Royal Tern (*Sterna maxima*). Although largest of the inshore feeders, their eggs still weigh less than 20% of adult body weight (*S. maxima* from Buckley and Buckley 1972). These species avoid aerial predation by sitting tight on their eggs, but their conspicuous guano-spattered colonies make them very susceptible if ground predators are present. Perhaps a small clutch is less wasteful should it prove necessary to desert the colony to avoid ground predators.

Clutch size determines the subsequent brood size and factors favouring a particular brood size such as feeding rate per chick may be the main selective force determining clutch size. Changing environmental conditions, especially those effecting food supply, may favour different brood sizes in some years, so that females of inshore-feeding species might lay one egg less or more than the mean. The variation in brood size be-



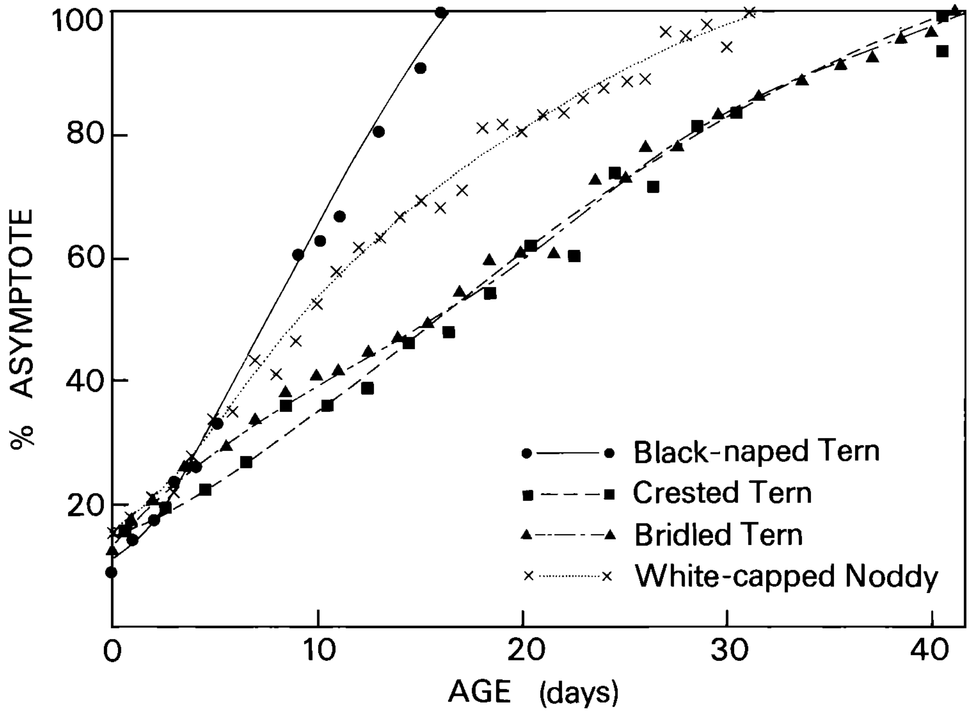


FIGURE 1. Tern chick growth curves as a percentage of asymptote.

TABLE 6
Egg Weight in Relation to Body Weight

Species	Egg weight (g)	Adult body weight ($\bar{x}$ g ± SD)	Egg weight/body weight (%)
Temperate			
Arctic Tern	19[a]	109 ± 1.30	17.4
Common Tern	20[a]	126 ± 1.82	15.9
Roseate Tern	20[a]	124 ± 2.08	16.1
Sandwich Tern	35[a]	229 ± 2.75	15.3
Tropical			
Black-naped Tern	–	110	–
Crested Tern	55	320 ± 350[b]	15.7–17.2
Bridled Tern	25	131 ± 1.80[b]	19.1
White-capped Noddy	23	114 ± 1.38[b]	20.2
Sooty Tern	34[c]	175[c]	19.4

[a] Lack 1968.
[b] Hulsman, pers. comm.
[c] Stonehouse 1963.

tween temperate nesting species in the same locality in the same season cannot be explained by chick mortality as they are exposed to the same environmental factors, including predators. The Common Tern and Sandwich Tern are both inshore feeders, yet the average brood size of the former is twice that of the latter. The growth constant in the Common Tern is greater in single chick broods, broods of two and three, with the exception of the first 10 days of the third chick, than in the single chick broods of the Sandwich Tern. The differences are not related to the greater adult weight (230 g) or asymptotic weight (189 g) of the Sandwich Tern, as the fitted slope is only steeper in the single chick broods of the Common Tern. In other brood sizes the fitted slope is almost identical with that found in the Sandwich Tern (Fig. 2). Also, the asymptote is reached at about 20 days in both species, with the Common Tern fledging at 22 days and the Sandwich Tern at about 25 days. The actual growth from hatching to asymptotic weight is about 5.65 g/day in the Common Tern and about 8.25 g/day in the Sandwich Tern. This means that with twice the brood size on average, the Common Tern will have collected about 37% more food than the Sandwich Tern, assuming that conversion rates are similar. In the Roseate Tern and Arctic Tern, with smaller brood sizes, the growth rates are about 4.6 g/day and 5.1 g/day, respectively.

Dunn (1979) gives comparative growth of temperate nesting species with K values of 0.300 and 0.258 for the Common Tern and Sandwich Tern, respectively. These values (derived from Ricklefs 1973, taken from Pearson 1968), are comparable to those made on Coquet Island, 28 km south of where Pearson made his observations. On Great Gull Island, North America, Common Terns had a lower constant (0.213) in 1967 and a higher one (0.241) in 1968, than that of the Sandwich Tern, asymptotes being reached earlier at 15 days, but fledging later at about 26 days at lower weight (LeCroy and Collins 1972). However, later studies in years with higher survival the results from Common Terns were more comparable (LeCroy and LeCroy 1974).

On Coquet Island, Sandwich Tern parents raised one and occasionally two chicks to one and a half times the weight of Common Tern chicks. Only broods of two Sandwich Tern chicks would have comparable daily increases in weight (16.50 g/day) with broods of three Common Tern chicks (16.95 g/day). Only in 1967, did these two brood sizes have a high success; in the two earlier years broods of one Sandwich Tern and broods of two Common Tern chicks were most frequent due to high mortality of 2nd and 3rd chicks, respectively (Langham 1972, 1974). In these two years, the daily weight increase of Sandwich Tern chick (8.25 g/day) was intermediate between single Common Tern chick (5.65 g/day) and that of a brood of two Common Tern chicks 11.30 g/day).

The other two temperate species considered, the Arctic Tern and Roseate Tern, appeared to feed mainly out to sea from the breeding colony (Langham 1968), but since this was still over the shallow water of the continental shelf, they were considered inshore-feeding species in contrast to the tropical pelagic-feeding terns. The growth constant is higher in the Arctic Tern with a slightly higher asymptote attained in 15 days. Although a few Arctic Terns lay three eggs, the commonest clutch size is two (76%) and most succeed in raising two chicks. The Roseate Tern lays equal numbers of one-egg and two-egg clutches, both with high success, and so half raise one chick and half raise two chicks. Given this dichotomy, one might expect all Roseate Terns to lay two eggs and have a slightly slower growth rate with a longer fledging period. Although in the three years studied the Roseate Tern enjoyed a high breeding success, it appeared more susceptible to climatic changes, probably because Coquet Island is near the northern extremity of its range (Langham 1974). The data on growth obtained by LeCroy and Collins (1972) is very similar, but the survival of chicks in broods of two was about half that in broods of one, although there appeared to be more two egg clutches. As in the Common Tern, the Roseates suffered from poor survival in 1967 (LeCroy, pers. comm.).

In the tropical species, only the Black-naped Tern had a growth rate similar to that shown by temperate tern species. The commonest clutch was two (78%) and the hatching and fledging successes (Table 2) are underestimates due to the difficulties experienced in locating eggs and chicks on the pebble-strewn beach. Its growth rate bears most resemblance to the Arctic Tern and Roseate Tern. It reaches its asymptotic weight in 16 days and fledges in about three weeks, with a daily weight gain of about 4.7 g/day.

The other three species show a much slower growth rate, including the Crested Tern which was mainly seen fishing in the surf zone near the reef edge, an inshore feeder. The situation on One Tree Island seems to be modified by the increase in Silver Gulls, partly associated with human occupation, as some of these are persistent predators of the Crested Tern, and to a lesser extent, Black-naped Tern eggs. In the case of the Crested Tern, certain gulls have become very adept at robbing adults returning to feed their chicks, and even attacking chicks, trying to force them to disgorge (Hulsman, 1976, pers. obs.). This persistent kleptoparasitism may have a significant effect on growth rate. Another factor is that the measurement of growth rate was made using one of the later subcolonies where conditions may have been less favourable. In this case, the asymptotic weight was not achieved until about 38 days, yet some chicks fledged as early as 35 days. In 1982, using the same asymptotic weight it was estimated the nine chicks, the total produced on One Tree Island, would attain this at 40 days, and were probably fledging at this age.

Although predominantly an inshore feeder, the Crested Tern normally lays one egg, a resemblance to tropical, offshore-feeding species. The other tropical species attain their asymptotic weight at a similar or shorter period than the Crested Tern, but the latter fledges much earlier, normally between 35–40 days. On One Tree Island, Bridled Terns and White-capped Noddies attained their asymptotic weights at about 38 and 29 days, respectively. Yet, the Bridled Tern fledged between 58 and 60 days and the noddy between 51 and 53 days. Ashmole (1962) gives a normal fledging age of about 45 days for the noddy but this may be delayed by shortage of food. Other tropical species feeding offshore have long fledging periods such as the Sooty Tern at about 60 days (Ashmole 1963a) and the Fairy Tern at about 83 days, on average (Dorward 1963). The growth of the two offshore species resemble the Sooty Tern when growth constant (K) is plotted against asymptotic weight in contrast to the other species studied (Figs. 2A,B).

In these slow growing tropical species, only one egg is laid which Lack (1968) thought was a result of sparser food and greater distances involved in fishing to feed young. However, it seems that energy requirements are not markedly affected by changes in growth rate where most energy is being required for maintenance with less than a third being devoted to growth (Ricklefs 1979a). Unlike the Common Tern, Ricklefs (1974, 1979b) found the total energy requirement of the Sooty Tern, a pelagic species with a slow-growing chick, reached a maximum early in growth and remained at that level until fledging. The prolonged period of growth occurs after the energy requirements have reached a maximum.

Ricklefs (1979a) speculates that mobility may be important in dense colonies of Sooty Terns where emphasis is on rapid development of legs followed by a slow growth rate of other body structures including flight feathers. Slower growth rate correlated with mobility might explain that found in Crested Terns as well as Sandwich Terns, in contrast to other inshore feeders, as chicks move out of the conspicuous nesting area soon after hatching. Although mobility is important in Bridled Terns, it is not required in the White-capped Noddy which stays put on its nest until fledging. A similar situation would seem to apply to Brown Noddies and Fairy Terns which are also sedentary until fledging, but have slow growth rates.

Another important aspect of a slow growth rate, is that the chick is less prone to starvation where food supply is liable to fluctuations. The advantage of slow growth rate and reduced metabolism (or torpidity) was mentioned for such species as the Swift (Lack 1956). It has been mentioned for the Sooty Tern on Ascension where some chicks were seen to survive for long periods with little food (Ashmole 1963a). In the present study, a period of cyclonic winds and heavy rain demonstrated that Bridled Tern chicks had a much higher survival than those of Crested Terns, even though the latter were near fledging. The chicks of the White-capped Noddies would prob-

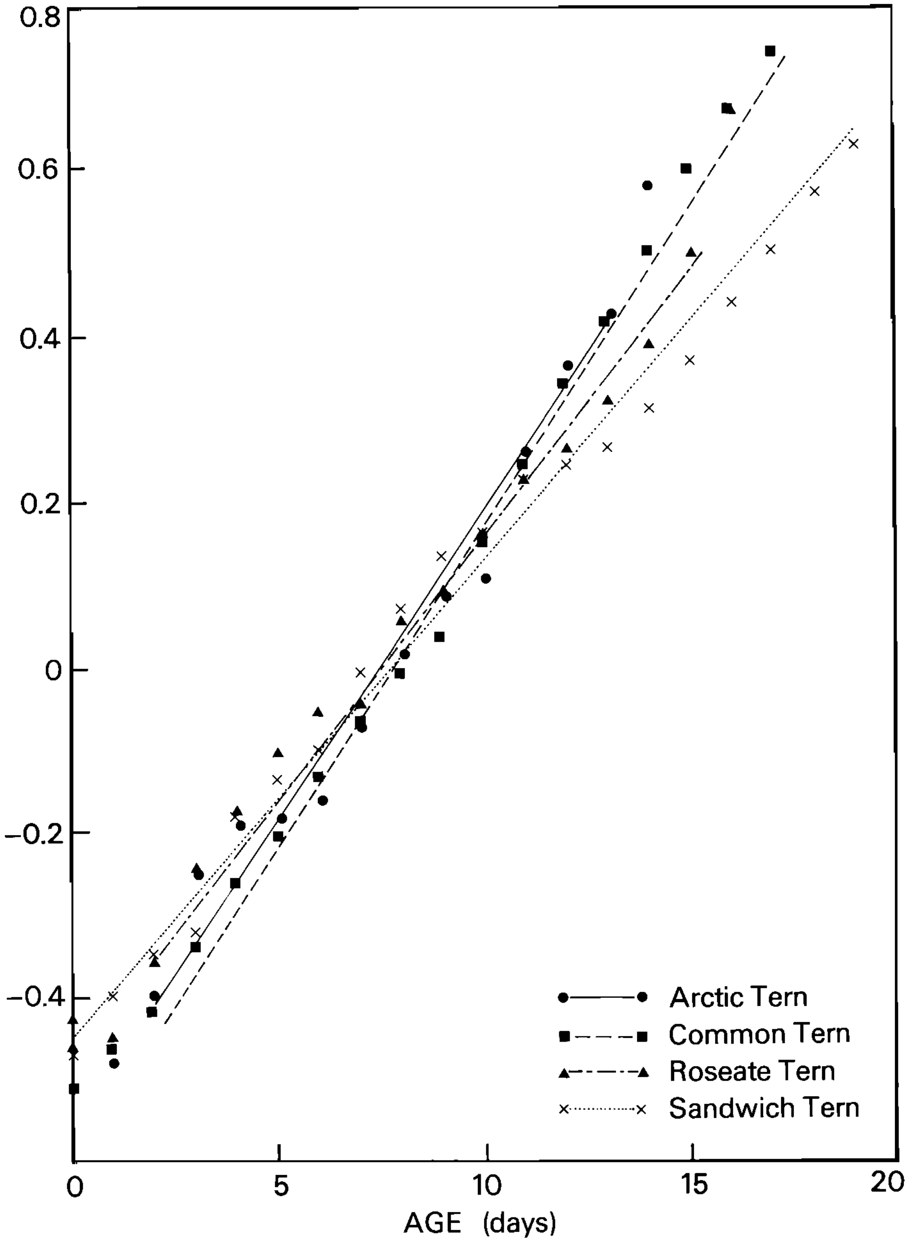


FIGURE 2A. Tern chick growth fitted to logistic or Gompertz curves.

ably have a similar resistance to fluctuating food supply, but the destruction of their nest sites by the cyclonic winds obscured this on One Tree Island. White et al. (1976) reported that Brown Noddies, *Anous stolidus* were unaffected by a storm, and young Sooty Tern chicks which were in more exposed situations died from the loss of insulation caused by the rain and wind, rather than starvation.

Semi-precocial development shown by seabirds such as terns means that parents are soon freed from brooding so that both can be involved in fishing. The chicks of many tropical species have a slower growth rate than temperate species,

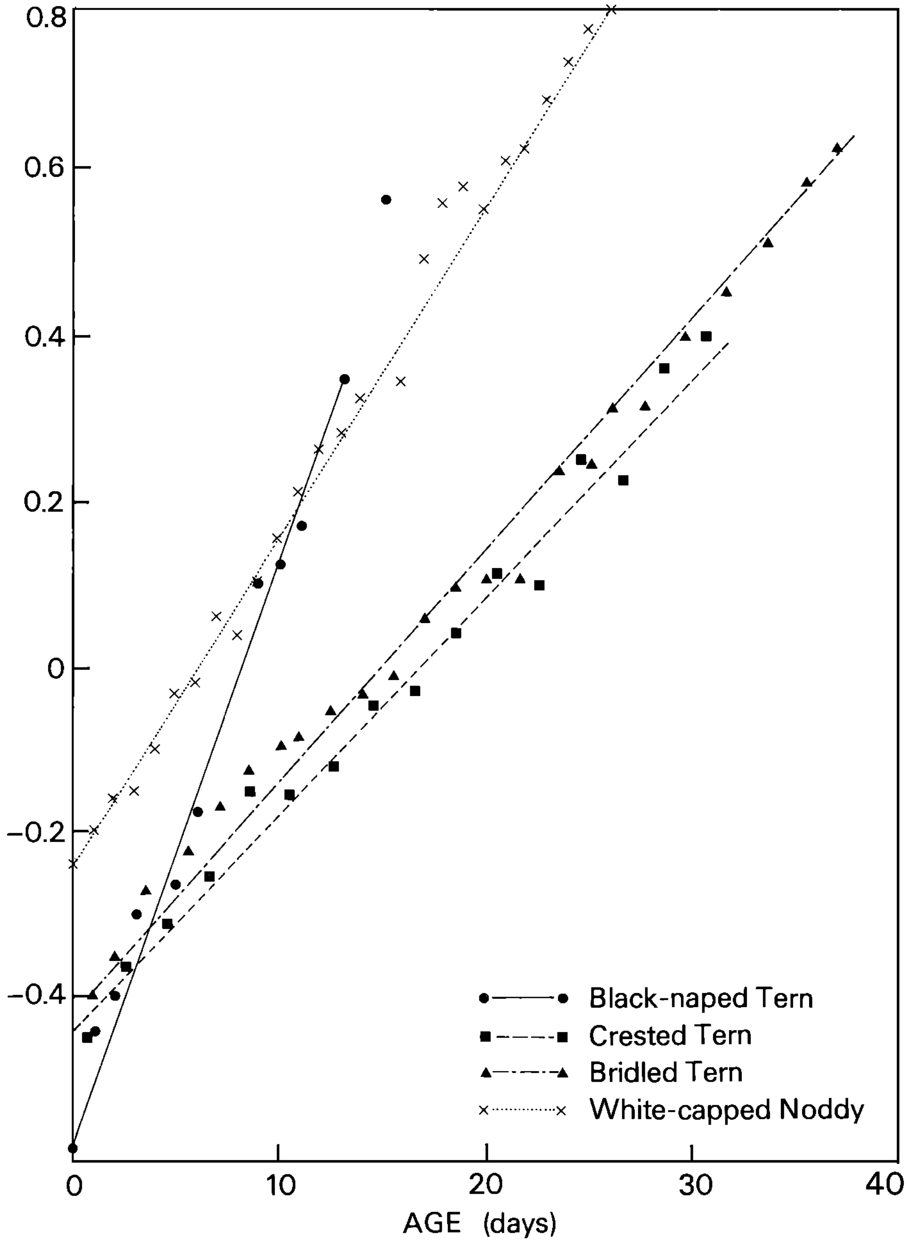


FIGURE 2B. Tern chick growth fitted to logistic or Gompertz curves.

as well as a smaller clutch size and subsequent brood size. These features suggest that predation has been relatively unimportant and that a slow growth rate for species laying a single egg is the only means of reducing food requirements still further (Ricklefs 1968). This is particularly important where food requires foraging over a wide area and is liable to fluctuations. The chicks of tern species rapidly acquire the ability to thermoregulate, and ground-nesting species have advanced development of the legs so that they can move away from the nest site to avoid intraspecific aggression, into cover to escape predators and food robbers, as well as sheltering from inclement weather. The subsequent long period to fledging shown by certain tropical species does not involve a marked increase in weight, since most energy requirements are required for maintenance. The latter part of development involves the growth of plumage, notably remiges and retrices, so that energy requirements remain fairly stable (Ricklefs 1979a). On One Tree Island, the growth rate of the tree-nesting and therefore stationary White-capped Noddy has a faster growth rate in terms of weight to attain asymptote than the Crested Tern or Bridled Tern. Common Noddies have a similar growth rate ($K = 0.153$) to reach asymptote shown by the White-capped Noddy (Ricklefs 1978), with a similar nest site, either a tree or cliff-ledge, involving little necessity for mobility until fledging.

The slower growth rate of offshore-feeding, tropical species is an adaptation to infrequent feeds when parents are required to search over wide areas of ocean where food maybe patchy and daylength short (Hulsman 1980). The Crested Tern has much more frequent feeds (Langham and Hulsman, in prep.) than Bridled Tern or White-capped Noddy, and the slow growth rate to asymptote of the former is accompanied by feather growth and other adult structures so that it can fledge soon after. Unlike the tropical offshore-feeding species, it is not capable of withstanding long periods without food, either because of dispersed food supply or prolonged bad weather, and in this respect resembles temperate marine tern species.

SUMMARY

The growth strategies adopted by marine terns in a temperate and a tropical regime were compared. Tern chicks are semi-nidifugous, being mobile and capable of thermo-regulation soon after hatching, but dependent on their parents for food. In England, the growth rates of Arctic, Common, Roseate and Sandwich Tern chicks were measured. In Australia, Black-naped, Crested and Bridled Terns and White-capped Noddy chicks were considered. The growth rates of all species, except the noddy, fitted a logistic curve. Temperate species lay one to three eggs and raise one to three chicks. The growth to asymptote is completed in all species in about 20 days, and temperate fledging a few days later taking longest in the Sandwich Tern. In the tropical species, the Black-naped Tern has a growth strategy resembling temperate species, with one or two chicks completing asymptotic growth in about 20 days and fledging occurring soon after. In contrast, the asymptotic growth of the young in the inshore-feeding Crested Tern resembled that of the offshore-feeding Bridled Tern, although the former fledges between 35–41 days and the latter at 58–60 days. The White-capped Noddy's single chick completed asymptotic growth in 29 days, but did not fledge until about 51–53 days.

The growth strategies employed are discussed in relation to clutch size and brood size, mobility, feeding rate, duration from asymptote till fledging and the ability to withstand periods of starvation caused by erratic food supply or bad weather.

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SOME CONSIDERATIONS ON THE REPRODUCTIVE ENERGETICS OF PELAGIC SEABIRDS

ROBERT E. RICKLEFS[1]

ABSTRACT.—I develop a model of the energetics of breeding seabirds that incorporates energy requirements at the nest site, rate of energy gathering at sea, and constraints on transporting energy between the feeding area and the breeding colony. Energy requirements are greatest during the period of chick brooding, but an upper limit to the volume or mass of food that parents can carry may ultimately limit brood size to one and preclude rapid growth in pelagic species. Meal sizes are typically 14–18% of adult mass. Feeding rate and energy density of the meal also influence rate of energy delivery to the chick. These considerations suggest that data on diet quality, meal size, and feeding frequency may provide a basis for comparing feeding ecology and corresponding breeding adaptations among species of pelagic seabirds.

Pelagic seabirds forage at great distances from their breeding colonies and return to feed their young at most once each day, and frequently less often. This definition applies to all species of Sphenisciformes (which are not considered here) and Procellariiformes, and many Pelecaniformes (boobies, frigatebirds, tropicbirds) and Charadriiformes (noddies, some terns, gulls, and auklets) nesting on remote islands at all latitudes. Most of these species share a set of reproductive characteristics (single-egg clutch, prolonged incubation period, and slow chick growth) that have suggested energy limitation (Lack 1968). This situation is thought of as arising from three sources: 1) patchy and sparse dispersion of food resources making prey difficult to locate and capture, 2) irregular and unpredictable fluctuations in food availability, requiring birds to adjust reproductive requirements to a minimum anticipated level, and 3) constraints on the ability of birds to transport food between the feeding and nesting site. Severe energy limitation is often regarded as limiting brood size in pelagic seabirds to a single chick. In most experiments in which brood size was increased from 1 to 2, parents did not rear the additional offspring (e.g., Rice and Kenyon 1962, Harris 1966). Slow postnatal development may be an additional means by which the energy demands of reproduction are reduced (Ricklefs, in press). Werschkul and Jackson (1979) have alternatively attributed slow growth rate in pelagic seabirds to the lack of sibling competition (but see Ricklefs 1982), in which case parents may benefit from the reduced daily energy requirement of a slowly growing chick. The accumulation of large quantitites of fat by the chicks of some seabirds, especially petrels, has been viewed as an adaptation to a fluctuating and unpredictable food resource (e.g., Lack 1968).

Balancing this view of seabird reproduction based on food limitation is the observation that pelagic seabirds are among the most long-lived of any group of animals of similar size (e.g., Ashmole 1971, Harris 1977). Hence, food shortages critical enough to threaten the lives of adult seabirds appear to be infrequent. One may argue that adults require less food when they are at sea during the nonbreeding period than they do when nesting, and that while at sea they may range widely in search of suitable feeding areas. If so, the low reproductive rates and long development periods of pelagic seabirds would appear to derive from the special circumstance of having to feed on the open ocean while tied by nesting to a particular locality. This circumstance may impose energy restriction in several ways. First, suitable feeding habitats close to nesting colonies may be less available than areas chosen from a broader area of the ocean. In particular, if local food resources fluctuate unpredictably, birds tied to a particular area must adjust their reproduction to the minimum expected resource level. Second, Ashmole (1963) suggested that the high concentration of seabirds around tropical nesting colonies may depress the local availability of food and thus affect reproduction through density-dependent feedback. Third, the limitation may be derived, not from the quality of the food resource itself, but rather from the problem of transporting food between the feeding area and the nest site.

In this paper, I develop a simple model of the reproductive energetics of pelagic seabirds, incorporating the problem of transporting energy. I then explore some of the implications of this model for reproductive adaptations. Although I have not proposed any new factors or circumstances to explain both the particular adaptations of pelagic seabirds as a group or variation in these adaptations among pelagic seabirds, I have treated energy requirement and food provisioning in a novel fashion that clarifies the problem of reproductive energetics in seabirds and suggests new avenues of investigation.

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[1] Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104.

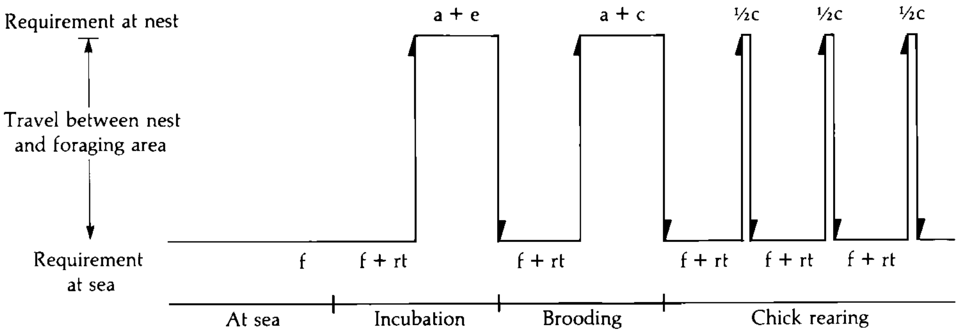

FIGURE 1. A model of the energetics of reproduction in pelagic seabirds based upon a species in which adults return to the colony either to exchange with their mates or feed their chicks after a 24-hour foraging cycle. f = energy required by adult during the foraging cycle, rt = energy required for one round-trip between the feeding area and the breeding colony, a = daily energy requirement (DER) of an adult at the nest, e = DER of the incubation cost of the egg, c = DER of the chick. The model could be modified for any length of foraging cycle.

THE MODEL

The model distinguishes foraging at sea and activities associated with reproduction at the breeding colony (Fig. 1). These activities are connected by round trips between the two areas. While foraging at sea, birds maintain a positive energy balance. That is, food intake not only supplies the energy required to forage but also provides a surplus of energy available to support travel between the feeding area and the nesting colony combined with the energy demands of reproduction at the nest. In my model, I define the energy provided for reproduction by each foraging bout as the net energy return of foraging minus the energetic cost of a single round trip between the feeding area and the breeding colony.

During the nonreproductive period, the energy balance of adults is potentially most positive because they do not have to support reproduction or travel between feeding and breeding areas; molt imposes an unknown cost at this time, however, and food supplies may be lower or less available during the nonbreeding than the breeding season. For breeders, the daily energy (power) requirements of individuals (adults plus eggs or chicks) at the nest site vary with stage of reproduction. During the incubation period, each foraging bout (including feeding and traveling between the nest and the feeding area) must supply the requirements of the adults' incubation bout. In all pelagic seabirds, both members of the pair share incubation and chick rearing, and so time during the incubation period is split roughly half and half between foraging or resting and incubation. After hatching, the energy demands of reproduction increase dramatically. Between the day the chick hatches and the end of the chick-brooding period, each day of foraging at sea must provide the adult with enough stored energy to supply a day's requirements of one brooding adult plus the chick. After the end of the brooding period, however, adults are no longer tied to the nest site, except briefly to feed the chick, and if need be they may devote all their time to foraging. During this period, until the chick leaves the nesting colony, each day's foraging need furnish only one-half the power requirements of the growing chick, the other half being supplied by the second member of the pair. As a result, during the rearing period, power requirements of reproductive activity at the nest are considerably reduced compared to those during the incubation and brooding stages.

The net energy available for reproduction could be increased by reducing the frequency of foraging trips between the feeding areas and the colonies, particularly if the distance were great. This option may be limited by restrictions on the amount of food that adults can carry per trip, as I shall discuss below. Before doing so, however, I shall provide some estimates for energy demands at the nest.

POWER REQUIREMENTS OF REPRODUCTION

The energetics of reproduction have been determined for only a few species of pelagic seabirds, and the available studies must be considered as very preliminary (e.g., Dunn 1980, Drent and Daan 1980, Ricklefs et al. 1980, Ricklefs and White 1981). Patterns of energy requirement likely vary considerably from species to species, but here I report data on the Sooty Tern (*Sterna fuscata*) to illustrate the basic pattern. I assume that the power requirement of an incubating adult

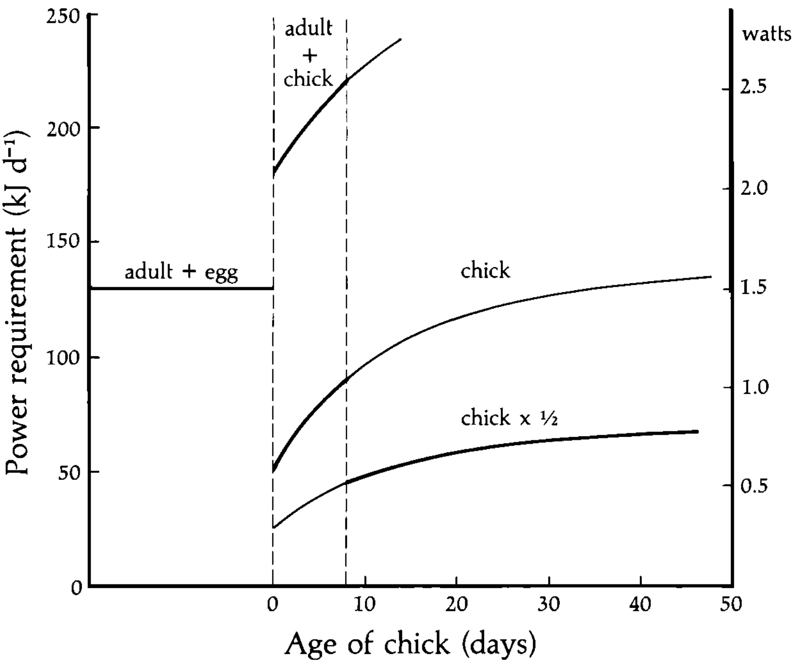

FIGURE 2. Power requirements for reproduction at the nest based on data for the Sooty Tern (after Ricklefs and White 1981).

Sooty Tern is approximately 1.5 times its standard metabolic rate, or SMR (see King 1974, Mugaas and King 1981). Using published allometric equations to estimate SMR (Aschoff and Pohl 1970) results in a value of about 130 kJ d^{-1} (1.50 W). Because Sooty Terns incubate a single egg in a warm climate, incubation probably requires little or no excess heat production by the adult. During the middle of the day, Sooty Terns spend more time shading their eggs than warming them by direct contact with the brood patch (Dinsmore 1972) and metabolism may be elevated over its thermoneutral level (MacMillen et al. 1977). The power requirement of the chick increases from approximately 50 kJ d^{-1} (0.58 W) at hatching to a maximum of 135 kJ d^{-1} (1.56 W) when the chick is fully grown (Ricklefs and White 1981). These estimates do not include activity by either the adult or the chick, but they probably accurately portray the relative power demands during different stages of the nest cycle (Fig. 2).

During the incubation period, the power requirement of the single adult is 130 kJ d^{-1} (1.50 W). During the chick brooding period, approximately eight days on the Dry Tortugas, Florida (Dinsmore 1972), the power requirements for brooding and of the growing chick sum to between 180 and 220 kJ d^{-1} (2.08 and 2.55 W). After the end of the brooding period, one-half the power requirement of the chick, which must be supplied each day by each parent, drops to about 45 kJ d^{-1} (0.50 W) initially and increases to almost 70 kJ d^{-1} (0.81 W) by the time the chick is fully grown. According to this model, the maximum power requirement during the chick-rearing period is approximately one-third the maximum during the brooding stage and about one-half the requirement of the adult during the incubation period.

If adults balanced their energy budgets during the incubation period and if the food supply did not vary over the nesting season, then we must conclude that during the chick-rearing period adults could usually gather much more food than the chicks require. Furthermore, if adults balanced their energy budgets during the chick-brooding stage—I know of no data concerning this point—the discrepancy between the amount of food adults can gather and what they have to provide for their chicks would be even greater. Under such circumstances, pelagic seabirds might be able to rear a second chick with little difficulty except, perhaps, during the brooding stage. The failure of twinning experiments (Palmer 1962, Rice and Kenyon 1962, Harris 1966) suggests, however, that the ability of parents to supply the chick's requirements are constrained by factors other than their ability to gather food. Although the quality of the diet, meaning the relative proportions of certain essential nutrients, may bear upon the growth rate of the chick, diet quality cannot itself be responsible for the small brood size, unless chicks made up potential dietary limitations of essential nutrients at rapid rates of growth by consuming more food rather than reducing growth rate. Therefore, either birds are not energetically constrained during the chick-rearing period and brood size is limited by factors other than rate of energy supply at that time, or the amount of energy that can be delivered to the chick is limited by the ability of adults to transport food between feeding areas and the nest site. I shall elaborate below that constraints upon feed size have less bearing upon the power requirement of the adult bird at the nest site because this demand can be satisfied by stored fat carried at a high energy density.

FEED SIZES IN PELAGIC SEABIRDS

The size of the feed brought to the chick is known for a small number of seabirds. In a few species, food samples have been obtained by regurgitation from adults returning to the nest site, but it is difficult to know whether such samples represent the full amount carried by the adult. Studies reporting the masses of regurgitated food samples rarely have verified by dissection that complete feeds have been obtained. The simplest and most reliable way to measure the size of the feed is by the increment of mass of the chick upon feeding. This technique is most practical for species that feed their chicks no more than once each day; sizes of feeds may be determined by periodically weighing the chick throughout the feeding period. Because meals are assimilated and water is excreted quickly, chicks must be weighed frequently so as not to underestimate grossly the size of the feed (compare Harper 1976 and Richdale 1965). Most of the studies reported here were based upon weighings at 3-hour or 4-hour intervals. Ricklefs (unpubl. data) estimated that about 25% of the mass of meals of Christmas Shearwater and Phoenix Petrel chicks was lost during a 4-hour period following feedings. If feeds occur half-way between weighings, on average, meal size would be underestimated by about 15%.

Unless feeding is observed directly, the investigator must judge whether a chick has been fed by one or both parents during the interval between weighings. In some species, such as some diving petrels (Pelecanoididae), in which feeding rates are high and both parents visit the colony during the same brief period each night, the recorded mass increment usually is twice the average meal size delivered by each parent. For species that feed their chicks infrequently, mass increments are more often due to a single feeding, and it is often possible to distinguish unusually large mass increases as resulting from two feedings. Although this technique has limitations, it is beginning to produce data that reveal certain patterns in the foraging ecology of pelagic seabirds.

Feeding rate and feed size are summarized in Table 1. One must remember that these are representative values only and that meal size and, especially, feeding rate may vary widely over seasons, years, and localities. The average feed size in most of the species falls between 14 and 18% of adult body mass. Lower values were recorded for the Northern Gannet (*Morus bassanus*), which feeds primarily inshore and may make several trips per day to the nest site, particularly during the early part of the development period (Montevecchi and Porter 1980), and for the Brown Noddy (*Anous stolidus*). Values about 18% have been reported only for the diving petrels. The median mass of 27 complete stomach samples of adult Adelie Penguins (*Pygoscelis adeliae*) collected during the chick-rearing period at Cape Crozier, Antarctica, was 500–600 g, or 14–17% adult mass (Emison 1968). Meal size, expressed as % adult mass, and adult mass appear to be unrelated (Fig. 3; excluding the gannet by virtue of its being an inshore feeder). Although some meals are much larger than the average, the available data (Table 1) suggest that seabirds, as a group, have a characteristic feed size and that the rate of energy delivery to the chick may be limited by the amount that can be carried by the parent. In the Sooty Tern, average feed size is approximately 25 g and meals have an energy density of between 4 and 5 kJ g^{-1} (estimated from compositional data in Ricklefs and White 1981). Hence feeds of between 100 and 125 kJ are provided to chicks at an average rate of 1.2 and 1.6 times per day in two studies; the total energy delivered (120–200 kJ d^{-1}, excreted energy not discounted) is on the same order as the estimated power requirement of a single, fully grown chick (135 kJ d^{-1}).

If feed size has an upper limit, it could be imposed either by 1) the maximum volume of the proventriculus, or other storage organ, 2) by the added energy required to transport additional food, or 3) by other aerodynamic considerations that prevent adults from lifting heavier meals. For the energetic cost of transporting additional food to impose an abrupt upper limit to feed size, cost of transport per gram of food carried would have to increase abruptly at large meal size.

TABLE 1
CHARACTERISTICS OF MEALS FED TO SEABIRD CHICKS

Species	Adult mass (g)	Feeding rate[b] (d^{-1})	Feed mass (g) Range	Feed mass (g) Mean (SE)	Sample size (*n*)	CV[c] (%)	% of adult mass	Method[d]
Procellariidae								
Pachyptila turtur (1)[a] Fairy Prion	111	ca. 1		16.6	57		15	I
Puffinus nativitatis (2) Christmas Shearwater	340	0.63	30–60	48.2 (2.4)	14	19	14	I (4)
Pterodroma alba (2) Phoenix Petrel	272	0.36	30–85	49.4 7.6)	8	44	18	I (4)
Hydrobatidae								
Oceanodroma leucorhoa (3) Leach's Storm-Petrel	45	0.27		6.3 (3.6)	34	58	14	I (3)
Oceanodroma furcata (4) Fork-tailed Storm-Petrel	60			7.5		32	13	
Pelecanoididae								
Pelecanoides georgicus (5)	105	ca. 1		18.6	9		18	I (3)
Georgian Diving Petrel (6)	105	0.89	13.5–36	22.3 (0.3)	149	15	21	I (3)
Pelecanoides urinatrix (6) Common Diving Petrel	127	0.94	10–31	26.0 (0.4)	146	16	20	I (3)
Phaethontidae								
Phaethon rubricauda (7) Red-tailed Tropicbird	650	0.49	55–125	96.1 (4.6)	26	24	15	I (4)
Sulidae								
Sula bassana (8)	3000		150–500	c. 250			8	R
Northern Gannet (9)	3263	1+		359		7	11	R
Sula sula (10)	1003			126			13	I (3)
Red-footed Booby (10)	982	0.45		144			15	I
(7)	900	0.74	65–200	142.0 (9.7)	23	33	16	I (4)
Sternidae								
Sterna lunata (7) Gray-backed Tern		1.0	8–19	13.1 (0.7)	28	27		I (4)
Sterna fuscata (11)	175	0.79	9–46	25.1 (2.5)	15	38	14	I (3)
Sooty Tern (7)	175	0.57	14–47	25.9 (2.4)	16	37	15	I (4)
Anous stolidus (11)	160	0.92		15.5			10	I (3)
Brown Noddy (7)	160	1.0	10–25	18.3 (1.4)	10	24	11	I (4)
Alcidae								
Ptychoramphus aleuticus (12) Cassin's Auklet	167	1.0	8.6–45.6	27.8 (2.1)	22	35	17	R

[a] (1) Harper 1976; (2) R. E. Ricklefs, unpubl. data from Christmas Island (Pacific Ocean); (3) R. E. Ricklefs, unpubl. data from Kent Island, New Brunswick; (4) Boersma et al. (1980); (5) Payne and Prince (1979); (6) D. D. Roby and R. E. Ricklefs, unpubl. data from Bird Island, South Gerogia; (7) R. Shea and R. E. Ricklefs, unpubl. data from Midway Islands; (8) Nelson (1978a); (9) Montevecchi and Porter (1980); (10) Nelson (1978b); (11) Brown (1975); (12) Manuwal (1972).

[b] Feeding rates expressed per parent.

[c] Standard deviation of feed mass divided by the mean.

[d] R = meals obtained from adults by regurgitation; I (h) = meal size estimated from mass increments over periods of h hours.

The effect of meal size on the power requirements of transport may be estimated as follows. Pennycuick (1969, 1975) describes the power requirement of level flight as

$$P = \frac{W^2}{2pS_dV} + P_p + P_o$$

where P = total power (watts, W), W = weight of bird (newtons, N = mass [kg] × 9.81), p = air density (1.22 kg m^3 at sea level), S_d = disk area (m^2), V = forward speed (m s^{-1}), P_p = parasite power required to overcome the drag of the body, and P_o = profile power required to overcome the drag of the wings as they are flapped. The first term of the sum is the induced power (P_i) required to keep the bird aloft against the pull of gravity. It is the only one of the three power terms that contains body weight as a variable.

The total energy required for travel between the feeding ground and nest site is the power

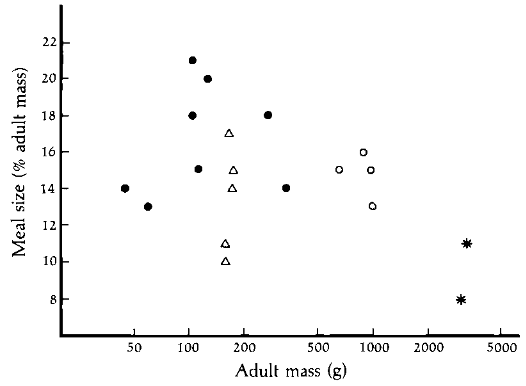

FIGURE 3. Relationship between relative meal size (% adult mass) and adult mass. Solid circles: Procellariiformes; open circles, Pelecaniformes (stars, Northern Gannet); open triangles: Charadriiformes. Data from Table 1.

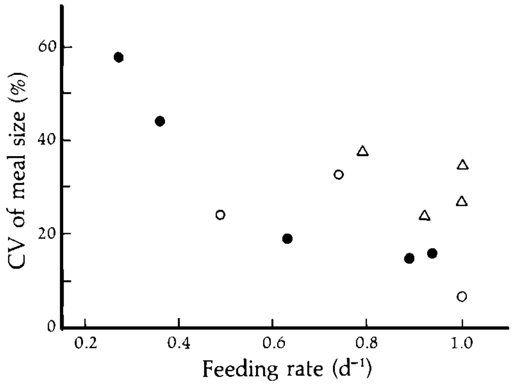

FIGURE 4. Coefficient of variation in meal size as a function of feeding rate per parent. Symbols as in Figure 3.

requirement times time (s), or *Pt*. The right-hand terms (P_p and P_o) in the equation for P are independent of body mass and may be considered as a constant (C) in calculating the effect of meal size on transport cost. Assume the following for Sooty Terns: wing span = 0.86 m (Tuck and Heinzel 1978) (therefore $S_d = 0.58$ m^2), flight speed (V) = 11 m s^{-1} (about 25 m.p.h.; guessed) and $t = 14 \times 10^3$ *s* (about 4 hours; guessed). For a Sooty Tern of average adult mass (0.180 kg), level flight requires 0.200 $W + C$, according to the equation for P. With a 0.025-kg meal, this cost increases to 0.260 $W + C$. Adding another 0.025 kg would increase the flight cost to 0.327 $W + C$, or approximately 0.06 W per meal equivalent. During a 4-hour flight, this cost amounts to about 840 J, which is trivial compared to the approximately 112,500 J contained in the meal. I take this result to indicate that the cost of transporting food to the chick, deriving from the effect of meal weight on flight energetics, is so small as not to pose an upper limit to meal size. Alternatively, either volume constraints or limits to the weight that seabirds can lift off the water could set upper limits to meal size.

VARIATION IN MEAL SIZE

Some of the studies presented in Table 1 provided data for calculating the coefficient of variation (CV) in the size of the meal delivered by individual parents. The CV is an index to the variability of food provisioning. Excluding the Northern Gannet, CVs were lowest for the diving petrels and the Christmas Shearwater, and they were highest for storm-petrels, the Phoenix Petrel, and the Sooty Tern. In general, as the frequency of feeds decreases among species, the variability in feed size increases, suggesting that the most pelagically feeding species are faced with the most variable food supplies (Fig. 4). Among the petrels, variability in feed size could be influenced by variation in the degree to which meals are partially digested at sea and concentrated with respect to their lipid content. Also, because feed size could reflect variation in the timing of the feed within the interval between weighings or in the amount of food accepted by the chicks, which may not always equal the full amount brought by the parents to the nest (see Harper 1976). The data in Figure 4 suggest that as a group, terns have greater variation in meal size than do petrels. Other comparisons are worth following up with more detailed field work. For example, the Red-footed Booby appears to have more variable meal size than the Red-tailed Tropicbird, even though the latter has greater intervals between feedings. The Phoenix Petrel and Christmas Shearwater were studied in the same colony at the same time; the shearwater exhibited both a higher feeding rate and lower variation in feed size. Such results suggest that ecological differences between such species may be revealed through a study of their feeding rates. Further resolution of components of variation into seasonal, night-to-night, and between-individual components should provide an index to the variability in the food supply, against which patterns of lipid deposition might be compared.

METHOD OF ENERGY TRANSPORT

Energy can be carried from the feeding area to the breeding colony as 1) assimilated energy deposited as lipid stores in the adult, 2) undigested food, or 3) some combination of, or intermediate between, these extremes. Lipid deposits can be utilized only by the adult itself to cover the costs

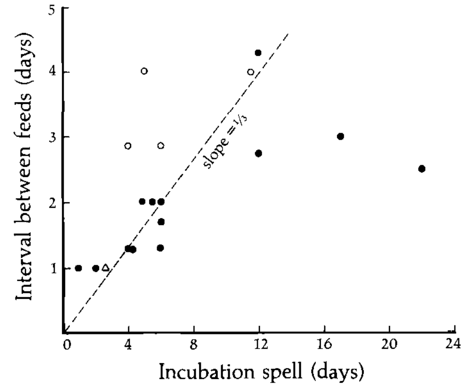

FIGURE 5. Relationship of interval between feeds to incubation spells in Procellariiformes. Data from Lack (1968), solid circles; Harris (1977), open circles; Roby and Ricklefs (1983), open triangle.

of incubation, brooding, and maintenance at the nest. Chicks consume regurgitated food, which may be fresh or partially digested. The manner in which energy is transported determines the amount that can be carried each trip. The energy equivalent of pure lipid is 38 kJ g^{-1}. A Sooty Tern with an incubation requirement of 130 kJ can satisfy that requirement by carrying less than 4 g of lipid from the feeding area to the nest site, i.e., less than one-sixth of the average meal size brought back to the chick. Meals of Sooty Terns were estimated to contain 4–5 kJ g^{-1} (Ricklefs and White 1981). The energy densities of fish average approximately 6 kJ g^{-1} (Watt and Merrill 1963), or about one-sixth of pure lipid. Species that consume prey having high concentrations of oil, particularly plankton-feeding seabirds at high latitudes, may have diets with considerably higher energy density. Petrels may further concentrate dietary energy by partial digestion of the meal and retention of lipids in the proventriculus, forming the familiar stomach oils (Ashmole and Ashmole 1967, Ashmole 1971, Clarke and Prince 1976, Warham et al. 1976).

One consequence of the higher energy density of lipid compared to fresh food is that adults may use fat deposits to sustain themselves for longer periods during incubation and the chick brooding stage than they could on an equivalent mass of food brought back undigested. Therefore, one might expect the length of the incubation spell, during which no food is transferred to the chick, to exceed the interval between feeds brought to the chick, where the amount of energy delivered is more severely limited by the size of the feed. In Figure 5, I have plotted the relationship between inter-feed interval and incubation spell for several species of Procellariiformes. Many of these species are distributed close to a line that represents a feeding interval one-third the length of the incubation spell bearing out the expectation.

LENGTH OF THE BROODING PERIOD

The model of power requirement portrayed in Figure 1 suggests that the maximum demands upon parents occur during the brooding period. At this time, the parent must support not only itself but also the increasing power requirements of the chick. If at any time during the nest cycle parents must accept a negative energy position, it is during the brooding period (the long fasts of incubating polar penguins excluded). The demands of brooding may explain the rather curtailed chick-brooding periods and early development of endothermy of many pelagic seabirds. The chicks of storm-petrels, which are left alone after 2–4 days of brooding, often in very cold environments, may represent the extreme. Although the power requirements of these chicks might be reduced by extended brooding, the total energy demands upon the parent, including its own maintenance requirements at the nest, may be too much to sustain.

A simple model will illustrate the factors bearing on the length of the brooding period. Assume that the mass of lipid carried to support the parent during brooding spells is negligible compared to the mass of food required by the chick. Assume further that the parent must deliver all the food required by the chick for a day during the brooding period but only half the food required by the chick during the subsequent chick-rearing period. If, under these restrictions, parents additionally can deliver only one-half the maximum amount of food required by the full grown chick, then the brooding period should extend no further than the age at which the chick requires half of its maximum energy consumption when full grown. For the Sooty Tern (Fig. 2), this level is is reached when the chick is only a couple of days old. In fact, when the chicks are finally left unbrooded during the day at eight days of age, the estimated power requirement of the chick (90 kJ d^{-1}) exceeds one-half of the maximum requirement of the full grown chick by about 30%. An energy budget calculated for Leach's Storm-Petrel (Ricklefs et al. 1980) indicates that chicks attain half their maximum power requirement shortly after hatching.

These considerations suggest that longer brooding periods should occur in species that hatch smaller chicks with lower power requirements, and in larger species. For the latter, the mass-specific metabolic rate is lower and a meal representing a given percentage of adult body mass can supply the power requirements of the chick for a longer period. Among seabirds in general, longer brooding periods are found primarily in larger species, notably penguins, albatrosses, giant fulmars, and Pelecaniformes. The pattern of power requirement by chicks of the inshore-feeding Double-crested Cormorant illustrates the pattern for a large altricial species, and shows that the initial requirement of the small chick is low and that one-half of the maximum power requirement is not reached until after 15 days of age (Dunn 1980). In the Northern Gannet, that point is not reached until 3–4 weeks after hatching (Montevecchi et al. 1983). Prolonged brooding usually is associated with altricial development which, in turn, usually is associated with a low chick power requirement, particularly during the early development period. The energy requirement of the chick and length of brooding period may be mutually adjusted according to relationships that are beyond our ability to model at present.

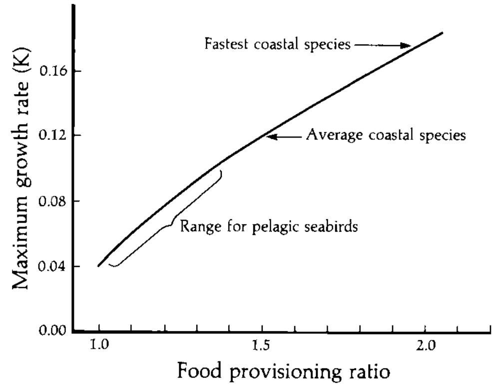

FIGURE 6. Relationship between maximum sustainable growth rate (rate constant of Gompertz equation) and food provisioning ratio (energy delivery rate per chick divided by power requirement of fully grown chick; from Ricklefs 1983a).

FEEDING RATE

The net energy returned to the nest site conceivably could be increased by increasing the interval between feeds hence reducing costly travel between foraging areas and the nest. When meal size is limited, however, by the mass that the adults can carry, to reduce feeding rate is to bring about a corresponding reduction in the rate of energy delivered to the chick. To some degree, this could be compensated by concentrating lipid in the diet through selective digestion. It is thought that procellariiform birds do this in producing stomach oils that are then regurgitated to the chicks (Ashmole and Ashmole 1967, Ashmole 1971). For Leach's Storm-Petrel, the chick's power requirement of 90 kJ d^{-1} could be satisfied by an average meal size of 6.3 grams and a feeding rate of 0.27 feeds per parent per day only if the energy concentration of the diet were about 26 kJ g^{-1}, or 70% of the value of pure lipid. The ability of parents to deliver such an energy-concentrated diet may depend in large part on their ability to select prey with high lipid contents. Hence feeding far at sea, tied to long intervals between feeding visits, may be intimately connected with diet selectivity and may be possible only in regions where certain types of prey are available. When the biochemical composition of the diet cannot be altered substantially by selective digestion, prolonging the period between feedings will reduce the energy available to the chick and may require a reduction in growth rate to balance the energy budget. Among Pelecaniformes frequency of feeding and rate of growth are strongly and positively correlated (Harris 1977, Nelson 1977, 1978). This may be related directly to the effects of foraging distance on food provisioning.

FEEDING RATE AND GROWTH RATE

I (Ricklefs, in press) have recently developed models describing how rapidly chicks can grow with different levels of food provisioning. These models are based upon sigmoid growth of Gompertz form (Ricklefs 1968) and the assumption that the maximum power requirement during the growth period cannot exceed the maximum potential level of food provisioning, which furthermore is assumed to be constant throughout development. I evaluated the model for a 1000-g seabird patterned after the Red-footed Booby. Maximum sustainable growth rate is related to the food delivery rate in Figure 6, where growth rate is expressed as the rate constant (d^{-1}) of the Gompertz equation and rate of food delivery is expressed as the ratio of the delivery rate to the power requirement of a fully grown chick. When the food delivery rate equals this level, and the ratio is thus 1.0, the maximum sustainable growth rate is 0.041 d^{-1}. As the level of food provisioning increases above this level the maximum sustainable growth rate increases rapidly, approximately doubling between food provisioning ratios of 1 and 1.2. When the ratio reaches 2, a growth rate of approximately 0.18 d^{-1}, 4.5 times faster than that at a ratio of 1, can be supported. The models developed by Ricklefs (in press) indicate that at ratios much in excess of 2, parents should double brood size at the expense of greatly reducing the growth rate of the two chicks.

The maximum growth rate predicted for any seabird the size of the Red-footed Booby is on the order of 0.18 d^{-1}, the minimum 0.04 d^{-1}. A survey of growth rates reveals that among 1000-gram species, the range of growth rates observed in pelagic seabirds rearing single chicks is approximately 0.04 to 0.10 (Ricklefs 1973, 1982), corresponding to food provisioning ratios of approximately 1 to 1.3 or 1.4. The average growth rate of inshore feeders rearing broods larger than 1 was approximately 0.12 d^{-1}, corresponding to a food provisioning ratio of 1.5 per chick, i.e., a total of 3 to 4.5 for most species. The highest observed growth rates were about that expected for a food provisioning ratio of 2 per chick, i.e., a total of 4 to 6.

If my model realistically assesses the relationship between growth and power requirement in birds, the observed growth rates of pelagic seabirds raise a number of issues. In particular, in no pelagic species does the food provisioning ratio appear to exceed about 1.4; we would expect to observe brood sizes of 1 among species with food provisioning ratios up to 2, or even more with high time-dependent chick mortality. Although pelagic seabirds may possibly be restricted to areas with uniformly low feeding conditions, the food provisioning ratio alternatively may be limited to below 1.4 by the amount of food that parents can carry. For a seabird the size of the Red-footed Booby, carrying 150 g meals at 5 kJ g^{-1} at a frequency of 0.45 meals per parent per day, the energy delivered (675 kJ d^{-1}) is 1.35 times the requirement of the fully grown chick (1.5 × SMR). At a feeding frequency of 0.74 meals per parent per day, the provisioning ratio is 2.22. For the Sooty Tern, similar calculations give ratios of 1.06 and 1.46 at the feeding frequencies reported in Table I (0.57 and 0.79). If observed feed sizes are close to upper limits, then these calculations lend force to the suggestion that the growth rate of pelagic seabirds is food-limited, directly so by the ability of the parents to carry food in species that feed their young frequently.

FUTURE WORK

Using the model presented in this paper to interpret aspects of seabird ecology depends in part upon its quantitative evaluation. Hence to increase the precision of the model is to increase our understanding of how seabirds interact with their environments. Current knowledge of seabird energetics and certain aspects of seabird reproduction is rudimentary, to the point of hindering substantial progress in the study of pelagic birds. In the context of the discussion presented in this paper, I believe that the following areas deserve close attention.

(1) Quantitative theory provides the appropriate context for field observation and experimentation. With minor exceptions, there has been no progress in the development of explicit theory for seabirds in two decades, since the work of D. Lack and N. P. Ashmole during the 1960s. Even many of their ideas on the evolution of reproductive rate and the regulation of seabird populations were not expressed in terms of easily testable predictions. Although seabirds are attractive for many kinds of work, biologists have continually been frustrated by their inability to study the ecology of their subjects away from breeding colonies. Until the techniques of satellite telemetry and on-bird microprocessing of activity data become inexpensive and accessible, we shall have to rely on assessing foraging ecology by indirect means at the nesting colony. To be useful, theories must be expressed in such measurable terms, at least for the present.

The more explicit the theory, the more precise and detailed must be the measurements used to evaluate models. All the relationships discussed in this paper should be written in more complex expressions, reflecting the real complexities of seabird biology. Sensitivity analyses will tell us how precisely we must measure each variable in order to optimally balance research efforts to answer particular questions. Without considering such models in further detail here, it is still possible to indicate some areas that require further work.

(2) Clearly, much of the discussion in this paper has been based on considerations of the power requirements of adults and chicks. These are poorly known, in part because few seabird colonies are amenable to physiological work. That situation is changing with the opening or upgrading of research stations and the increasing portability of apparatus. Where possible, investigators should measure power output directly by the doubly-labelled water technique. It is particularly important to obtain data on incubating and brooding adults, and on chicks both at the end of the brooding period and at the age of maximum power requirement.

(3) A major part of the power requirement of the chick is the accumulation of energy in the tissues of the body. These requirements can be measured only by biochemical analysis of a series of chicks collected during the nesting period. Such specimens could also reveal information on the management of energy reserves by nestlings, particularly of Procellariiformes, which store large quantities of fat as chicks.

(4) The discussion in this paper assumed that adults balanced their energy income and expenditures during the nesting cycle. It is possible, however that they may accept energy deficits for short periods of high power requirements, particularly the chick-brooding period. Trends in

adult mass during the nesting cycle may indicate such periods and their potential effect on the energy budget.

(5) Meal size and feeding rate are particularly revealing of feeding ecology, and their study should be pursued vigorously. Because these measurements are likely to be extremely variable over seasons, years, and localities, their estimation will require a large effort. In many species, this effort might be considerably reduced by continuous recording of chick masses on the nest (e.g., Poole and Shoukimas 1982, Sibly and McCleery 1980), coupled with time lapse photographic records of parental feeding.

(6) Data on food delivery are only as useful as estimates of the energy and nutrient composition of meals are accurate. Recent biochemical work on seabird diets, especially of the food consumed by chicks, must be greatly expanded and incorporated routinely in studies of other aspects of breeding biology.

The model discussed in this paper distinguishes between the food delivered to chicks and the energy carried by parents to fulfill their power requirements at the nest. Direct measurements of the latter by biochemical analysis of adults at the beginning and end of incubation bouts are indicated.

(7) Finally, additional information on growth rate, development of endothermy, parental care of the eggs and chicks, and patterns of fat deposition and utilization will enrich the phenomenology of seabird adaptations and increase the statistical power of comparative and correlative analyses. Measurements of breeding success and adult survival, in experimental studies where practical, will tell us the demographic outcome of the interaction between adaptations of seabirds and their environments, and provide a basis for evolutionary interpretations of the great diversification of seabird biology.

SUMMARY

I developed a model that matches the energy requirements of reproduction (i.e., of the eggs, chicks, and adults at the nest site) to the ability of parents to transport energy from the feeding area to the breeding colony. The greatest energy requirement relative to the ability of the parents to provide food occurs during the chick brooding period. At this time, the energetic demands of the nestling are increasing with chick growth while adult foraging is still constrained by the requirement of one parent to remain at the nest site. The ratio of energy demand to supply is also high during the incubation period, when the adult must spend half its time at the nest. Relative energy demands are lowest for each parent during the chick-rearing period, but brood size and the growth rate of the chick may be limited by the ability of the parents to carry sufficient unassimilated food between the feeding and nesting areas.

This view of reproductive energetics suggests that problems involved in transporting food over long distances, rather than the foraging ability of adults, may limit the reproductive output of seabirds. During the incubation and brooding stages, adults can carry energy needed to maintain themselves at the nest site in the form of stored fat which has a high energy density. Chicks, however, require regurgitated, relatively fresh food transported between the feeding and breeding areas at a low energy density. Measurements of feed sizes in a variety of pelagic seabirds indicate a characteristic feed size on the order of 14 to 18% of adult body mass. The product of the feed size and its energy density sets an upper bound to the amount of energy that can be provided to the chick, assuming one feed per parent per day. In species that feed their young at intervals of more than one day, rate of energy provisioning may be severely reduced. By partial digestion of meals and retention of lipids in the foregut, petrels may have been able to increase the energy density of their feeds, thereby permitting extended foraging bouts. This strategy may be available only to species having high-lipid diets. The models suggests that seabird biologists should pay attention to the size and biochemical composition of feeds, as well as to the energy requirements of reproduction, in order to interpret adaptations of seabirds to their marine environments.

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CONTRASTS IN BREEDING STRATEGIES BETWEEN SOME TROPICAL AND TEMPERATE MARINE PELECANIFORMES

J. B. NELSON[1]

ABSTRACT.—The climatic and feeding conditions to which marine pelecaniforms are subject largely determine the nature of each species' breeding strategy. An individuals lifetime strategy 'should' (presumably) be to produce the greatest number of fit young at the least cost. To achieve this a complex set of breeding adaptations must evolve such that everything the individual does enters the equation between the energetic cost and the net result of the activity. Thus viewed, we may investigate the nature of the differences in breeding strategy between temperate and tropical pelecaniforms. These include deferred breeding, frequency and timing of breeding, size of egg, clutch and brood, the detailed composition of the breeding cycle, the nature of the attachment to breeding area, breeding site and partner and the size and spatial and social characteristics of the breeding group. Few of these relate exclusively to temperateness or tropicalness. Foraging mode (inshore and distant) is a critical determinant of breeding strategy and does not relate exclusively to latitude. But the adaptive advantage of flexibility in breeding under tropical feeding conditions and of predictability under temperate markedly affects breeding regimes and the behavior systems which subserve them.

The breeding strategies employed by an individual largely determine its life's productivity. In genetic terms, this includes its contribution to the breeding success of relatives, with whom it shares genes (Hamilton 1963, 1964, 1970). Breeding strategies must be subject to strong selection pressures. Therefore we may expect that environmental conditions, which so greatly affect foraging and feeding for example, will play an important if not decisive role in shaping breeding strategies. Tropical and temperate regions impose widely different foraging methods and selection pressures. This contribution aims to examine the nature of some of the adaptive responses in the marine pelecaniforms.

Breeding strategies are only part of a species' web of adaptations, evolving along with hormones, respiration, egg-physiology, the shape of wings, beaks and feet and the entire behavioral repertoire of the species. The Great Frigatebird *Fregata minor* of the Galapagos occasionally incubates for 17 days continuously, but, whilst this may be required in order that its partner may forage widely to locate food, the species' physiology must enable it to withstand long periods without food or water. Lack (1967) called this intricate web of relationships 'a new and exciting development in ornithology.' Since then, the complexity has been confirmed but the web has not been untangled.

In elucidating these relationships and the nature of breeding adaptations there can be no substitute for long, detailed and genealogical field studies. In addition, such studies provide the only means by which conflicting theories about evolutionary mechanisms can be resolved. For example, the argument about whether population control occurs by optimal productivity and density-dependent mortality or by intrinsically (socially) controlled recruitment (Lack 1954, Wynne-Edwards 1962) can be fully resolved only through reliable data about the phenomena involved. *Do* some seabirds take "rest" years? Precisely what is the phenomenology of deferred breeding? These and scores of similar questions need answering before interpretation is possible. And in the field of sociobiology, where interpretation tends to precede facts, it would be useful to know *which* individuals are most successful, and why. Life-history data can be used, also, to suggest why certain strategies, for example cooperative breeding and lekking, are common in landbirds but absent in seabirds.

Pelecaniforms are excellent subjects for such comparative ecological and behavioral research because they breed in colonies with great intraspecific variability, thus offering opportunities to study social aspects of breeding success; many species are widely distributed, offering opportunity to study the relationship between breeding and different climatic and environmental conditions; and many aspects of breeding biology vary widely within, and especially between, families. Additionally, once breeding haunts are reached, colonies are usually accessible, with readily quantifiable ecological and behavioral parameters.

In this limited survey of breeding strategies, I include all activities which are a necessary part of breeding, as against merely the maintenance of life in general. Breathing, defecating, preening, thermo-regulation, feeding, etc. are thus excluded, but activities preceding laying, which are often unjustifiably ignored, are here included. Every component of breeding costs time and energy, and thus may involve risks and has potential rewards. As mentioned above, the nature and availability of food is a major determinant of breeding strategy. Other factors, such as climate,

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[1] Zoology Department, University of Aberdeen, Scotland AB9 2TN, U.K.

predation and availability of nest sites can also be important but are usually of more local significance.

My objective is to bring out the nature of adaptive differences in breeding strategies of marine pelecaniforms by means of examples, with special reference to the role of tropical and temperate conditions. I have excluded most pelican species and the anhingas because their inland and fresh water feeding habits introduce complications and their omission does not affect my theme. At the end of each section I provide a brief conclusion, which facilitates cohesion between sections.

Breeding strategies involve: 1. Age at which breeding is first attempted. 2. Activities which precede the first breeding attempt. 3. Frequency of breeding. 4. Timing of breeding. 5. Size of egg, clutch and brood. 6. Composition of the breeding cycle (site-establishment, pair-formation, nest-building, incubation, care of young from hatching to fledging, postfledging care of young). 7. Nature of attachment to breeding area, breeding site and mate. 8. Size and spatial characteristics of the breeding group.

AGE OF FIRST BREEDING

For maximum productivity a seabird "should" breed as soon as it is fit and competent, in terms of hunting ability, local lore and social behavior. This rejects deferred breeding as an intrinsic regulator of recruitment, which is inconsistent with individual and kin selection, and because a simpler explanation exists. The difficulty lies in assessing 'full' fitness. We cannot yet assess physiological fitness to enable us to compare breeders, non-breeders and pre-breeders, and except by inference, we will never be able to assess "skill" and "lore." Nor would it be enough merely to demonstate that individuals of a given age *can* rear young, but that many do not attempt to do so. Some 5 or 6 years olds may be "fitter" than others.

Some phalacrocoracids and pelecanids can breed when two years old (e.g., Brown, Urban and Newman 1982) and none absolutely require more than three years before breeding. Yet it is thought that frigates do not breed before they are seven and may require up to eleven years (Diamond 1975a). In between, Red-billed Tropicbirds *Phaethon aethereus* breed when four or five (Harris 1969a), boobies between two and four and gannets between three and six (Nelson 1978). Within the sulidae, circumstantial evidence (Nelson and Powell, unpubl. data) suggests that the far-foraging Abbott's Booby *Sula abbotti* has the longest deferred breeding period. It also has the slowest growth. The other sulids with slow growth, notably the Red-footed Booby *Sula sula* but to some extent the Masked Booby *Sula dactylatra* also have longer deferred breeding periods and are more pelagic than their inshore congeners, notably the Blue-footed *Sula nebouxii* and Peruvian *Sula variegata* Boobies.

Long-deferred breeding does not correlate with size and weight, feeding mode, nesting habitat, colony size and density or social complexity. It does, however, correlate with foraging habit. With one exception, the Atlantic Gannet *Sula* (*s.*) *bassana,* all pelecaniforms which delay breeding until they are five years old or more have in common the habit of foraging far from the colony. This in turn means that tropical marine pelecaniforms tend to show longer deferred breeding periods than temperate ones. Pelagic feeders forage over ocean areas which are often vast and apparently impoverished. Within these areas they must find perhaps transiently productive zones, presumably using many subtle cues. Long experience may count for more, here, than in species which forage in restricted, often rich areas. The Atlantic Gannets' intense competition for a breeding site, unique within the order, may prevent younger individuals (especially males) from breeding (Nelson 1978). Sex differences in age of first breeding (females usually breeding before males) remain to be explained but may have to do with the latter's site-establishing role.

Conclusion

The length of the deferred breeding period correlates positively with the tendency of breeding adults to forage far from the colony and is usually, therefore, longer in tropical than in temperate marine pelecaniforms.

ACTIVITIES PRECEDING FIRST BREEDING ATTEMPT

CLUBS

In general clubs are gatherings of non-breeding (usually pre-breeding) individuals, including many in immature plumage. Sometimes they contain off-duty breeders. Usually club birds congregate near to, but separate from breeders. They are distinguishable from roosts and aggregations of "loafers" by the territorial and incipient nest building activities which occur there. At roosts and loafing areas the main activities are preening, bathing and sleeping and any agonistic behavior is merely to maintain individual distance. In no pelecaniform is it known that permanent pair bonds are first formed in the club, after which the pair transfers to a breeding site, though this is claimed for some gulls. A review of clubs in seabirds remains to be written.

Within the pelecaniforms they are reasonably well documented only in Atlantic Gannets, where they are highly conspicuous. In this species they may contain more than 2000 individuals, packed more densely but less regularly spaced than in the breeding colony to which they are adjacent. Club members perform the species full repertoire of agonistic and sexual behavior, including copulation. They land and depart frequently, with attendant risk of injury, and Gannet clubs cannot be dismissed as mere aggregations of resting birds. There is no special relationship between clubs and either tropical or temperate pelecaniforms. Two possible predisposing factors may be large colony size and complex social structure. The latter may include relatively permanent attachment to site and mate since clubs may facilitate, by practice, site-establishment and pair-forming behavior.

PROSPECTING, AND PRE-BREEDING OCCUPATION OF SITE

The establishment of a breeding site and pair proceed in steps which, though little known (see Hunt 1980, for a recent review of mate selection and mating systems in seabirds) are clearly very different in different pelecaniforms. Prospecting for the 'right' colony and segment within the colony is a preliminary step but because that activity is essentially part of site establishment and this links closely with pair-formation, the whole process is considered under those headings. Most pelecaniforms and indeed most seabirds attempt to breed in the first season in which they establish an adequate site. Only where the site is unusually important would it be worth spending a full season establishing it. This is known to happen only in the Atlantic Gannet. It would be practicable only where seasonally predictable food allows the owner to return predictably to re-occupy the site. In impoverished tropical areas in particular, the cost, in time taken from foraging, would be high. It may be that the Atlantic Gannets' combination of circumstances is unique.

CONCLUSION

No pelecaniform is known to form definitive pairs in "clubs." No tropical marine pelecaniform invests a season in occupying a definite nest site before breeding on it. At least one temperate sulid (the Atlantic Gannet) does so.

BREEDING FREQUENCY

SUCCESSFUL BREEDING

Although in seabirds an annual seasonal cycle is normal in temperate latitudes, many tropical seabirds, including pelecaniforms, have modified the length of their breeding cycles and therefore their breeding frequency, to suit local conditions. Some tropical pelecaniforms breed more than once a year, thus increasing the number of cycles within their lifetime whilst others are compelled as a consequence of their particular feeding adaptations, to breed less than once a year. For almost all species, data from banded individuals and pairs are lacking. The Flightless Cormorant *Nannopterum harrisi* may attempt to breed several times within a calendar year (seven times within 24 months for one male and eight clutches within 36 months for a female, Harris 1979). In some areas Brown *Sula leucogaster* and Blue-footed boobies fit more than one breeding cycle into a calendar year (Nelson 1978). In several cormorants, for example Little Black, *Phalacrocorax sulcirostris,* Black-faced, *P. fuscescens,* Pied, *P. varius,* Little Pied, *P. melanoleucos,* Long-tailed, *P. africanus,* Bank, *P. neglectus,* and Cape, *P. capensis,* according to area, the population breeds either continuously or at two seasons of the year, though more than annual breeding has not been proved for identifiable pairs. The Common Cormorant *P. carbo* breeds more or less continuously in tropical Australia (Serventy, Serventy, and Warham 1971) but strictly annually and seasonally in Britain and western Europe (e.g., Cramp and Simmons 1977).

Six pelecaniforms (the five frigate species and Abbott's Booby) breed only once every two years, although the male Magnificent Frigatebird *Fregata magnificens* on Barbuda probably breeds more often by abandoning one cycle part-way through and beginning another with a new female (Diamond 1972). The same species can be an annual seasonal breeder in one area (Red-footed Boobies on Christmas Island, Indian Ocean), but breed less often than once a year and largely aseasonally in another (Red-footed Boobies on Tower Island, Galapagos) (Nelson 1969, 1978). However, no pelecaniform is known to breed successfully both more *and* less than once a year, in different localities.

Breeding frequency depends partly on the length of the cycle and this correlates chiefly with the time taken to rear offspring to independence, which is longer in pelagic than inshore feeders. Thus, the seven marine pelecaniform species (five frigates and two sulids) which breed less often than once a year are all pelagic feeders, usually tropical with scarce and/or unpredictable food and therefore with slow growing young.

Some frequent breeders with relatively short rearing periods are inshore feeders (cormorants, some populations of Blue-footed Boobies) or species with readily available and dependable food (gannets, Peruvian Boobies). The Brown Boobies of Ascension Island appear to be a special case (Simmons 1967) in that, although living under extreme tropical, blue-water conditions, with unpredictable food shortages, most pairs occupy their breeding sites continuously. Pairs without eggs or chicks then lay whenever food becomes plentiful. Thus, although in extreme cases young are dependent for longer than those of almost any other sulid, in general this population breeds more frequently than any other sulid. Several tropical marine pelecaniforms, which are also pelagic feeders (tropicbirds, Masked Boobies and several populations of Red-footed Boobies) breed only approximately once a year, but as populations only very loosely seasonally. There apparently are no predictable advantages to strictly seasonal breeding.

The evidence uniformly suggests, as Lack (1954) predicted, that despite different strategies, each species rears as many young as it can feed. There is no positive evidence to the contrary. However contra Lack there is nothing to support the idea that the number of young reared is always density-dependently controlled. In fact, whilst density-dependence is difficult or impossible to prove, it can sometimes readily be demonstrated that the number of young reared, at least to independence, is NOT density dependently controlled. For example. both in tropical pelagic feeders such as frigates and Red-footed Boobies on the Galapagos, and in inshore feeders of more productive areas such as the Peruvian Boobies, Guanay Cormorants *Phalacrocorax bougainvillea* and Chilean Pelicans *Pelecanus* (*O.*) *thagus* of the Humboldt Current, the food shortages which occur are unequivocally *not* due to the size of the bird population. Oceanographic factors and not birds cause the temporary disappearance or shortage of food, which often suddenly reappears. The size of the bird population is supremely irrelevant either in causing the shortage or in coping with it.

FAILED BREEDING

The response to a failed breeding attempt is another aspect of breeding strategy. Options are: remain on site and replace the clutch or brood within the time required to develop new eggs (genuine replacement); abandon the attempt, disperse, perhaps molt and return again at the normal seasonal time if there is one; or lay again *before* this would otherwise have happened but later than genuine replacement would require.

The first option is adopted by most if not all temperate marine pelecaniforms. However, replacement clutches are useful only if young are not produced, or thrown on their own resources, at an impracticably hostile time and if the energy cost to the female can be readily met (or, if it cannot, stress is acceptable). In highly seasonal latitudes there is a cut-off point beyond which lost clutches or broods are not replaced. In the Atlantic Gannet on Bass Rock 70% of eggs lost to experienced females were replaced if lost within a month after laying. After 43 days of incubation, replacement laying did not occur. When (as here) the egg is only 2.9% of the female's weight and food is abundant, the cost of each egg is small. Late eggs are not replaced, presumably because the chicks would fledge too late to have a reasonable chance of surviving. Similarly, Shags (*Phalacrocorax aristotelis*) replace half incubated clutches but do not re-lay after losing a brood (Snow 1960). Tropical pelecaniforms by contrast, are largely free from seasonal constraints. Presumably as a consequence, the first and third options are most commonly adopted by them. Replacement laying within two or three weeks of egg loss may occur in all three pan-tropical boobies and Blue-footed Boobies on the Galapagos. On the other hand failed breeding attempts may be abandoned, and a variable period may ensue, in, for example, the Galapagos Red-footed Booby, the Ascension Island Brown Booby, the Flightless Cormorant and the Red-billed Tropicbird of the Galapagos. Dispersal, return and laying at a strictly pre-determined seasonal period, as in temperate pelecaniforms, could be positively *maladaptive* for tropical species, since it removes the opportunity of using food as a proximate stimulus for initiating a new breeding attempt and thus responding sensitively to its unpredictable fluctuations (Nelson 1968).

Replacement laying remains to be conclusively demonstrated in Great Frigatebirds or most pelecaniforms. My own evidence with Galapagos birds was circumstantial and Reville (1980) claims emphatically that on Aldabra this species and also the Lesser Frigatebird *Fregata ariel* did not replace lost eggs. Apparent replacements were laid by second females. Stonehouse and Stonehouse (1963) however showed with marked individuals that Ascension Frigatebirds *F. aquila* re-layed in 20–25% of instances. The environmental circumstances of frigates seem to point to replacement laying as a predictable strategy. Thus the egg is but a fraction of the cost of the offspring which adults were 'prepared' to meet. Seasonal constraints are mild and largely irrelevant since the offspring will be fed for more than a year and, finally, the biennial breeding regime and long-deferred breeding already minimize lifetime productivity and to wait even one year instead of replacing the egg would further decrease this.

Nevertheless, all five frigate species are either markedly or loosely seasonal breeders and if, for some as yet unidentifiable reason, replacement laying is usually ineffective, their seasonal programming would lead them to wait until the following year.

On occasions, all tropicbirds lay new eggs to replace lost eggs or small chicks, but appear to require longer than other marine pelecaniforms (1–2 months, Red-tailed *Phaethon rubricauda* on Christmas Island, Pacific Ocean, (Schreiber and Ashmole 1970), 23–30 days, White-tailed (*P. lepturus*) on Ascension (Stonehouse 1962), 40–56 days, Red-tailed on Aldabra and 42–51 days, White-tailed on Aldabra (Diamond 1975b)). The proportion doing so is not known but was at least 10% on Aldabra and few on Ascension. The Red-billed Tropicbirds of the Galapagos sometimes adopt the 'intermediate breeding' strategy. On Daphne Island, for example (Snow 1965), many nests failed due to competition for sites and many of the failed adults nested again after 3–4 months, although interestingly, they did not display this flexibility on nearby Plaza Island (Harris 1969a).

"Rest" Years

Do experienced adults refrain from breeding despite retaining last season's site and mate? Good data are extremely scarce, but on Ascension Island, Dorward (1962) had good evidence that some Masked Boobies did. Kepler (1969), on Green Island (Kure Atoll) reported that all such pairs *attempted* to breed but Woodward (1972) recorded 20 birds that bred one year, turned up again the following year, but didn't breed. Among those, it is almost certain that there would be both individuals from previous pairings though there is no hint that they remained together in the non-breeding year. Some 90% of Masked Boobies on Kure changed sites, and often territories, in successive years (Kepler, loc. cit.) and many pairs were disrupted. This is the best available data for any tropical pelecaniform and falls short of demonstrating that intact pairs take "rest" years. For the Atlantic Gannet the data, now extending 21 years for a marked group, is quite unequivocal: rest years do not occur in intact pairs (Nelson, unpubl. data). Non-breeding years enforced by loss of mate or site are another matter.

There are many indications for a wide range of seabirds that adult weight and breeding success are positively correlated and that pre-breeding feeding conditions affect laying date. It is conceivable that pre-breeding feeding might be too poor to raise some individuals to a required physiological threshold. The probability of success, below this threshold, could be too low to justify a breeding effort. Critical physiological data are needed. Since it is now possible to record accurately and automatically the weight of an adult every time it comes to the nest, exciting advances should be made concerning adult fluctuations in weight and fine details of chick growth. I suspect that species differ in the height of the "fitness threshold," below which they will not breed. I speculate that those adults in which stress and reduced longevity is a "fair price" for increased productivity (probably the inshore feeders with large broods) will breed when further below normal weight than do the tropical pelagic pelecaniforms. There are subjective data (Kortlandt, unpubl. data) for the Common Cormorant, that breeding does severely stress adults of some species. However, other evidence also suggests that in some tropical pelagic feeders (frigates, Abbott's, Masked, and Red-footed Boobies, Nelson 1966, 1969, 1978) the adults maintain body weight even when the young are starving. Presumably natural selection operates by taking into account pre-breeding mortality (it is of relatively little benefit to rear a chick which is 95% likely to die before breeding); life-expectancy of adults; capacity of the female to respond to fluctuations in food by modifying brood-size; readiness with which adults can regain lost-condition outside the breeding season; and many other factors.

There is scope here for the mathematic modeller and I suggest that although increasing productivity by "allowing" adults to stress themselves is likely to be a valid strategy in some inshore, temperate pelecaniforms which tend towards the "r" end of the 'r- and K-selected' spectrum, it is not valid for most tropical, pelagic pelecaniforms.

However it is increasingly clear that non-breeding years, where they occur, are not devices for reducing recruitment but for maximising it, by mitigating stress or re-stabilizing social relationships after disruption.

Conclusion

Tropical and temperate pelecaniforms contrast strongly in breeding frequency, both as regards successive, successful cycles and also in strategies adopted in response to failed attempts. There is no equivalent among temperate, marine pelecaniforms to the tropical pelecaniform strategies of breeding successfully more than once a year, less than once a year and strictly only once every two years. As regards failed breeding, tropical pelecaniforms have more options available than do temperate ones, due to lack of seasonal constraints.

THE TIMING OF BREEDING

Seasonality

Birds lay at those times of year which produce the most survivors to breeding age (e.g., Lack 1966). This, at one point or another, is most often determined by food. In strongly seasonal latitudes breeding seasons are sharply defined by changes in photoperiod and temperature. Most seabirds' mean annual laying dates are remarkably consistent, albeit at the level of local populations rather than species. Laying dates may coincide with a flush of food, often for rapidly growing young. For example, the period of most rapid growth of Shags on Lundy Island, England, coincides with the movement of sand-eels, *Ammodytes spp.* into the area (Snow 1960); the young of most seabirds on the Farne Islands hatch in June and early July, coinciding with the arrival inshore of *Ammodytes tobianus* and *A. lanceolatus* (Pearson 1968); the growing period of the young of both British and Canadian gannets coincides with the arrival inshore of the mackerel (*Scomber scomber*) shoals. As mentioned, local differences in food affect laying dates. Bass Rock Gannets lay two to three weeks earlier than birds on Ailsa Craig; Shags from southeast Scotland lay two weeks earlier than Shags from southwest Scotland (Potts 1969) and puffins (*Fratercula arctica*) from the Isle of May (southeast Scotland) lay two or three weeks earlier than birds from St. Kilda (northwest Scotland) (Harris 1978). These differences also affect growth rates in some species. Post-fledging survival is often age-specific in the first year, thus providing strong selection pressure for early laying.

By contrast, all tropical pelecaniforms show a wide spread of laying times. In some cases laying may seem entirely aseasonal but in fact usually favors certain months. For example, on the relatively aseasonal Christmas Island (Pacific Ocean), Schreiber and Ashmole (1970) show that the six breeding pelecaniforms, (Red-tailed Tropicbird, Masked, Brown and Red-footed Boobies, Great and Lesser Frigatebirds) may all have eggs in any month. Nevertheless each species has a detectable, albeit broad peak, or peaks. That of the tropicbird, for example, lasted six months, three of which consecutively produced by far the most eggs.

Where waves of laying in tropical pelecaniforms are triggered by an upturn in food there can be no guarantee that favorable conditions will last. Subsequent abandonments of breeding, or mass starvation of chicks, are on record for marine pelicans, boobies, tropicbirds and frigates. On a practical point, chick-banders waste much extremely valuable information on age-dependent mortality if they fail to note estimated age of chicks which they band.

Some interesting points emerge from a comparison of timing in the Atlantic Gannet (temperate) and Abbott's Booby (tropical). The gannet (at the local population level) has a highly consistent mean annual laying date varying by only ±5 days. Its chick, fed on a seasonal flush of oily mackerel, grows faster than that of any other sulid, despite being the heaviest. This hastens fledging and provides substantial fat deposits, in place of postfledging feeding. I have suggested that early fledging is so important that competition for a socially adequate site, which facilitates this, dominates the gannet's breeding behavior. To acquire and maintain its site, the gannet attends it for three or more months before laying and for an equivalent period after offspring have departed. Furthermore, gannets sustain their site-defense displays to an extent unparalleled among seabirds. If early laying is so important, the spread of laying (late March to early July on the Bass Rock) may seem anomalous. However, the appropriate adaptation to a variable environmental factor is a variable response, not a fixed one. In many seabirds, clutch size is variable because the factors which determine breeding success are variable. In some years smaller clutches outproduce larger ones and this maintains a stable polymorphism. The same argument applies to the spread of laying. The main cause of mortality among recently-fledged Atlantic Gannets is starvation due to bad weather. In the North Sea and North Atlantic weather is highly variable. No fixed laying date is practicable and could avoid bad conditions. In some years, birds fledging earlier or later than the mean will survive best, hence the maintenance of the spread of laying. In addition, the later-laying of first-time breeders contributes to the variability.

Abbott's Booby's unusual breeding strategy does precisely the opposite in that instead of fledging young in time to avoid the monsoons (on Christmas Island, Indian Ocean in November-March) laying is so late and chick growth so slow that by November the chick is still downy (Nelson, 1971). This leaves two options, both apparently maladaptive: It could launch its energetically-costly single fledgling without post-fledging care and without fat deposits, into the monsoonal Indian Ocean in December or January, presumably with little chance of survival. This assumes post-fledging care at sea is impractical. Certainly no sulid shows it. Or adults could try to feed the chick on the island, through the monsoons, until conditions improve in April/May. The chick could then be restored to good condition by August/September when it could become independent at 56–60 weeks, compared with the gannet's 12–13. Abbott's Booby has adopted this second option. Between January and March, 60–90% (it varies from year to year) of dependent, fully grown young starve to death. Each chick represents some 8 months investment by its parents. Moreover, this long cycle means that Abbott's Booby can breed only once every two years. The key to the entire strategy is the timing of laying (mainly June/July) coupled with extremely slow growth. If Abbott's Boobies laid in March and grew at the normal rate for a pelagic sulid the chick could fledge before the monsoons, as do Brown and Red-footed Boobies on this same island. Presumably a relatively slight shift in weather pattern could significantly affect the survival rate of fledglings between December and April. The strongly-postulated southward drift of Christmas Island due to plate tectonics might conceivably have had an effect by distancing Abbott's from its major feeding area. Perhaps Abbott's now-aberrant breeding strategy accounts for its relict status.

SYNCHRONY

Some 93% of seabirds are colonial (Lack 1966). All pelecaniforms with the partial exception of Abbott's Booby are colonial and their colonies without exception known to me, show at least sub-group synchrony in laying.

One may distinguish between types of synchrony, causes and functions. First, synchrony may, but need not, imply seasonal timing. It represents clustering in time and this may be seasonally consistent, as in temperate species, or largely non-seasonal as in tropical pelecaniforms. Second, clustering can be in relation to the whole colony ("Colony" is a difficult concept/fact to define.) or to parts of it (sub-group synchrony). There is an important difference between these two. A colony may show only slight overall synchrony but marked sub-group synchrony. This is partly because most colonies of seabirds are not homogeneous but are spatially sub-divided. I know of no pelecaniforms for which this is not true except some colonies of Gannets (all three allo-species). But even in topographically homogeneous colonies of Gannets in which nests are regularly distributed (a rare phenomenon but closely approached in some Atlantic and Australasian (*Sula* (*bassana*) *serrator*) gannetries) there is still sub-group synchrony. It is possible to demarcate 'clusters' of chicks whose ages are closer to each other than is the average 'closeness' within the whole colony. Sub-group synchrony is so widespread in colonial seabirds that one may suspect it to be universal.

In marine pelecaniforms of high latitudes the principal 'coarse' timer of reproductive behavior is presumably photoperiodic. Local availability of food certainly affects yearly timing (onset, spread and mean annual date of laying) at the local level but there have been no investigations of differences in timing, between years in the same colony, and linked to food. Social factors are also involved, especially in sub-group synchrony, for example in the Atlantic Gannet (Nelson 1978). Social synchronisation requires far more critical study than it has so far received. It may be regarded as a 'fine' timing mechanism, reducing the spread of laying by bringing laying forward in potentially late females (its probable role in bringing forward the whole group is a separate consideration).

One factor which may be involved in the initiation of sub-group synchrony is the initial attraction ('peer' attraction) between individuals which are all at the same, early stage of breeding. Knopf (1979) has indicated that this occurs in the White Pelican (*Pelecanus erythrorynchos*) and Burger (1979) has analysed it more fully for the herring gull (*Larus argentatus*). That peer-attraction is a widespread phenomenon emerges from many incidental observations in the seabird literature (e.g., Nelson 1970, 1978). Once such a peer group has formed, tighter synchrony can develop. The role of behavioral facilitation in this has remained almost totally unanalysed because of the difficulty of isolating and quantifying its contribution, but videorecording and time-lapse photography now provide useful tools. We need standardised behavioral profiles for different social groupings of the same species. These would have useful applications, for instance, in relating behavior to the probability of egg-laying.

In tropical pelecaniforms, photoperiodic timing presumably does not apply. An internally controlled circannual rhythm could presumably provide 'coarse' timing if this is adaptive but we need to know much more about the possibility of broadly rhythmic fluctuations in external factors. Sudden changes in the availability of food certainly initiate (and terminate) waves of laying in several Galapagos seabirds, including some pelecaniforms (Nelson 1969, Harris 1969b, Nelson and Snow, unpubl. data) but these are not of an annual nature. The tropical marine pelecaniforms have, therefore, a more flexible timing system than temperate species. Socially mediated synchrony is almost certainly involved in sub-groups and a pioneer analysis of this phenomenon in the Great and Lesser Frigatebirds of Aldabra, by Reville (1980) is worth summarizing here.

Overall, colonies of all five frigate species can be seen to consist of sub-groups within which (usually) they seem to be further sub-divided into clumps or clusters, often related to discontinuities in the habitat. I suggested (Nelson 1968) that the clumps of nesting Great Frigatebirds on Tower Island, Galapagos, resulted from nuclei of displaying males. Diamond (1975a) similarly described Great and Lesser Frigatebirds on Aldabra as nesting in groups. Reville's analysis, however, showed that the Lesser Frigatebird did *not* clump when occupying an unbroken stretch of suitable habitat in which there were no Great Frigates. Instead they tended to be regularly spaced, whereas Great Frigatebirds clumped at 15–23 sites per clump. This difference correlates with the two species' different criteria for selecting sites and affects subsequent synchrony and breeding success. Simply, Lessers fill the patches of suitable habitat which they are going to use, simultaneously. That is, social factors (such as the number and density of displaying males in each patch) do not cause other males, and subsequently females, to prefer some patches over others. In Great Frigates this is emphatically not so and females chose patches with initially many males rather than those with few. Patches of Great Frigates therefore filled up one after the other sequentially rather than simultaneously and the distribution of nests follows the same pattern as the distribution of the (initially clumped) displaying males. Lesser Frigate males, however, continued to settle among pairs that had already formed, until regular dispersion, whether at high or low density, resulted.

The function of synchrony depends on the species. It may (theoretically) 'swamp' predators, reduce interference by conspecifics or have no major function as such but merely result from laying to a tightly-defined mean seasonal date, the seasonality rather than the synchrony being adaptive.

For differential mortality related to time (seasonal) of fledging there is in temperate birds as a whole, abundant evidence. Emlen and Demong (1975) stress the role of information transfer as the benefit of close synchrony in Bank Swallows, (*Hirundo riparia*) those individuals fledging either early or at the peak of synchrony emerge to find a stream of conspecifics flying between the colony and local, ephemeral food sources. Ward and Zahavi (1973) claimed information-transfer as perhaps the function of coloniality but it probably applies much less widely to seabirds than they propose. In my view, neither colonial breeding nor synchrony function in this way in most seabirds, especially pelagic ones.

In the frigates of Aldabra, the two contrasting spatial patterns permitted comparison of synchrony and breeding success in the two species. In the Lesser Frigate, females settling later did not subsequently require less time before laying, whereas in the Great Frigate they did. Therefore laying in Great Frigates was more synchronized than in Lessers. The increased synchrony in Greats, Reville suggests, reduced conspecific interference and increased hatching success (54.5% over two years in the Great Frigate, 20.1% in the Lesser). Moreover, in the Great Frigate, the most synchronized groups had the highest hatching success. Reville suggests that clustering makes a localised group of nests less attractive to potential usurpers and so reduces conspecific interference.

On the major question of why the Lesser Frigate does not cluster Reville comments that the female cannot afford to be as male-selective as the female Great Frigate, because there appear to be more males than females in the Great population but a 1:1 ratio in Lessers. Coupled with Diamond's (1972) discovery of the skewed sex ratio in the Magnificent Frigate (*Fregata magnificens*) this piece of work appears to provide fresh insight into frigate breeding strategies. Why the sex ratios differ in frigate species is another question.

CONCLUSION

Temperate marine pelecaniforms exhibit seasonal timing, and synchrony of laying. Tropical pelecaniforms are relatively non-seasonal but nevertheless show marked sub-group synchrony. The functions of sub-group synchrony (as opposed to seasonal timing) may be several and do not relate especially to either tropical or temperate conditions but more to social phenomena common to both.

THE SIZE OF EGG, CLUTCH, AND BROOD

The pelecaniforms exhibit a wide range of egg and clutch size, presumably reflecting their great adaptive radiation into different feeding and breeding niches. The correlation between large eggs (in relation to female weight) and small clutches (usually one egg) and far-foraging is well known. Conversely, inshore feeders lay relatively smaller eggs and larger clutches. So tropicbirds and frigates are invariably uniparous and lay relatively large eggs, pelicans and cormorants are almost invariably polyparous and lay smaller eggs, whilst gannets and boobies fall in between. Within the sulidae it is not only the range (1–4) of clutch size that is interesting but the fact that some species never lay more than one egg per clutch, others never more than two, whilst yet others lay clutches of variable size. Within this family, a major correlation between clutch size and foraging simply mirrors the general one within the order. The same principle may be further demonstrated by the fact that even within uniparous boobies such as the Red-footed (and also in tropicbirds), egg size varies with locality; eggs are larger where food is scarcer (Snow 1965, Nelson 1969).

Because far-foraging is a widespread adaptive response to breeding in blue-water tropical regions (though not necessarily confined to such) it is to be expected that tropical marine pelecaniforms will tend towards relatively larger eggs and smaller clutches. This is so, although there are important exceptions, principally concerning tropical pelecaniforms with notably inshore feeding habits (all tropical cormorants and pelicans and three tropical boobies). Conversely, temperate marine pelecaniforms are, with the exception of the three gannet allo-species, polyparous inshore feeders. These generalisations and exceptions may be pursued using specific examples.

Tropicality and foraging method interact instructively within the sulidae. All six breed largely or entirely within the tropics although four (the Red-footed, Masked, Brown, and Abbott's) are essentially more tropical than the Blue-footed, and Peruvian. The latter two breed within or close to colder, more productive waters and breeding birds forage less widely than the other four. Consequently the four tropical boobies are all strictly single-chick species although only the Red-footed and Abbott's are actually uniparous. In the Masked and Brown Boobies, which lay either one *or* two, the two-chick broods are always reduced to one by fratricide, the essential point being that the elimination of the younger chick by its sibling is early in life, by active persecution and in no degree dependent on the food available at the time. Thus whether by laying one relatively large egg as do the Red-footed and Abbott's Boobies, or two smaller ones which, if both hatch, are soon reduced to a single chick, as in the Masked and Brown Boobies, these four tropical pelagic sulids are adopting essentially comparable strategies.

The Blue-footed (1–3 eggs) and the Peruvian (2–4 eggs) not only lay these larger clutches but may rear 2 chicks (Blue-footed) or even 4 (Peruvian). Even where the Blue-footed breeds on the same island as the Masked, or the Brown, it does not exhibit obligative brood reduction as they do, although in times of food shortage the smaller sibling may starve. Obviously, the food-scarce blue-water environment and associated foraging habits of the Masked and Brown Boobies have converted facultative into obligative brood reduction by penalising those pairs in which both young survived, even if only for a few days. The Peruvian Booby normally loses none of its brood, although in Niño years, the whole brood and its parents normally starve to death. Clearly in all six boobies, the size of the brood which is reared is low in tropical far-foragers and higher in the less-tropical, more inshore foragers.

It might be expected that the 3 gannet allo-species (Atlantic, Australasian and African (*Sula* (*bassana*) *capensis*) would be polyparous but, instead, they are strictly uniparous. But they are not truly inshore feeders. Although they are not truly pelagic either, they forage at considerable distances from the breeding colony. Moreover, they endow their offspring with considerable fat reserves in lieu of post-fledging care and (at least in the Australasian and African) this makes it difficult for them to feed more than a single offspring.

Brood reduction, both through sibling murder and through differential starvation is found in other pelecaniforms. In the White Pelicans (*Pelecanus onocrotalus*) of Dassan Island (South Africa) the older chick actually kills its sibling (Cooper 1980) whilst differential starvation occurs in the Brown Pelican (Schreiber 1979) as it does, also, in many phalacrocoracids (e.g., Kortlandt *in litt.* for the Common Cormorant, Snow (1960) and pers. observ. for the Shag).

Obligative brood reduction may be seen as a mechanism to optimise productivity. If both chicks were allowed to grow strong during a period of plenty, they would later compete strenuously when food became scarcer and before one succumbed both would be weakened. If the probability of temporary food shortage is high enough, natural selection will ensure that chicks which have not been thus weakened survive best. To interpret brood reduction as a mechanism for reducing production is precisely the opposite of the case. Although brood reduction by competition for food among siblings is widespread in birds, for example in raptors, corvids and herons, (see O'Connor, 1978) it is, in these birds, never completely obligatory within the first few days. This is understandable since no land bird is subject to selection pressures comparable to those facing highly pelagic, blue-water seabirds.

Conclusion

Tropical marine pelecaniforms tend to have larger eggs and smaller broods than have temperate members. This correlation exists largely as a result of the differing foraging methods used in these two environments. Therefore it is subject to many exceptions, since inshore and offshore foraging do not correlate precisely with temperate and tropical environs respectively.

COMPOSITION OF BREEDING CYCLE

Although breeding frequency is partly determined by the length of the breeding cycle, cycles of equal length may be sub-divided differently. It is the investment in each component that amounts to a strategy. When comparing these components in different pelecaniforms the premise is that natural selection shapes the details of energy-expenditure on a lifetime basis. Most fieldwork is unavoidably crude by comparison with the admirable physiological studies of, for example, Whittow (1980) on the correlates of prolonged incubation, Dunn (1980) on the energy allocated to feeding nestlings or Ricklefs (1974) on the energetics of clutch-size and chick-growth. However, behavioral field data can facilitate interpretation. Whilst it would be interesting, for example, to know what it costs a gannet to spend 5 months of each year displaying on its empty site, thereby performing roughly 15,000 display-acts, in comparison with a frigatebird's few days of display, the conclusions which may be drawn do not depend on such quantification. Here, I will contrast some tropical and temperate marine pelecaniforms with respect to the characteristics of the following components of the breeding cycle: (i) pre-laying activities, (site-establishment, pair-formation and nest building), (ii) incubation, (iii) care of pre-fledged young, (iv) care of post-fledged young and (v) post-breeding activities.

PRE-LAYING ACTIVITIES

In tropical pelecaniforms pre-laying breeding activity is highly compressible whereas those of more seasonal latitudes spend longer on this component. Full comparative data are extremely patchy so it is appropriate to select examples.

In the Brown Pelican the male selects the site (Schreiber 1977), as is the case in most other pelecaniforms (certainly in sulids, frigates and at least some phalacrocoracids). In 1–4 days, during which he is seldom absent, the male Brown Pelican attracts a female. After a further 4–10 days the nest has been built (material gathered solely by the male) and 1–3 days after this (some 6–17 days after he first stations himself on site) the first egg is laid. During this brief period there is little overt fighting between neighbors, no frequent, ritualised threat and no specific site-ownership display. This may be a phylogenetically primitive procedure, brief, labile and lacking a complex repertoire of behavior. The male finds a suitable perch, sits on it using a simple head-swaying display until a female joins him, bonds almost immediately and quickly builds a nest. Pelicans in general are not faithful to a particular site nor usually to a breeding area (Vestjens 1977, Knopf 1979) and correspondingly they invest little in it.

Great Frigates show this relationship between site and effort even more clearly. Males display in groups, each on his perch, and those which are unsuccessful in attracting a female fly off and join, or initiate, a group elsewhere. Thus the display site may not be, initially, a firmly established, potential breeding site. It is far more labile than in any other pelecaniform. Almost all the frigate's pre-laying activities are sexual, directed to females and not territorial, directed against other males. The site changes with each breeding attempt and little effort is devoted to its maintenance. There is, for example, no special site-ownership display. A male may join a display group, attract a female, form a pair and build a nest all within a few days (Reville 1980, Nelson 1968).

Similarly, in the Flightless Cormorant pre-laying activities may take as little as 10 days from the first display by the male, on the sea, to egg-laying (Harris 1979). Here, too, site establishment and pair-formation take place anew with every breeding attempt, of which there may be several in one year.

By contrast, some high-latitude pelecaniforms, for example, Common Cormorants, Shags, Atlantic, and Australasian Gannets, spend weeks or months attending and refurbishing their sites. In these species the pre-laying period is never highly compressed. Moreover, the incidence of strictly territorial activity may be extremely high. For example, the male Atlantic Gannet attends his site on average 60% of all daylight hours in the six weeks before laying. During this period he fights several times with intruders or neighbors and performs both a ritualised threat display and the complex and energetic site-ownership display approx. 1500 times each (these figures derived from standard checks extrapolated to a 15-hour day). In addition he makes more than 100 visits with nest material. This is a considerable investment of time and energy, repeated in each of the 15–20 years for which an Atlantic Gannet keeps his site.

The Shag begins to attend either the precise site of former years or the same locality, perhaps a ledge or gulley, up to 70 days before laying (Snow 1960), the mean period being 38 days. Territorial display is frequent.

Species which have permanent sites usually have permanent pairs and the site, established by the male, is used by him for sexual display, first to attract a female and in succeeding years as the focus for reunion. This scenario is highly appropriate for consistently seasonal breeders, which is presumably why it applies so widely to seabirds of high latitudes. Conversely, the pre-eminent adaptation to the extreme tropical regime is flexibility in the timing of breeding and in its components, so that these can be modified when food dictates. This opportunism is inconsistent with fidelity either to site or mate and consequently affects the behavior which subserves such fidelity. The adaptive strategy is to abandon the fixed annual cycle, take advantage of upturns in food, use these as proximate timers and evolve the capacity to buffer fluctuations in food by retarded growth, large-egg (to give starvation resistant chick), brood-reduction, and extensive post-fledging feeding. However, many tropical areas are by no means aseasonal and correspondingly, breeding may be loosely seasonal.

The concomitants of these two basically different strategies are that those behaviors which maintain site and pair-bond are extensively developed in species in which attachment to site and mate is highly durable, e.g., Atlantic Gannet, Abbott's Booby, Shag; and less developed or minimal where it is ephemeral, e.g., all frigates, Brown Pelicans, and tropicbirds. Some pelecaniforms, for example most boobies and cormorants, fall somewhere between the two extremes, as indeed does the strength of their attachment to site and mate.

The frigates do not have permanent sites because these are incompatible with their biennial cycle, in which essentially two populations use the same breeding area, and those pairs which are absent from the colony are in no position to maintain their sites. The shifting nuclei of displaying males are incompatible with the reunion of former partners. Males readily accept females soon after display begins. They attend display sites almost continuously for days on end (some are present for a month before pairing) and the odds are heavily against a former partner coming to the colony and finding "her" male, at the previous site and still unattached. So pairs usually last for only one breeding attempt, and, after the first 3 or 4 days following the initial encounter, and the short nest-building period, there is no pair-bonding behavior. During these first three days Reville (1980) observed that the time which the pair spent together decreased from 90% to 44% of each day and that male sexual display (beak clattering) decreased by half in day two to none in day three. After nest-building, incubation and intensive chick care, the frigate's lengthy foraging absences and brief visits to the nest make meeting somewhat improbable. Despite this apparent lack of pair-bonding behavior the bond between parent and offspring is strong enough to ensure that parents feed their young for longer than almost any other seabird.

In tropicbirds, too, sites and pairs are notably impermanent and pair formation is flexible. Red-billed Tropicbirds in the Galapagos breed at different times on different islands, and on some islands laying occurs all year round. Harris (1969a) showed that on Tower Island sudden scarcity of food caused some adults to desert their young and delayed the onset of breeding in others. This fluidity, together with strong competition for holes, is not conducive to regular re-occupation of sites and re-formation of pairs. Territorial and pair-bonding behavior is so minimal that no worker has commented on anything other than the overt competition for holes and the well-known flight-display, which establishes, rather than maintains, the pair-bond.

In the Brown Pelican, egg-laying in a single colony can occur over a period of at least six months and at many colonies birds remain all year. The records of pelican colonies changing location, and the state of flux within colonies as new breeders arrive and breeding continues, show that sites and pairs last merely for one breeding attempt. Pelican courtship is relatively simple and its undifferentiated nature is well captured by Schreiber's (1977) account. The male selects the site and displays to females but after pair-formation, as in frigates and tropicbirds, there is no specifically pair-bonding behaviour.

Most pelecaniforms with impermanent sites and pairs invest relatively little in them, behaviorally, but the Flightless Cormorant is an exception. Its nest-relief ceremony, involving ritualised presentation of seaweed, is well documented (Eibl-Eibesfeldt 1960). Correspondingly, although it readily shifts site and changes its mate, it frequently does retain the same site and mate in successive nestings ($^{57}/_{112}$ and $^{52}/_{136}$ males and females respectively remained in the same nesting place for successive nestings; in 31 instances the same partners nested together twice and in one case three times (Harris, 1979). It is, of course, highly sedentary and its foraging absences are short. Both factors increase the likelihood of re-pairings, compared with frigates and tropicbirds.

In sulids the male establishes the site and displays both territorially and sexually on it. Unlike the frigates, tropicbirds and pelicans, sulids have evolved not only a sexual advertising display by which males attract females but also an extensive repertoire of displays performed by the pair on the site, particularly before egg-laying but also at the nest-relief ceremony. Correspondingly, attachment to the site is strong and the pair bond often endures for successive nestings. Abbott's Booby compares interestingly with the frigates in that it, too, nests in trees and breeds only once in two years. Yet is has a permanent site and keeps the same partner. It can do so because, unlike the frigates, it is a dispersed breeder with a precise location to which partners can return. Although the nest itself usually disintegrates in the monsoons, the exact location is used in successive nestings. Return to the island is highly seasonal and the partners therefore have both the environmental timer and the precise location necessary for reunion.

In the Atlantic Gannet 94% of pair bonds remain intact from year to year. Extreme aggression is shown in defence of site and, both overtly and in ritualised form, by male to female. This aggression, by becoming linked to sexual behavior, may actually strengthen the pair bond. Consequently, aggressive males, which presumably are more successful in site competition, are not penalized in the pair context. Copulation is accompanied by vigorous nape-biting *only* in the Gannets (three allo-species) and the act itself lasts on average 24 seconds, which is 3–6 times as long as in any other pelecaniform. It is accompanied by massive tactile stimulus (tramping movements of the webs on the female's back). Also, the Gannet's elaborate meeting ceremony is preceded by napebiting and the display itself incorporates ritualised aggression. This simple example illustrates the sort of interactions—here between site-attachment behavior and pair-bonding behavior—which must operate on an unimaginably complex scale in the evolution of breeding strategies. The Gannets system works only because the feeding environment allows reliable and early return to the site each year.

The third pre-laying activity is nest-building and associated behavior. The practical functions, in pelecaniforms, are to provide sites for copulation and to protect and insulate eggs and young. The function of nest-building in those species in which the structure is of no practical use is to strengthen the pair-bond. Even where, as in the Atlantic Gannet, the nest is obviously valuable, its pair-bonding function should not be overlooked. On Ailsa Craig the act of landing was the commonest cause of death accounting for more than 300 adults in one season, (Wanless 1979). Yet Gannets bring in nest material far more than appears to be necessary. The pair-bond must justify these visits. Conversely, frigates build flimsy, barely adequate platforms of dead twigs. The young frigate has prehensile feet and nest building probably has little pair-bonding function, so the minimum suffices. Also, frigates have considerable temperature-regulation problems and the open lattice work may help air-flow over egg and young chick. Abbott's Booby needs a substantial nest to give the chick a stable footing as far into the monsoon period as possible. Its bulky cradle is built from large, living twigs plucked with great effort and significant risk from the jungle canopy. In addition, each return with nest material involves mutual greeting and a highly ritualised presentation of the twig, after which both partners build it into the nest structure. Presumably this helps to cement the pair-bond which is highly durable (Nelson and Powell, unpubl. data).

The same combination of practical and symbolic factors applies to the many cormorants and to the pelicans. As nidicolous species, all require a structure, be it land vegetation, twigs, seaweed, pebbles, flotsam or guano. Many phalacrocoracids, however, use nest material in mutual building interactions and continue to build through incubation and part of the nestling period. Correspondingly, nests are often re-used and in some species pair-bonds may endure for more than a season.

As part of breeding strategy, therefore, one may view nest building in relation to the pair-bond (and therefore the relative permanency of the site) as well as in relation to the physical functions of the nest. Through this link, it relates to opportunism in breeding, or the lack of it. Tropical marine pelecaniforms, being mainly opportunistic and with transitory attachments, are constrained largely by the availability of material, the energetics of building and the physical functions of the nest. Temperate species, with more durable bonds, add the social (pair) dimension to their nest-building activities.

INCUBATION

Aspects relating to incubation include: the method, egg-recognition, duration of incubation, length of individual incubation stints and interactions between partners. Of the fact that gannets, boobies, cormorants and pelicans have no brood patch and incubate eggs beneath webs (gannets and boobies) or on them (cormorants and pelicans), whilst frigates and tropicbirds have a median brood patch, I can say little in relation to breeding strategies. Obviously, the small feet of frigates in particular, but also tropicbirds, could not incubate the large egg. Of the difference between sulids and phacrocoracids one may note that the reduced clutch of all the sulids with the partial exception of the Peruvian Booby, permits incubation underfoot whereas this becomes difficult with more than two or three eggs and many phalacrocoracids, as inshore feeders, lay clutches of four or even more. But there is no evidence that incubation beneath the webs is more efficient than on top. The only pelecaniform in which individuals apparently recognise their own egg is the Red-tailed Tropicbird (Howell 1978) which in 27 out of 35 choice-tests retrieved its own rather than another egg. These eggs are variable in color whereas most pelecaniform eggs are plain, stained or nondescript. The competition for nest holes which occasionally leads to the deposition of two eggs in one hole many select for recognition. The duration of incubation is positively correlated with the yolk reserves of the egg and large eggs, in turn, correlate with slow growth of the young. Both large eggs and slow development are adaptations of far-foraging seabirds and will be discussed later in this section.

Long incubation stints, also, go with pelagic rather than inshore feeding and can be used as a measure of foraging behavior. Frigates, tropicbirds and Masked and Red-footed Boobies are often recorded far from the nearest breeding station. In areas such as the Galapagos where evidence of periodic and severe food shortages is incontestable, incubation stints in all pelagic species are unusually long when compared with those of conspecifics elsewhere. There is no reason to doubt that birds absent from the colony are indeed foraging. Within a species, populations with longer incubation stints also have chicks which grow more slowly than others—for example, chicks of Great Frigates on Tower Island (Galapagos) with mean incubation stints of 10 days grow more slowly than those on Aldabra, with incubation stints of 6.5 days. Similarly, Red-footed Boobies on Tower Island have incubation stints 2 or 3 times as long as their congeners on Christmas Island (Indian Ocean) and their chicks take 140 days as against 105 to fledge.

Within the marine pelecaniforms, long incubation stints predictably correlate with low clutch and brood size since both are adaptations to pelagic feeding. All uniparous pelecaniforms have incubation stints well in excess of 24 hours, many exceed 48 and some average more than 5 days. With the exception of two sulids, both of which are single-chick species even though they lay clutches of two, no polyparous pelecaniform averages as much as 24 hours.

There are two possible functions (pair-bonding and coordination of change-over) of the ritualised behavior which may occur at nest relief and these are sub-served by distinct displays. Some marine pelecaniforms show no special behavior at change-over. Incubating frigates and tropicbirds simply vacate the nest to the incomer. Brown Pelicans, at least in early incubation, interact briefly and simply and usually without contact, head-swaying and bowing (Schreiber 1977). This interaction diminishes as incubation and the guard stage progress. Among phalacrocoracids there is no marked greeting ceremony but there is a distinctive pre-flight display. In all four families, with a few exceptions amongst the cormorants, pair bonds are for only one season and pair bonding displays weak or absent. Among sulids, nest relief is much more elaborate, incorporating both pair-bonding display and ritualised pre-departure display. The most marked cases are the Atlantic Gannet and Abbott's Booby in both of which the ecstatic mutual greeting display is prolonged, noisy, and elaborate. In both species, pairs are permanent or highly durable and their nest-relief display may be considered to be an extension of the bonding behavior which they show during pair-formation. The pre-departure behavior in the Atlantic Gannet is also highly conspicuous but its function is to ensure that the partner (as shown by its own behavior) "registers" this intention and therefore remains behind. Departure of both birds could easily result in the loss of egg or chick. It seems anomalous that cormorants and sulids presumably require pre-departure display (since they have evolved them) but frigates, for example, do not. No direct link with foraging and the tropical or temperate habitat can explain this difference which may relate to the vulnerability of the temporarily unguarded nest of ground-nesting pelecaniforms to predation and stealing by conspecifics. But frigate nests are also vulnerable.

The adaptive aspects of the different degrees and forms of pre-departure behavior are not understood. Complex greeting behaviour at nest relief, however, does appear to relate to permanence of site.

PRE-FLEDGING CARE OF YOUNG

The length of the intensive guard spell during which the young are seldom or never unattended, the frequency of feeding and the period for which young are fed before fledging all lend themselves to adaptive modification in relation to food and foraging behavior.

In pelecaniforms with nidicolous altricial young (all of them except the Phaethontidae, which probably is the most primitive family) some intensive brooding is inescapable. The common practise is to brood the young until they can thermoregulate, which is approximately between 4–6 weeks. But they are still highly vulnerable to attacks from conspecifics and predators such as raptors and introduced mammals. There is now considerable evidence that, among seabirds, interference by conspecifics, either predatory (as in some gulls) or social (as in sulids) is of major significance. In frigates (Nelson 1968, 1976, Stonehouse 1962, Diamond 1975a and Reville 1980) the intrusion of adult males, presumably non-breeding or intending to breed out-of-phase with the main body, causes loss of eggs and of unattended chicks on a large scale. In tropicbirds (Snow 1965, Harris 1969) eggs and chicks are lost as a result of competition for sites and it may be that the unusually long guard spell in these species is to protect chicks from intraspecific interference. The downy young, protected from extremes of temperature in their holes or beneath vegetation, would otherwise seem to need less brooding.

Adults which invest less time in intensive guarding obviously have more time to forage and in tropical pelagic species this is of paramount importance. Nothing else could account for frigates or Masked Boobies, for example, leaving their defenceless young (30–35 days old) as soon as these can thermoregulate. Among temperate species the Gannet's unique investment in guarding its offspring continuously until it leaves the nest and colony (which it does abruptly and with no return) is notable. That it is even possible for one of the parents to remain constantly on guard, thus halving the food-gathering potential of the pair, depends on the timing of breeding such that chicks grow during the period when the shoals of the exceptionally nutritious and principal prey, mackerel, move inshore and become available. But this does not, in itself, explain why Gannets should trade away half their food-gathering potential. What is the benefit? The only convincing suggestion is that in a dense colony of such a highly territorial species, in which there is intense pressure on breeding sites, unattended nests, and their contents, would be under serious threat. Also, even pilfering of nest material by neighbors would greatly jeopardise small chicks. For these reasons, extended guarding, made possible by abundant food, has evolved. I know of no comparable case in any other seabird.

The habit of forming crêches or pods of unfledged young is entirely restricted among pelecaniforms to pelicans and some cormorants. The function of pods is not clear but may relate to temperature control. Feeding is strictly of one's own offspring. Pods can form only where parents will feed their young away from the nest site. Apparently (and excluding the hole-nesting tropicbirds) all pelecaniforms, except two sulids will do so. Only the Gannet superspecies and Abbott's Booby restrict feeds to the nest, or in Abbott's Booby when the nest disintegrates, to the precise location of it. The reasons are, however, very different in these two cases. In Gannets it is impracticable for young to move off the nest. On cliffs, they might fall, and on flatter ground the attacks of densely packed breeding adults would be fatal. Also, given their method of fledging (one abrupt, irrevocable departure) there would be no gain. In Abbott's Booby where free-flying young are fed for 9 months and most die of starvation, there must be extremely strong selection pressure against feeding intruding young. Restriction to the precise nest site should help prevent this. As in the Gannet, the adults' attachment to their site is strong and highly durable, which will tend to focus feeds on the site.

Perhaps the most obvious difference in chick care to be expected between tropical pelagic pelecaniforms and temperate (and tropical) inshore feeders is that the former will return with food much less frequently than the inshore feeders. As a result, the chicks of the former grow more slowly and single-chick broods are the rule. The frequent feeds, rapid growth and large brood size of inshore feeding Peruvian Boobies, with abundant anchovies *Anchoveta engraulis* in the Humboldt upwelling contrast markedly with the three pan-tropical pelagic sulids and make the point that it is food and foraging which control these parameters. The marine phalacrocoracids, inshore feeders and predominantly temperate, simply emphasise this point. They feed their young frequently and these grow quickly compared with all the tropical pelagic pelecaniforms. As this contribution repeatedly demonstrates, a principal casual factor in determining breeding strategy is the nature of foraging—inshore or pelagic—and often (but not always) this in turn correlates with temperate or tropical distribution.

POSTFLEDGING CARE OF YOUNG

Post-fledging care, whilst in one sense an extension of incubation and pre-fledging care (and the duration of these three components correlate positively) is nevertheless a very important variable in breeding strategy, with complex costs and benefits. Seabirds have four options in the care they give to their fledged young. Parents can: continue to feed the free-flying juvenile at the site, matching the period to the difficulty of the juvenile's transition to independence; take it to sea, free-flying or otherwise, and feed it there; provide it with reserves to fuel it during the transition to independence; or do nothing for it after fledging and provide no reserves. These options are not independent of prefledging care, which in seabirds may last anywhere from 2 days to 11 months (reviewed by Burger 1980). The procellariforms feed their single young for up to 11 months (Wandering Albatross *Diomeda exulans*) but none feed young after fledging. Penguins either provide fat reserves or launch their offspring to coincide with a seasonal flush of readily-caught crustacea; but adults do not feed young after fledging even if they are not fully grown by then. Some gulls and terns favor extensive post-fledging feeding (Ashmole and Tovar 1968). Some auks go to sea with their young, which in some cases carry out most of their growth there (see Sealy 1973). Not surprisingly, no seabird unequivocally adopts the fourth option (above). It would be maladaptive to invest so much in producing a chick only to fail with near certainty at the final stage. The reason lies in the nature of seabird feeding which, even in the simplest cases, is more difficult to perform than in birds (or mammals) whose young receive neither reserves nor post-fledging (or equivalent) care. These are all herbivores, gramnivores, omnivores or insectivores. Either the food is stationary and beneath their noses, or abundant and obtainable by stereotyped, innate or quickly learnt (by rapid trial and error) behavior. Also, the young of such species are usually led to feeding areas by their parents. Among land birds the best parallel to seabirds is the raptors, where post-fledging feeding is, as in many seabirds, prolonged.

Pelecaniforms adopt the first and third of the four options listed above. The phylogenetically primitive strategy in pelecaniforms, in conjunction with a clutch of several eggs (uniparity being derivative) may have been to feed the mobile, free-flying or free-swimming young for a variable period at, or away from the site. The cormorants and pelicans still do this, though only the former extends feeding to free-flying young. Tree nesting populations of the Brown Pelican do not feed their young once these have left the nest (Schreiber 1977) but the young at 11–12 weeks are late in flying, and may have accumulated reserves (my speculation only). Many pelecaniforms, however, have departed from this simple pattern of feeding mobile young on- or off-site and prolonging the period where and when necessary. All tropical, pelagic pelecaniforms except tropicbirds have evolved long periods of post-fledging feeding. In the classic example, the frigatebirds, with up to 14 months post-fledging feeding and commonly 9–12 months, this huge parental investment demonstrably relates to the great difficulty experienced by newly independent young in securing prey for themselves. Nelson (1968) documented a drop in body weight to 640 gm for juvenile Great Frigates on the Galapagos even after several months of post-fledging support by their parents. Similarly, in all four tropical boobies (Masked, Red-footed, Brown and Abbott's) postfledging feeding is either on occasion or (in the case of Abbott's) always, more than 6 months in duration. The tropicbirds are seemingly anomalous in being classically tropical, pelagic and specialised (plunge divers) and yet lacking post-fledging feeding. Harris (1969a) *contra* Fleet (1974) makes this clear for the Red-billed and certainly the Christmas Island (Indian Ocean) race of the White-tailed did not feed their fledged young (Nelson, unpubl. data). However, Red-billed Tropicbirds, even in the Galapagos, reached weights of 120% adult weight, so presumably they fledge with reserves. I speculate that there are strong inhibitions preventing young of hole-nesting species from returning there, once fledged.

The most extreme departure from post-fledging care and concomitant provision of reserves and fat for their offspring is found in the Atlantic Gannet (Nelson, 1978). Laden with up to 1500 gm of perivisceral and sub-cutaneous fat, the young Gannet literally throws itself from the cliff top and flies for a variable distance before landing on the sea, from whence it is unable to rise until it becomes lighter. Its parents remain behind on the site. Australasian and Cape Gannets are intermediate between this extreme and the practice, amongst all boobies, of some post-fledging care. Some Australasian juvenals wander to the edge of the colony, exercise, and return to be fed for up to three days before fledging (Nelson, unpubl. data) after which they are on their own. Neither of these two allo-species fledge with as much fat as the Atlantic and both are less adapted to cliff nesting, which makes return impossible (details in Nelson 1978).

As mentioned earlier, the adults of pelagic feeders, those pelecaniforms with the typical syndrome of single-chick broods, slow-growth, long-deferred breeding and high chick mortality, do not lose weight when feeding young even when these are starving. It would not pay off for a long-lived, slow-reproducing adult to stress itself in any one breeding attempt. For inshore feeders, with a different adaptive syndrome, the trade-off will be different and, using hypothetical but reasonable figures, this difference can readily be demonstrated. For them, it may be worthwhile to stress the parents and thereby produce more young.

ATTENDANCE AT BREEDING AREA AFTER DISPERSAL OF YOUNG

Adults which leave the site immediately after the young are independent save energy and gain nomadic foraging time, and can better exploit dispersed and patchy food offshore. All tropical pelagic pelecaniforms therefore abandon the breeding colony at this time. Even frigates, which require land for roosting, wander widely, roosting on many islands where they do not breed. The frigates that are always in evidence at some colonies are probably pre-breeders, breeders and immatures rather than immediately post-breeding adults. Tropical pelagic sulids turn up thousands of kilometres from the place where they last bred (Nelson 1978).

The implications of this essential requirement of tropical pelagic seabirds to spend significant periods of time as nomadic feeders have perhaps been largely overlooked by seabird workers. It is an item that has to be budgeted for in the reproductive lifetime strategy. It is especially important that the newly independent young of such seabirds have a long period during which they can wander at will, feeding opportunistically, unrestricted by the need to spend time and energy returning systematically to a fixed point. I would suggest that this requirement, more than any other, explains why seabirds lack cooperative breeding. Cooperative breeding is common among land birds especially those in rigorous, food-poor environments. Tropical pelagic seabirds would appear to be ideal subjects for cooperative breeding, but an essential prerequisite is that the young do not disperse, but remain in the parent's "territory" (= "breeding colony") and help with subsequent breeding attempts. This, I suggest, is precisely what the young of pelagic seabirds cannot do without serious risk of starvation. They need a larger foraging area and maximum time to forage if they are to survive. I am not aware that the almost complete absence of this major breeding strategy, among such seabirds, has received comment, though it surely deserves it. Even among the inshore feeding marine cormorants and pelicans, there is considerable movement of adults and even greater movement of young birds, presumably for the same reason.

The only pelecaniforms which have incorporated into their breeding strategy a lengthy period during which the site is not only occupied but displayed-upon at high frequency and intensity are the gannets, especially the Atlantic Gannet. This species' three-month period of occupying the site after offpsring have departed is merely consistent with other evidence of the site's importance, which I relate to social stimulation and the timing of breeding.

ATTACHMENT TO BREEDING AREA

I refer here to a species' tendency to restrict further breeding to a precise locality, having once bred there. Philopatry, or the tendency of offspring to return to breed where they were born is a separate phenomenon. Both are part of breeding strategy but in different ways. The former enables an individual to adapt to local conditions by learning, whilst the latter, theoretically, holds the possibility of genetically adapted local populations. Philopatry is important in the context of group selection, one of the main requirements of which is that local populations should be adequately isolated. The other requirement is that groups should go extinct often enough to make it a viable alternative to individual selection. There is some data from pelecaniforms on the first of these issues.

Species with permanent sites and mates obviously cannot change breeding localities but those with ephemeral attachments have this option. Conversely, if any factor compels a species to change its breeding locality at intervals, then a permanent site and mate would be ruled out. This seems rarely to apply to pelecaniforms.

The substantial advantages of remaining faithful to a locality in which one has bred successfully may be its safety and the knowledge of local feeding areas and conditions. The disadvantages may include denial of the opportunity to discover a better area, perhaps less crowded or safer, or nearer to good feeding areas and possibly (with time) increased risk of predation. An appropriate strategy might be for an individual to explore in the pre-breeding phase, visiting perhaps several colonies, but to remain settled once a choice has been made. Many seabirds do precisely that, and of course range extension and recolonization demand such pioneers. Perhaps because the advantages of remaining true to a locality having once bred there are great, and the strategy so widely adopted, there are no clear correlations between this habit and the tropical or temperate regime.

Among phalacrocoracids, Guanay Cormorants constantly shift breeding locality (Murphy 1936, Hutchinson 1950). This is partly due to extensive human disturbance but perhaps also to the build-up of parasites in these teeming colonies. Common Cormorants and Shags, by contrast, are strongly attached, as individuals, to traditional localities though pre-breeders move between localities. Some marine (Brown) pelican colonies are traditional (Schreiber 1979) and presumably the same individuals remain there for life. Among sulids, the same individual adult Red-footed Booby has been captured whilst breeding on two widely separated islands (Woodward 1972) in different years. This sort of information is so extremely difficult to obtain that it might be unwise to assume that it only rarely happens. Masked and Brown boobies do commonly shift their territories within the colony (Kepler 1969, Nelson 1978) but this is not a colony shift. The Atlantic and Australasian gannets do not change colonies once they have bred; the proportion of marked individuals which return each year shows this unmistakably (Nelson 1978; Robertson, pers. comm.). Among frigatebirds, the Great and Lesser on Aldabra congregated densely in favored localities but, between years, did move several km. The possibility has been canvassed (Harris 1969b) that in the Galapagos and perhaps elsewhere, experienced breeding individuals of the Great and Magnificent Frigatebirds may move between colonies which are temporally out-of-phase and thus breed more frequently than once in two years. This seems unlikely if only because of the extreme length of the period of parental care and the need for breeding adults to moult and rest. The argument that such extremely K-selected species would be strongly disadvantaged if adults stressed themselves applies forcibly here.

The restriction of the *fulvus* race of the White-tailed Tropicbird to the Indian Ocean Christmas Island shows that it doesn't change breeding locality, but in the Galapagos the existence of different breeding regimes among Red-billed Tropicbirds on adjacent islands (Snow 1965, Harris 1969a) suggests that some interchange may occur. For example, birds returning for a new breeding attempt may be expected to go where there are most available sites and conspecifics in the appropriate phase of reproduction.

The tendency of pre-breeders to explore and attach themselves to a colony other than the one in which they were born is probably much stronger than that of experienced breeders to change colony. Banded cormorants, Shags, Atlantic Gannets, Red-footed, Masked and Brown

Boobies have all been recovered at non-natal colonies. Moreover, in the Atlantic Gannet the population increases at several colonies demonstrate, beyond doubt, the influx of very substantial numbers of immigrants (details in Nelson 1978). A study of Ailsa Craig Gannets (Wanless 1979) appears to show that many pre-breeders establish, defend and consistently attend sites among breeders for a season and then leave the colony and (presumably) go to another one. This finding, if corroborated, would have several important implications, not least for demography, but as yet is not fully acceptable. Undoubtedly, however, large numbers of pre-breeding gannets (as do many other seabirds) visit non-natal colonies and many settle there. On Clipperton Island, after pigs had been exterminated, the population of Masked Boobies rose dramatically within two or three years, presumably by an influx of pre-breeders.

Conclusion

Marine pelecaniforms show variable but usually strong attachment to a breeding colony, having once bred there, although many species move sites within the colony. Usually they return to breed in the colony of their birth but many visit other colonies as pre-breeders and may cause sudden and large increases in the breeding population. The degree of attachment to a colony and of philopatry is extremely difficult to determine but may be weakest in opportunistic breeders, which are usually tropical species.

SIZE AND SPATIAL CHARACTERISTICS OF THE BREEDING GROUP

The marine pelecaniforms congregate in colonies which may number less than 10 pairs (many phalacrocoracids) to several millions (mixed cormorant/booby/pelican colonies in Peru). Obviously, new colonies begin with one or two pairs but even long-established colonies, within most pelecaniforms, range greatly in size. Given the apparent lack of stringent selection pressure on absolute colony size, can any guiding principles be discerned? First, are colonies merely imposed by lack of sites, conferring, otherwise, no special advantages? Clearly this is not the case, since colonial seabirds are strongly attracted to colonies as such. The advantages may be proven safety and also social in nature. If social advantages are important, what are they and would they (and the safety factor) be expected to lead to ever-increasing colony-size until some limiting factor intervened? Such factors could be shortage of sites and density-dependent pressure on food within the colonies' foraging areas. Are small colonies as successful as large colonies? Are there differences in their respective social structures? These questions move well into little-researched territory which requires a fuller review than is possible here. I will merely suggest some answers to these questions with particular reference to tropical versus temperate marine pelecaniforms.

A social advantage in large colonies is the greater pool of individuals available, for example, to newly established males "advertising" for females and to females prospecting for site-owning males. This saves time and effort and, if there is a mechanism for assessing individual fitness, a large colony applies this differential to a greater number, thus optimizing its effectiveness. It is not known whether, in seabirds, males or females are able to differentiate between "fit" and "less-fit" potential partners but some mammals and birds can make astonishingly subtle distinctions. Male Wood Pigeons (*Columba palumbra*), for example, can distinguish between females that have recently been courted by another male and those that have not (Rissman 1983). Among gulls there are significant differences in breeding potential between individuals. Thus, for example, the age of the male Red-billed Gull (*Larus novaehollandiae*) affects the female's clutch size (Mills 1973). Also, larger colonies presumably provide greater social stimulation and so colony size may help determine the timing of breeding and its synchrony in ways favoring larger colonies. Conversely, large colonies presumably increase interference by conspecifics. Social advantages, however, appear undeniably too slender to account for the presence of very large colonies. But, together with safety and limited availability of breeding locations, they could favor large colonies, the limits on which may then be imposed by site availability and by food. These are often impossible to disentangle.

First, sites themselves may run out. This clearly happened in several Peruvian seabird islands and operates in some Atlantic gannetries. Here enters the little-studied matter of site-quality. Seabirds undoubtedly select sites on the basis of many features. A cliffnester such as the Shag, although breeding on sites with a wide range of qualities such as distance from and above the sea, width and inclination of ledge, presence of protuberances and cracks, nearness to conspecifics, and other factors, is nonetheless applying different criteria than Gannets nesting on the same island. Optimal sites may run out. In tropicbirds, site requirements are such that demand outstrips supply. This accounts not only for the small size of tropicbird colonies but also for the notable competition (intra- and interspecific) and thus for the tendency of tropicbirds to utilize unsuitable sites such as holes in dense-jungle trees far inland on Christmas Island, Indian Ocean. Another population of this species nests in cliff crannies miles inland in the Waimea Canyon of Kauai (Hawaiian Islands) and yet others on the open ground beneath *Casuarina* trees.

Second, food may limit colony size. The incontestable logic of the inevitability of density-dependent competition is one of degree rather than of decree. Species which forage close inshore must fairly soon begin to compete for food unless this is superabundant. Thus Common Cormorants normally form colonies of less than 200 pairs, whereas colonies of Quanay Cormorants of the rich Humboldt Current commonly number 200,000 or more. The one is probably in density-dependent competition for food, whilst the other probably is not. Among highly pelagic pelecaniforms density-dependent competition for food is also highly unlikely to be a factor in determining colony size. There is clear evidence that the role of food, vital though it is in determining breeding success in many tropical pelecaniforms, operates via oceanographic influences independently of bird numbers. In sum, therefore, the wide range of colony size in many pelecaniforms arises because a wide range of factors determine it and these operate in different combinations for different species and circumstances. There is a correlation between colony size and foraging habit, but loosely, if at all, between colony size and tropical or temperate distribution.

Is breeding success higher in larger colonies? Probably there is a difference only between very small colonies and larger ones. The breeding success of a very small and inaccessible Atlantic gannetry in Britain (at Bempton) increased with colony size but only until the colony reached about 40 pairs (Nelson and Fairhurst, unpubl. data). There is no reason whatsoever to suspect that large colonies of any species are, because of size, less successful than very large ones.

There may be differences in social structure between colonies of different size in at least some pelecaniforms. The Bempton colony of Atlantic Gannets, which was growing rapidly, contained a higher proportion of immature individuals, adult-plumaged pre-breeders and young breeders than did certain sub-sections of the Bass colony. But that was a function of growth rather than colony size, and in fact a rapidly-growing part of the Bass also exhibited the Bempton syndrome. No comparisons have been made between stable large colonies and stable small ones. Existing studies of colony structure in seabirds have all concentrated on ecological factors such as breeding success in relation to edge/centre position, age and experience, body-weight, pair-status and the spatial pattern of the breeders. Most of these are on gulls. In pursuit of the role of social structure and social stimulation we need also ethological longitudinal studies of the differences in frequency and intensity of named behavior patterns in individuals of different social status (age, experience, position, nature of pair-bond, etc.).

Colony density is much more consistently species-specific than is colony size. Large or small, colonies of all pelecaniforms show recognizable typical densities. Topography places obvious constraints upon density but the latter is nevertheless under strong selection pressure in its own right. It cannot relate to food since it can make no difference whether Atlantic Gannets nest one meter apart or two. But they always choose the former. Where density is intra-specifically variable it may relate to available space. Thus, on some islands Cape Gannets pack much closer together than on others, but Atlantic Gannets maintain the standard spacing regardless of available space. Rather than food or space, social factors are most likely to "explain" observed density at the proximate level. These, however, have been largely neglected and I am unable to quote a single reference which relates the two (see below).

Conclusion

Colony size, enormously variable within and between species, relates to availability of sites, foraging mode, and social factors, rather than directly to tropical or temperate regime. Density is more species-typical and relates more strongly to social factors and colony size, but remains largely unexplored in terms of social behavior.

FUTURE WORK

I suggest that the following areas deserve study:

1. A comparative approach to breeding and stress. It must be significantly more worthwhile for breeding adults of some species, than for others, to subject themselves to harmful stress for the sake of increased productivity in the short term. Data are required on:

(a) The characteristics of first-time and experienced breeders (age, weight, behavior profiles) and their breeding success in temperate and tropical regimes. If field-cum-physiological data could establish quantifiable differences between breeders and non-breeders, and between breeders at the beginning and end of a cycle, we would have a powerful tool.

(b) The relationship between parental weight throughout a breeding attempt and egg/clutch size and chick growth.

(c) The nature and role of "rest" years on a widely comparative basis. The objective of these studies would be to understand the cost/benefits of the alternative strategies of higher productivity involving stress and a shorter breeding life or lower productivity but avoidance of stress and a longer breeding life. These may be studied between species and in relation to tropical (aseasonal) or temperate (seasonal) breeding regimes and also, possibly, within a species, where different strategies could comprise local adaptations. Group-selection may again become an issue in seabird biology.

2. The hitherto unremarked but intriguing absence of cooperative breeding in seabirds invites comment. There must be compelling reasons for this and my suggestion (that newly independent juvenals would be too heavily handicapped if they were to remain within the limited foraging area available to colony-attached birds rather than wandering more widely during this critical period) is only one.

3. Social behavior (discrete, defined and quantifiable behavioral items) in relation to colony size and density, social status, overall and subgroup synchrony, permanence of site and pair bond and productivity should be studied over the lifetime of known individuals.

The social aspects of coloniality remain little understood and, in conjunction with a more sophisticated approach to the matter of site-quality in physical terms, could help to define the causes of colony-size and spacing in seabirds, at the proximate level. Perhaps the most conceptually important data will come from that demanding and time-consuming project, the long term study of local populations and marked individuals, for which the pelecaniforms are so well suited.

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