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The Diets of *Sula dactylatra*, *Sula sula*, and *Fregata minor* on Christmas Island, Pacific Ocean[1]

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ABSTRACT: The diets of the Blue-faced Booby (*Sula dactylatra*), the Red-footed Booby (*Sula sula*), and the Great Frigatebird (*Fregata minor*) were studied by analyses of regurgitation samples. Flying fish and squid composed the majority of the diets, but the Frigatebirds also consumed numerous Sooty Tern (*Sterna fuscata*) pulli. These data allow comparison with similar earlier studies of the smaller bird species that inhabit the atoll and indicate that resource partitioning occurs through the percentage of fish and squid taken and the size of the prey items taken, with the larger species of birds eating larger fish and squid.

ANALYSES of regurgitation samples provide valuable data on the comparative feeding ecology of birds. These data are useful to persons who are studying the food of seabirds, whose actual feeding behavior is difficult to study (Ashmole and Ashmole, 1967, King 1974). The Ashmoles collected regurgitation samples from eight species of small seabirds nesting on Christmas Island, central Pacific Ocean (1° N, 157° W) between February 1963 and June 1964 (Ashmole and Ashmole 1967, Ashmole 1968, Ashmole and Ashmole 1968). Their study was concentrated on two small islets in the lagoon. The results clearly show that the size of the bird is directly related to the size of the food items and that resource partitioning is accomplished through species differences in feeding methods, feeding zones, and feeding times.

Three Pelecaniformes (Blue-faced Booby, *Sula dactylatra*; Red-footed Booby, *Sula sula*; and Great Frigatebird, *Fregata minor*) are the largest abundant seabirds breeding on Christmas Island and are concentrated on mainland areas of the atoll (Schreiber and Ashmole 1970). From May through August 1967, Schreiber collected regurgitation samples from these species. In this paper we document their diets, because these data combined with those of the Ashmoles offer a glimpse into the feeding strategies of the major members of the avifauna of this midocean atoll.

Methods

All samples were collected between 1800 and 0300 hours from adults, subadults, or nestlings. Because of the advanced state of digestion in many samples, only 175 of 288 (collected individually and preserved in 10 percent Formalin) were analyzed in detail: 57 percent of 63 from *Sula dactylatra*, 51 percent of 98 from *Sula sula*, and 70 percent of 127 from *Fregata minor*. The larger number of samples collected from *F. minor* indicates more time spent working with these birds and does not mean necessarily that this species regurgitated more readily than did the boobies. Differences in the condition of the samples may indicate that boobies have a more rapid digestion process, that they are feeding earlier in the day or farther from land, or that frigates feed later into the evening. These subjects need further study. Frequency of regurgitation in the field was not recorded.

Only food items classed into digestion grades 1 or 2 (see Ashmole and Ashmole 1967) were analyzed. Frequency of occurrence and length of all food items were recorded. For squid, the mantle was measured; for fish, the standard length was measured. Weights of total samples and individual items were taken to the nearest 1 g on an O'Haus beam balance. Volumes were measured by water displacement to the nearest

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TABLE 1

FISH SPECIES IDENTIFIED IN REGURGITATION SAMPLES FROM THREE SPECIES OF PELECANIFORM BIRDS, CHRISTMAS ISLAND, PACIFIC OCEAN, 1967

FISH TAXA	DISTRIBUTION CATEGORY	BLUE-FACED BOOBY, *Sula dactylatra* no.	%	RED-FOOTED BOOBY, *Sula sula* no.	%	GREAT FRIGATEBIRD *Fregata minor* no.	%
Chanidae							
Chanos chanos (Forskål)	I	0	0	0	0	2	3
Exocoetidae		23	96		91		78
Euleptoramphus viridis (van Hasselt)	P			28		44	
Exoceotus volitans Linnaeus				2		1	
Cypselurus spilonotopterus (Bleeker)				1		1	
Prognichthys albimaculatus (Fowler)				1		1	
Serranidae							
Epinephelus merra (Bloch)	I	0	0	0		2	3
Coryphaenidae							
Coryphaena sp.	P	0	0	1	3	4	7
Acanthuridae							
Acanthurus achilles (Shaw)	P	0	0	0	0	1	2
Scrombridae							
Euthynnus affinis (Cantor)	P	1	4	0	0	1	2
Tetraodontidae							
Arothron meleagris (Lacépède)	I	0	0	1	3	1	2
Diodontidae							
Chilomycterus sp.	I	0	0	0	0	2	3
Balistidae							
Xanthichthys sp.	P	0	0	1	3	0	0
Total Number of Fishes Identified in Samples		24		35		60	

NOTE: Distribution categories of fishes: P, pelagic; I, inshore.

1 cc. Data for June and July have been combined for presentation, since study priorities precluded few samples being collected during these months.

Fishes were identified (Table 1) to the lowest taxonomic level possible and categorized as inshore (those that spend their adult lives closely associated with coral reefs or lagoon waters) or pelagic (open-water inhabitants) species. The Acanthuridae and Balistidae are inshore forms as adults but pelagic as larvae. As only the larval forms of members of these families were present in the samples, they have been categorized as pelagics. Although some species of Tetraodontidae and Diodontidae are known to be at least occasionally pelagic, the two species encountered in this study have been categorized as inshore species.

Fishes have been deposited at the University of South Florida. The squid were lost in transit, so that we are unable to identify them to family or species.

Results

The number, volume, size, and identification of food items are shown in Tables 2–6.

Discussion

On Christmas Island, a greater difference exists between the diets of *Sula dactylatra* and *S. sula* in the percentage of fish and squid taken and in the size of fish taken than exists between the sulids and *Fregata minor*. *Sula dactylatra* generally had the fewest items per sample but

TABLE 2

QUANTITATIVE DATA ON REGURGITATION SAMPLES FROM THE BLUE-FACED BOOBY, *Sula dactylatra*, NESTING ON CHRISTMAS ISLAND, PACIFIC OCEAN, 1967

ITEM	MAY	JUNE–JULY	AUGUST
Total Number of Samples	9	12	15
Average Number of Food Items per Sample	3.6	4.3	5.9
Average Sample Weight	160 g	167 g	203 g
Average Sample Volume	138 cc	149 cc	192 cc
Percentage of Squid by Weight	3.1	12.5	3.1
Percentage of Squid by Volume	2.6	13.4	2.6
Percentage of Fish by Weight	96.9	87.5	96.9
Percentage of Fish by Volume	97.4	86.6	97.4
Squid			
Present in Number of Samples	2	10	5
Average Number per Sample	0.33	2.2	0.4
Average Length Taken	8.3 cm	9.6 cm	7.7 cm
Average Weight Taken	15 g	9.6 g	12.5 g
Average Volume Taken	12.7 cc	9.2 cc	10 cc
Fish			
Present in Number of Samples	9	12	15
Average Number per Sample	3.3	2.2	5.4
Average Length Taken	13.1 cm	16.3 cm	13.6 cm
Average Weight Taken	46.6 g	67.3 g	36.6 g
Average Volume Taken	44.3 cc	59.5 cc	34.5 cc

TABLE 3

QUANTITATIVE DATA ON REGURGITATION SAMPLES FROM THE RED-FOOTED BOOBY, *Sula sula*, NESTING ON CHRISTMAS ISLAND, PACIFIC OCEAN, 1967

ITEM	MAY	JUNE–JULY	AUGUST
Total Number of Samples	16	17	17
Average Number of Food Items per Sample	8.3	5.9	5.6
Average Sample Weight	76 g	105 g	105 g
Average Sample Volume	69 cc	95 cc	93 cc
Percentage of Squid by Weight	26.7	34.3	15.4
Percentage of Squid by Volume	25.8	34.8	14.9
Percentage of Fish by Weight	73.3	65.8	84.6
Percentage of Fish by Volume	74.2	65.2	85.1
Squid			
Present in Number of Samples	15	16	17
Average Number per Sample	4.6	3	4.2
Average Length Taken	5.8 cm	7.1 cm	6.2 cm
Average Weight Taken	5.2 g	14.1 g	9.2 g
Average Volume Taken	4.6 cc	12.9 cc	7.9 cc
Fish			
Present in Number of Samples	16	17	17
Average Number per Sample	4.6	3.2	3.8
Average Length Taken	7.4 cm	8.5 cm	9.9 cm
Average Weight Taken	12.3 g	21 g	23.2 g
Average Volume Taken	11.4 cc	18.9 cc	20.8 cc

TABLE 4

QUANTITATIVE DATA ON REGURGITATION SAMPLES FROM THE GREAT FRIGATEBIRD, *Fregata minor*, NESTING ON CHRISTMAS ISLAND, PACIFIC OCEAN, 1967

ITEM	MAY	JUNE–JULY	AUGUST
Total Number of Samples	34	30	25
Average Number of Food Items per Sample	7.8	7.0	5.0
Average Sample Weight	105 g	122 g	115 g
Average Sample Volume	96 cc	108 cc	111 cc
Percentage of Squid by Weight	41.2	27.3	21.9
Percentage of Squid by Volume	41.8	23.6	20.7
Percentage of Fish by Weight	58.8	56.8	64.0
Percentage of Fish by Volume	58.2	60.6	65.7
Percentage of Bird Material by Weight	0	15.9	14.1
Percentage of Bird Material by Volume	0	15.8	13.6
Squid			
Present in Number of Samples	25	18	17
Average Number per Sample	6.5	6.2	5.5
Average Length Taken	6.5 cm	6.9 cm	8.2 cm
Average Weight Taken	9.0 g	7.8 g	10.1 g
Average Volume Taken	8.5 cc	6.8 cc	9.3 cc
Fish			
Present in Number of Samples	32	23	23
Average Number per Sample	3.1	3.7	2.1
Average Length Taken	9.9 cm	11.1 cm	21.6 cm
Average Weight Taken	20.3 g	26.1 g	75.3 g
Average Volume Taken	18.5 cc	23.3 cc	72.1 cc
Bird Material			
Present in Number of Samples	0	9	8
Average Number per Sample	0	1.4	0.7
Average Weight Taken		45 g	81 g
Average Volume Taken		39.4 cc	75 cc

TABLE 5

SIZE DISTRIBUTION OF FISH IN REGURGITATION SAMPLES FROM THREE SPECIES OF PELECANIFORM BIRDS NESTING ON CHRISTMAS ISLAND, PACIFIC OCEAN, 1967

SPECIES AND MONTH	STANDARD LENGTHS (cm) 0–5	6–10	11–15	16–20	21–25	26+	TOTAL
Blue-faced Booby, *Sula dactylatra*							
May	1	5	11	7	3	2	29
June–July	0	3	5	3	4	0	15
August	0	2	26	13	4	0	45
Total	1	10	42	23	11	2	89
Red-footed Booby, *Sula sula*							
May	6	17	3	1	0	0	27
June–July	1	9	8	3	0	0	21
August	0	10	48	3	0	0	61
Total	7	36	59	7	0	0	109
Great Frigatebird, *Fregata minor*							
May	0	33	36	17	5	4	95
June–July	0	8	41	24	2	2	77
August	0	15	40	30	1	1	87
Total	0	56	117	71	8	7	259

TABLE 6

SIZE DISTRIBUTION OF SQUID IN REGURGITATION SAMPLES FROM THREE SPECIES OF PELECANIFORM BIRDS NESTING ON CHRISTMAS ISLAND, PACIFIC OCEAN, 1967

SPECIES AND MONTH	SQUID MANTLE LENGTH (cm) 0–5	6–10	11–15	16+	TOTAL
Blue-faced Booby, *Sula dactylatra*					
May	1	1	1	0	3
June–July	4	8	0	0	12
August	0	3	1	0	4
Total	5	12	2	0	19
Red-footed Booby, *Sula sula*					
May	0	26	0	0	26
June–July	0	20	0	0	20
August	9	20	3	0	32
Total	9	66	3	0	78
Great Frigatebird, *Fregata minor*					
May	15	91	39	5	150
June–July	2	80	30	0	112
August	8	60	19	0	87
Total	25	231	88	5	349

TABLE 7

BODY WEIGHT AND CULMEN LENGTH OF FOUR SPECIES OF PELECANIFORM BIRDS ON CHRISTMAS ISLAND, PACIFIC OCEAN, 1967

SPECIES	MEAN CULMEN LENGTH AND RANGE (mm) AND NUMBER MALES	FEMALES
Blue-faced Booby, *Sula dactylatra*	104 (102–105), $N = 9$	104 (99–107), $N = 8$
Red-footed Booby, *Sula sula*	76 (71–82), $N = 28$	82 (75–86), $N = 28$
Great Frigatebird, *Fregata minor*	91 (81–99), $N = 85$	108 (100–116), $N = 78$
Red-tailed Tropicbird, *Phaethon rubricauda*	65 (59–68), $N = 17$	

SPECIES	MEAN WEIGHT AND RANGE (g) AND NUMBER MALES	FEMALES
Blue-faced Booby, *Sula dactylatra*	1733 (1550–2000), $N = 9$	1620 (1550–1700), $N = 8$
Red-footed Booby, *Sula sula*	825 (700–1050), $N = 28$	1025 (850–1200), $N = 28$
Great Frigatebird, *Fregata minor*	914 (675–1100), $N = 25$	1183 (950–1750), $N = 31$
Red-tailed Tropicbird, *Phaethon rubricauda*	635 (540–725), $N = 13$	

NOTE: Numerals in parentheses represent ranges. Data for *Phaethon rubricauda* represent both males and females.

its average sample volume was the largest of all three species, and this corresponds well with the relative sizes of the bird species (Table 7). *Sula dactylatra* takes more and larger fish (by weight and volume) than does *S. sula* but the latter takes more squid than does *S. dactylatra*. Of the three species studied here, *S. sula* had the least sample volume and least weight per sample. *Sula sula* is the smallest of the three bird species. *Fregata minor* had only slightly larger sample volume than did *S. sula* and was intermediate between the two sulids in number of items per sample. Its size tends to be intermediate between the two sulids (Table 7). In comparing average length, weight, and volume of squid and fish from regurgitation samples, we found that *F. minor* generally lies between the two sulids.

The larger species of birds studied here obviously take larger food items than do the small terns and procellarids studied by the

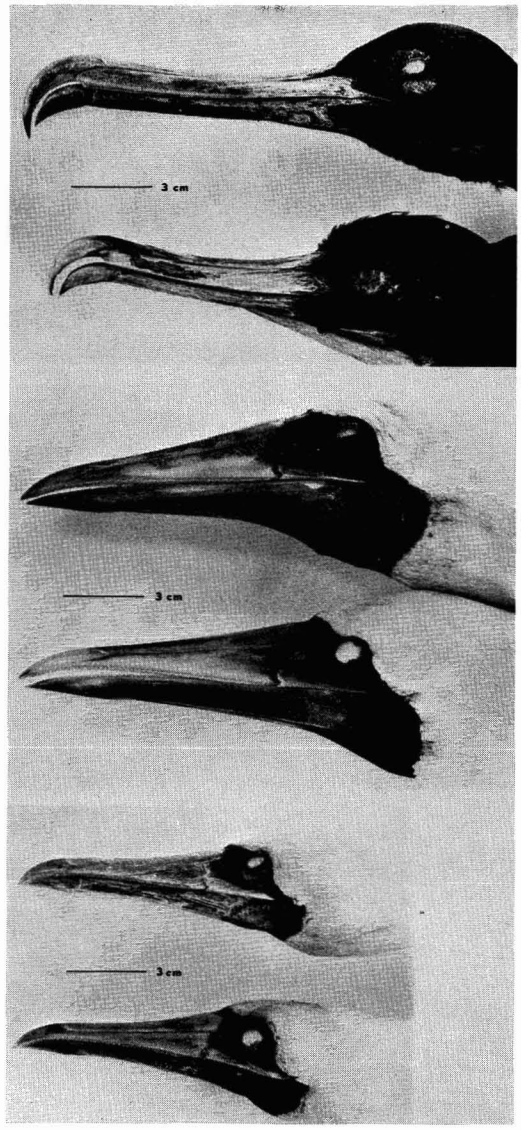

FIGURE 1. Bills of three species of pelecaniform birds. Top pair, *Fregata minor*; middle pair, *Sula dactylatra*; lower pair, *Sula sula*. In each species pair the female is uppermost. All six bills are shown to scale. All are specimens in the National Museum of Natural History, Washington, D.C.

Ashmoles (1967), and our data confirm their conclusions regarding size of predator and size of prey items. We were also able to compare the diet of the Red-tailed Tropicbird, *Phaethon rubricauda*, with those of the sulids and of *Fregata minor* on Christmas Island. Body size and bill length of these four species of birds gathered by Schreiber in 1967 on Christmas Island are shown in Table 7. Bill shapes of the boobies and frigates are shown in Figure 1, which should be compared with figure 6 in Ashmole and Ashmole (1967: 71). *Phaethon rubricauda* took fewer items per sample, and sample weight and volume were smaller than was the case with the other three Pelecaniformes on Christmas Island. Squid composed a much greater proportion of the diet of *Phaethon*, and smaller squid were present in its diet. The fish eaten by *Phaethon* were generally similar in size to those taken by *Sula sula*, except that several very large fish were taken by *Phaethon*. One of these fish (40–42 cm long) was the largest fish found during either of these studies. These conclusions further confirm the Ashmoles' suggestions regarding size of prey and size of predator and are what one would predict, i.e., large birds take large prey items.

Sula dactylatra, *S. sula*, and *Phaethon rubricauda* plunge-dive and pursue fish under water, possibly to some depth. *Fregata minor*, however, never enter the water but swoop from a considerable height and at a steep angle to snatch fish from very near the water surface, probably no deeper than 6 inches. The boobies and tropicbirds may be independent of predator fish as Ashmole and Ashmole (1967: 64) suggested, but we suggest that the frigatebirds may be more dependent on such marine predators as tuna and porpoise chasing smaller fish to near the water surface than are the other bird species.

Data that record observations of the feeding zones for the Christmas Island populations of these bird species do not exist. There is a summary of observations for the Hawaiian Island populations (King 1970) which is relevant to the Christmas Island area, although the latter area is somewhat complicated by the presence of the equatorial countercurrent. In Hawaii *Sula sula* is found predominately within 50 miles of land; *S. dactylatra* has been observed less frequently within 50 miles than it has over 100 miles from land; numbers of *Fregata minor* decrease gradually with increasing distance from land; the density of *Phaethon rubricauda* remains the same regardless of distance from land, and this species has been found primarily as widely

scattered individuals. None of the Pelecaniformes have been found in appreciable numbers in mixed species flocks.

As pointed out by Ashmole and Ashmole (1967: 101), the ability to exploit a wide variety of prey and prey size is important to the existence of these marine bird species. The presence of Sooty Tern pulli in the diet of *Fregata minor* on Christmas Island in June–August 1967 confirms the ability of this species to exploit a readily available food source. Schreiber and Ashmole (1970) noted that frigatebirds ate essentially all the chicks in one Sooty Tern colony on the island but did not consume those from the other tern colonies. Terns were found in the material regurgitated by the frigatebirds only in their nesting area near this tern colony. The cleptoparasitic habits of frigatebirds have received considerable comment. However, the information summarized here indicates that the *Fregata minor* population on Christmas Island in 1967 was feeding on several species of fish that the boobies—the species frigates chased most (Schreiber, unpublished data)—were not eating. Also the frigates were feeding on size-classes of both fish and squid different from those of the boobies. Thus, we conclude that during the period of this study frigates were making their own living without resorting to cleptoparasitism. Our data from regurgitation samples are confirmed by the relative scarcity of Schreiber's observations of frigates' harassing other bird species during his stay on the island. However, he did note some of this activity. It may well be that cleptoparasitism is an important behavior during periods of food stress when the ability to rob other species of birds of their fish and squid may mean the difference between survival of an individual or its ability successfully to rear young. Such a food stress situation did not exist on Christmas Island in 1967 (Schreiber, unpublished data).

Summary

Our data clearly indicate that resource partitioning of food between the pelecaniform birds on Christmas Island occurs through (1) differences in the percentages of fish and squid taken and (2) the size of prey items taken. Spatial partitioning in feeding zones may also occur, but we have no data on this point and believe that further studies are warranted. It is obvious, however, that the size of food items is related to the size of the predator. Thus, the larger bird species take the larger species of fish and squid. Fish species identifications indicate that these species of birds are eating the prey with which they come in contact. These data also indicate that the more closely related species (*Sula dactylatra* and *S. sula*) differ more in their diet than they do compared with the more distantly related species (*Sula* compared to *Fregata* and *Phaethon*), although the differences between the two sulids may occur entirely because of the body size differences.

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