

THE DIET OF THE MAGNIFICENT FRIGATEBIRD DURING CHICK REARING¹

ITZIA CALIXTO-ALBARRÁN AND JOSÉ-LUIS OSORNO²

Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, A.P. 70-275, México, D.F. 04510, México, e-mail: jlosorno@servidor.unam.mx

Abstract. We describe the diet of the Magnificent Frigatebird *Fregata magnificens* at Isla Isabel off the Pacific coast of Mexico based on 158 regurgitates (555 prey items) from males, females, chicks, and juveniles. The diet included 50 species of fishes (21 identified to genus only), 1 species of squid, and 2 species of crustaceans. *Diplectum pacificum* and *Anchoa lucida* were the most frequent species of fish in the frigatebird's diet. No differences in prey composition or prey size were found between males and females, but females disgorged 62% more food. This difference mirrors the bigger size (15% larger than males) and larger contribution of females to chick feeding. Flying juveniles consumed prey in different proportions than the adults and disgorged marginally more food. Juveniles may obtain food in different patches than adults and complement this source with maternal feedings, or they may be more likely to regurgitate. Diet composition of males, females, and flying juveniles changed during the 4-month period of this study, but the mass of regurgitates did not change as the breeding season progressed, suggesting that availability of prey species changes over time. Most of the diet of this population probably comes from opportunistic feeding on fisheries, because the variety of fishes disgorged is remarkably similar to the published list of fishes discarded by prawn-fishing boats in the area. If our assumption is true, kleptoparasitism and direct fishing are only marginally represented in the diet of this population.

Key words: diet, foraging techniques, *Fregata magnificens*, Magnificent Frigatebird, sea birds.

INTRODUCTION

Frigatebirds (*Fregata* spp.) forage by surface dipping, kleptoparasitism, and opportunistic feeding such as scavenging from fisheries. These methods have been described in several species (Nelson 1975, Osorno et al. 1992, Gilardi 1994), particularly in the Magnificent Frigatebird (*Fregata magnificens*). Some cases of opportunism include hunting small turtles (Sage 1995), seabird chicks, and other items naturally occurring or associated with human disturbance (Diamond 1973). Most accounts, however, have focused on feeding events, rather than on describing the diet of frigatebirds in particular populations (Diamond 1973, Nelson 1975, Schreiber and Clapp 1987).

Diet composition is expected to vary according to food availability and to the feeding technique used. Where dipping is the most common technique, the frigatebird's reported diet is restricted to squid and flying fish (Diamond 1975, Schreiber and Hensley 1976). A more diverse diet but still made-up only of surface-dwelling

species is the diet reported for the Great Frigatebird (*Fregata minor*) in Hawaii. This species consumed 23 fish families and a single squid. The most frequent prey were flying fishes, jacks, and squids (Harrison et al. 1983). In contrast, kleptoparasitic foraging is expected to increase the diet composition according to diet of the parasitized species, but this has not been documented.

Morphological differences between sexes, and different feeding skills associated with age and experience are known to influence the diet of individuals in marine birds (Orians 1969, Gilardi 1994). In the Magnificent Frigatebird, the reversed sexual size dimorphism (females are 15% bigger than males; Osorno 1996) and the different rearing roles between the sexes (Diamond 1973, Trivelpiece and Ferraris 1987, Osorno 1996) may produce sexual differences in diet composition.

Here we describe the diet of the Magnificent Frigatebird during the chick-rearing period based on adult, juvenile, and chick regurgitates. We compared the diet of males and females, and of adults and flying juveniles, and assessed whether this diet varies during the breeding season.

¹ Received 30 March 1999. Accepted 10 January 2000.

² Corresponding author.

METHODS

The study was conducted during the chick rearing period of a large breeding population (3,600 pairs; Osorno, unpubl. data) of the Magnificent Frigatebird at Isla Isabel, off the Mexican Pacific Coast (21°52'N, 105°54'W) from April to June 1991.

Diet was described from 158 regurgitations. Birds disgorged when handled or approached. Although stomach contents are likely to be a more accurate method of analyzing diet, that method necessitates sacrificing the birds. In Red-faced Cormorants (*Phalacrocorax urile*), no differences were detected using regurgitations or stomach contents (Schneider and Hunt 1984), suggesting that regurgitations are a good indicator of diet. We choose this method because of the minimal disturbance to birds, easy collection, and easy replication. In our study, all regurgitations were obtained during the day (08:00–18:00), collected in plastic bags, and wet weights obtained using an electronic Ohaus scale (± 1 g). Samples were fixed in 10% formalin. Date, wet weight of the regurgitation, sex, and age class of the bird were recorded. In the laboratory, samples were rinsed and preserved in 70% alcohol.

Regurgitations came from 7 reproductive males and 28 reproductive females, 21 flying juveniles, and 102 chicks (30 to 150 days old). Some chick regurgitations were obtained immediately after the chicks were fed by the father ($n = 6$) or the mother ($n = 44$); these items were assumed to represent the diet of the parent. Consequently, total sample sizes were 13 males, 72 females, 21 flying juveniles, and 52 chicks.

PREY IDENTIFICATION

Fish species were determined in each regurgitation using keys and catalogs by Hildebrand (1946), Walls (1975), Castro-Aguirre (1978), Thomson et al. (1979), Randall (1983), and Nelson (1984). Seventy percent of prey items were identified to species, 88% to genus, and 99% to family level.

We used biometrics in fish identification to determine: (1) number of branquispines in the first brachial arch (prominent expansions of variable size also known as rakers; Rojo 1991), (2) the number of scales in the lateral line, (3) the form and position of the fins (ventral, thoracic or jugular), (4) the dorsal, pectoral, and anal fins

formula (number of spines and radii), and (5) the presence of adipose fins, photophores, and barbells.

Size of 135 prey items was directly measured ($n = 93$), or obtained by linear regression ($n = 42$) when the state of digestion of the fish precluded direct measurements. Meristic data were: (1) total length (the distance between the mouth and the tip of the tail), (2) standard length (the distance between the mouth and the tip of the caudal peduncle), (3) head length (the distance between the mouth and the end of the operculum), (4) maximal height (measured from the base of the dorsal fin to the base of the pelvic fin), and (5) the diameter of the eye (Rojo 1991).

DATA ANALYSES

In order to quantify the relative abundance of prey, we used both the numeric (i.e., abundance) and frequency of occurrence methods proposed by Ashmole and Ashmole (1967), Harrison et al. (1983), and Duffy and Jackson (1986). In the numeric method we counted the number of items of each prey type per regurgitation. This number was added for all samples (regurgitations) to obtain the total number of items of each species. This value was divided by the total number of prey of all types ($n = 555$). The result is expressed in percentage to indicate the relative abundance of each prey type in the frigatebird's diet.

The frequency of occurrence method was determined by counting the number of regurgitations including a particular type (species or order) of prey. The resulting number expressed as a percentage of the total number of regurgitations ($n = 158$) indicates the number of birds regurgitating a particular prey type, but it does not indicate its absolute abundance. We also calculated the average number of items of each prey species per sample.

We compared (a) prey composition, (b) food amount (wet weight), and (c) prey size by date (month), sex and age of the bird disgorging any of the six most frequent orders (when sample sizes were appropriate) and at the level of the seven most frequent species in the sample of 158 stomach contents. Chick regurgitates ($n = 52$) were excluded from these analyses because we did not know the identity of the parent delivering the food, thus sample size for analyses was 13 males, 72 females, and 21 flying juveniles (n

= 106, but 158 for general description of the population's diet).

We used *t*-test or two-way ANOVA to analyze prey size and food amount or their normalized equivalent (logarithm or square root) of males and females. Nonparametric tests were used when small sample sizes precluded normalization of data. We applied Generalized Linear Models (GLM; Crawley 1993) to analyze prey item composition of males, females, adults, and juveniles. Specifically, we applied a binomial distribution model with a LOGIT link function. Critical values are reported as Chi-square values. For the analyses of the temporal variation in the wet weight of the regurgitation, we pooled all the regurgitations of males, females, and juveniles, and used a nonparametric comparison (Kruskal-Wallis test) because samples were not normally distributed even after transformation. All comparisons were two-tailed. Mean \pm SE and percentages are reported when appropriate. In our statistical comparisons of frequencies, we included one item of each order or species of prey per stomach only. Thus, each regurgitation in a particular statistical test was represented only once.

RESULTS

DIET DESCRIPTION

Every stomach contained on average 3.5 ± 0.3 items and 1.7 ± 0.1 different species. The average wet mass of 155 regurgitations regardless of the species and age class (3 items were not weighed) was 104.6 ± 4.3 g. Of all the recovered items ($n = 555$), 96.8% were fish, 2.3% were cephalopods, and 0.9% were crustaceans (0.5% decapods and 0.4% stomatopods). Fish belonged to 11 orders, 26 families, 36 genera, and 50 species (the complete list of species can be obtained from the authors on request). In 21 cases, we were unable to determine the fish species, but determined the genus.

Fish of the families Serranidae (48.7%), Triglidae (24.7%), Bothidae (13.3%), and Synodontidae (10.1%) were the most frequent in the 158 regurgitations. These families were represented by the following species: *Diplectum pacificum* (45.6%), *Prionotus quiescens* (12.7%), *Synodus scituliceps* (9.5%), and *Citharichthys* sp. (7.0%). Seven species were present in at least 5% of the regurgitations and were deemed the most frequent species (Table 1).

The four most abundant fish families were Serranidae (31.0%), Triglidae (14.2%), Engraulidae (10.6%), and Bothidae (8.3%). The more abundant species of these families were *D. pacificum* (29.7%), *Anchoa lucida* (10.3%), *P. quiescens* (8.8%), and *Citharichthys* sp. (5.2%). The relative abundance of most prey species was less than 2%. Only eight species (two species were identified up to genus) were more abundant than 2% and accounted for 65.7% of the total sample of 555 items (Table 1).

We measured the total length of the head and the ratio of the total length/maximal height of 93 complete prey of the three more frequent species. Based on these measurements we were able to estimate the total length of the head and/or the maximal height of another 42 prey items which were not in an advanced state of digestion. We estimated these measurements based on linear regressions of each fish species. The average total length of these 135 prey items was 12.5 ± 0.4 cm.

SEX DIFFERENCES

Prey type. Frigatebirds disgorged different proportions of the six more common orders ($\chi^2_5 = 356$, $P < 0.001$), but the relative ingestion of these by males ($n = 13$) and females ($n = 69$; three females ingested rare/unidentifiable fish) was similar ($\chi^2_5 = 8.6$, $P = 0.13$). Orders were Clupeiforms, Siluriforms, Aulopiforms, Batrachoidiforms, Scorpaeniforms, and Perciforms. These included the prey species consumed in at least 5% of the total sample. Fish of the seven most frequent species were consumed in different proportions by frigatebirds ($\chi^2_6 = 276$, $P < 0.001$), but males and females consumed similar proportions of these ($\chi^2_6 = 5.3$, $P = 0.51$).

Prey size. We compared the size (total length) of prey from 6 males and 26 females taking into account the fish family. The analysis included only those families represented in at least two regurgitates. For this analysis, when more than one measurable prey per stomach was available, we used the average size of each prey species. We did not compare the longest prey because this may be meaningless, as it is uncertain whether the longest prey in a given sample is the longest prey a bird can capture. Males and females captured same-sized prey considering the specimens of the three most common families in the sample (Carangidae, Serranidae, and Triglidae) (females: 13.3 ± 0.7 cm, $n = 26$;

TABLE 1. Most abundant and most frequent fish orders and families regurgitated by the Magnificent Frigatebird during the chick-rearing period (1991).

Order Family Species	Frequency ^a (%)				Abundance ^b (%)			
	Males	Females	Juveniles	Chicks	Males	Females	Juveniles	Chicks
AULOPIFORMS								
Synodontidae	3 (1.9)	9 (5.7)	1 (0.6)	3 (1.9)	3 (0.5)	14 (2.5)	1 (0.2)	3 (0.5)
<i>Synodus sciuticeps</i>	3 (1.9)	9 (5.7)	1 (0.6)	3 (1.9)	3 (0.5)	14 (2.5)	1 (0.2)	3 (0.5)
Other Synodontidae	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.6)	0 (0.0)	0 (0.0)	0 (0.0)	2 (0.4)
								1 (0.2)
BATRACHOIDIFORMS								
Batrachoididae	1 (0.6)	8 (5.1)	1 (0.6)	3 (1.9)	1 (0.2)	12 (2.2)	1 (0.2)	3 (0.5)
<i>Porichthys notatus</i>	1 (0.6)	8 (5.1)	1 (0.6)	3 (1.9)	1 (0.2)	12 (2.2)	1 (0.2)	3 (0.5)
Other Batrachoididae	0 (0.0)	4 (2.5)	1 (0.6)	2 (1.3)	0 (0.0)	7 (1.3)	1 (0.2)	2 (0.4)
	1 (0.6)	4 (2.5)	0 (0.0)	1 (0.6)	1 (0.2)	5 (0.9)	0 (0.0)	1 (0.2)
CLUPEIFORMS								
Engraulidae	1 (0.6)	5 (3.2)	3 (1.9)	8 (5.1)	1 (0.2)	26 (4.7)	26 (4.7)	22 (4.0)
<i>Anchoa lucida</i>	0 (0.0)	1 (0.6)	1 (0.6)	2 (1.3)	0 (0.0)	19 (3.4)	24 (4.3)	16 (2.9)
Other Engraulidae	0 (0.0)	1 (0.6)	1 (0.6)	1 (0.6)	0 (0.0)	19 (3.4)	24 (4.3)	14 (2.5)
Clupeidae	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.6)	0 (0.0)	0 (0.0)	0 (0.0)	2 (0.4)
	1 (0.6)	4 (2.5)	2 (1.3)	6 (3.8)	1 (0.2)	7 (1.3)	2 (0.4)	6 (1.1)
<i>Ophistonema libertate</i>	0 (0.0)	3 (1.9)	0 (0.0)	3 (1.9)	0 (0.0)	5 (0.9)	0 (0.0)	3 (0.5)
Other Clupeidae	1 (0.6)	1 (0.6)	2 (1.3)	3 (1.9)	1 (0.2)	2 (0.4)	2 (0.4)	3 (0.5)
PERCIFORMS								
Serranidae	9 (5.7)	64 (40.5)	18 (11.4)	44 (27.8)	26 (4.7)	124.2(2.3)	23 (4.1)	82 (14.8)
<i>Diplletrum pacificum</i>	5 (3.2)	39 (24.7)	9 (5.7)	24 (15.2)	8 (1.4)	91 (6.4)	14 (2.5)	59 (10.6)
Other Serranidae	4 (2.5)	37 (23.4)	9 (5.7)	22 (13.9)	7 (1.3)	88 (5.9)	14 (2.5)	56 (10.1)
Polynemidae	1 (0.6)	2 (1.3)	0 (0.0)	2 (1.3)	1 (0.2)	3 (0.5)	0 (0.0)	3 (0.5)
<i>Polydactylus opercularis</i>	1 (0.6)	5 (3.2)	0 (0.0)	3 (1.9)	1 (0.2)	5 (0.9)	0 (0.0)	4 (0.7)
Other Polynemidae	0 (0.0)	4 (2.5)	0 (0.0)	1 (0.6)	1 (0.2)	4 (0.7)	0 (0.0)	1 (0.2)
Other Perciforms	3 (1.9)	20 (12.7)	9 (5.7)	17 (10.8)	0 (0.0)	1 (0.2)	0 (0.0)	3 (0.5)
					17 (3.1)	28 (5.0)	9 (1.6)	19 (3.4)
PLEURONECTIFORMS								
Bothidae	0 (0.0)	8 (5.1)	3 (1.9)	11 (7.0)	0 (0.0)	9 (1.6)	5 (0.9)	33 (5.9)
<i>Citharichthys spp</i>	0 (0.0)	7 (4.4)	3 (1.9)	1 (0.6)	0 (0.0)	8 (1.4)	5 (0.9)	33 (5.9)
Other Bothidae	0 (0.0)	2 (1.3)	2 (1.3)	7 (4.4)	0 (0.0)	2 (0.4)	4 (0.7)	23 (4.1)
Other Pleuronectiforms	0 (0.0)	5 (3.2)	1 (0.6)	4 (2.5)	0 (0.0)	6 (1.1)	1 (0.2)	10 (1.8)
	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.2)	0 (0.0)	0 (0.0)

Table 1. Continued.

Order Family Species	Frequency ^a (%)				Abundance ^b (%)			
	Males	Females	Juveniles	Chicks	Males	Females	Juveniles	Chicks
SCORPAENIFORMS								
Triglidae	4 (2.5)	29 (18.4)	2 (1.3)	10 (6.3)	5 (0.9)	45 (8.1)	5 (0.9)	24 (4.3)
<i>Prionotus quiescens</i>	4 (2.5)	23 (14.6)	2 (1.3)	10 (6.3)	5 (0.9)	45 (8.1)	5 (0.9)	24 (4.3)
Other Triglidae	2 (1.3)	9 (5.7)	2 (1.3)	7 (4.4)	2 (0.4)	21 (3.8)	5 (0.9)	21 (3.8)
Other Triglidae	2 (1.3)	14 (8.9)	0 (0.0)	3 (1.9)	3 (0.5)	24 (4.3)	0 (0.0)	3 (0.5)
SLURIFORMS								
Ariidae	1 (0.6)	3 (1.9)	0 (0.0)	2 (1.3)	1 (0.2)	3 (0.5)	0 (0.0)	3 (0.5)
Other Fishes	1 (0.6)	3 (1.9)	0 (0.0)	2 (1.3)	1 (0.2)	3 (0.5)	0 (0.0)	3 (0.5)
Other Fishes	0 (0.0)	9 (5.7)	3 (1.9)	6 (3.8)	0 (0.0)	17 (3.1)	8 (1.4)	11 (2.0)
Total Fishes	19 (12.0)	129 (81.6)	31 (19.6)	87 (55.1)	37 (6.7)	250 (45.0)	69 (12.4)	181 (32.6)
Total Invertebrates	1 (0.6)	4 (2.5)	0 (0.0)	3 (1.9)	1 (0.2)	13 (2.3)	0 (0.0)	4 (0.7)
Total	20 (12.7)	133 (84.2)	31 (19.6)	90 (57.0)	38 (6.8)	263 (47.4)	69 (12.4)	185 (33.3)

^a Number of regurgitations including a particular type (species or order) of prey (percentage in relation to the 158 frigatebirds included in the sample).
^b Number of items of each prey type per class (percentages refer to the total 555 prey items recovered).

males: 12.5 ± 1.1 cm, $n = 6$; two-way ANOVA, effects: sex $F_{1,28} = 0.3$, $P = 0.57$; fish family $F_{2,28} = 4.5$, $P = 0.01$; interaction $F_{2,33} = 3.5$, $P = 0.04$).

Food amount (wet weight). The amount disgorged by females (96.2 ± 5.9 g, $n = 72$) was 63% more than the amount of food disgorged by males (58.8 ± 10.5 g, $n = 13$; t -test, $t_{83} = -3.1$, $P = 0.003$ on a log transformed variable).

AGE DIFFERENCES

Frequency of prey of the four most frequent orders from 75 adults (13 males and 62 females; in 10 cases, females consumed non-frequent orders) was compared to prey from 18 flying juveniles (3 juveniles did not consume the most frequent orders). Orders were consumed in different proportions ($\chi^2_5 = 438$, $P < 0.001$) and the relative consumption by adults and juveniles was also different ($\chi^2_5 = 36.1$, $P < 0.001$). At the level of the seven most frequent and abundant species, the trend was the same: adults and juveniles captured a different proportion of the different species ($\chi^2_6 = 14.4$, $P < 0.03$) and some species were consumed more frequently than others ($\chi^2_6 = 307$, $P = 0.001$).

Prey size. Length of two fish families (Serranidae and Triglidae) disgorged by 30 adults (4 males and 26 females) did not differ from that of fish disgorged by flying juveniles (adults: 13.5 ± 0.6 cm; juveniles: 14.8 ± 1.3 cm, $n = 6$; 15 juveniles consumed other rare fish families; two-way ANOVA: age $F_{1,32} = 0.2$, $P = 0.64$; fish family $F_{1,32} = 0.9$, $P = 0.35$; interaction $F_{1,32} = 1.7$, $P = 0.2$).

Food amount (wet weight). The 20 weighed juvenile regurgitations (103.2 ± 7.4 g) had on average 15% more mass than adult regurgitations (90.5 ± 5.4 g, $n = 85$) but the difference was not significant (Mann-Whitney U -test, $Z = 1.7$, $P = 0.07$). The power of an equivalent t -test was only 0.06, indicating we need to take this result with caution.

TEMPORAL VARIATION IN DIET

Not surprisingly, prey belonging to particular orders or species were consumed more often than prey from different taxa (orders: $\chi^2_6 = 443$, $P < 0.001$; species: $\chi^2_5 = 471$, $P < 0.001$). More interestingly, the six most frequent orders and the seven most frequent species of prey were caught in different proportions across the 4 months of the study (orders: $\chi^2_6 = 79$, $P =$

TABLE 2. Prey families of the items regurgitated by Magnificent Frigatebird according to habitat use. This classification is based on Ashmole (1971), Yañez-Arancibia (1988), and Drummond (unpubl. data). Demerso-benthonic, demersal, and pelagic-neritic correspond to strict bottom dwelling, bottom foraging, and surface dwelling, respectively.

Demersals	<i>n</i>	Demerso-benthonic	<i>n</i>	Pelagic-neritic	<i>n</i>
Balistidae	11	Arridae	7	Atherinidae	1
Gerreidae	2	Batrachoididae	17	Belonidae	1
Haemulidae	6	Bothidae	46	Cefalopoda	13
Sciaenidae	16	Cichlidae	1	Exocoetidae	13
Priacanthidae	1	Cynoglossidae	1	Hemiramphidae	1
		Decapoda	3	Scombridae	5
		Ophichthidae	4	Carangidae	31
		Polynemidae	10	Clupeidae	16
		Serranidae	172	Engraulidae	59
		Stomatopoda	2	Stromatidae	5
		Synodontidae	21		
		Trichiuridae	4		
		Triglidae	79		
Total ^a	36		367		147
(%)	(6.5)		(66.7)		(26.7)

^a Total number of prey is 550. In five cases the family of the prey was not determined.

0.001; species: $\chi^2_{15} = 290$, $P < 0.001$). For instance, Perciforms and Scorpaeniforms were abundant in May, whereas Clupeiforms and Batrachoidiforms were abundant in July. The mass (wet weight) of regurgitations did not change as the reproductive season progressed (April: 81.9 ± 19.2 ; May: 89.3 ± 5.5 ; June: 105.5 ± 10.0 ; July: 103.0 ± 11.7 ; Kruskal-Wallis $H = 4.5$, $P = 0.2$).

DISCUSSION

The diet of the Magnificent Frigatebird at Isla Isabel is the broadest diet reported to date for this genus. Flying fishes and squid, commonly reported as the diet of frigatebirds (Diamond 1975), were relatively uncommon prey items of the frigatebirds at Isla Isabel. In an attempt to determine the relative importance of the different feeding techniques in the diet of this bird, we classified the fish items in our sample according to their reported typical habitat in the water column. We considered three categories: organisms demerso-benthonic, demersals, and pelagic-neritic corresponding to strict bottom dwelling, bottom foraging, and surface-dwelling, respectively (Yañez-Arancibia 1988). Frigatebirds are only able to capture prey (through dipping) within the top 15 cm of the water column (Ashmole 1971) and cannot swim or dive because their feathers are not waterproof. Thus, we assumed that all the pelagic-neritic prey items came from direct surface fishing. The pe-

lagic prey reported commonly in the diet of the boobies, particularly Blue-footed Boobies, *Sula nebouxii* (H. Drummond, unpubl. data), which is the preferred kleptoparasitized bird at Isla Isabel (Osorno et al. 1992), were attributed to kleptoparasitism. Finally, typically demersal and demerso-benthonic prey were attributed to opportunist feeding near prawn-fishing boats pulling nets in an extensive zone around the island. These bottom fish are commonly described as part of the ichthyofauna associated with the shrimp fisheries (Amezcuca 1985, van der Heiden 1985).

According to the habitat categories, 6.4% of prey in the diet of this frigatebird population were organisms typically demersals, 66.9% were demerso-benthonic, and 26.3% were pelagic-neritic (Table 2). If our assumption about the prey type potentially accrued using each feeding strategy is correct, the most important source of food for this population seems to be opportunism on prawn-fishing boats. Another explanation may be that frigatebirds take advantage of the fishes driven up by predatory fishes or boobies, but this explanation hardly accounts for the frequency of bottom dwelling prey, and there are no data to support this idea. Flying fishes and squid are the expected diet of a surface feeder such as frigatebirds. However, opportunism on fisheries may be the most profitable feeding tactic in this population. Harrison et al. (1980) reported a broad diet, but still the most frequent

prey species were flying fish and squid, suggesting that direct fishing is the most important feeding technique in that population. We propose that kleptoparasitism and direct fishing can represent at best, a small fraction of the total diet of the Magnificent Frigatebird on Isla Isabel. This analysis and the poor kleptoparasitic success reported for this population (Osorno et al. 1992), suggest that kleptoparasitism is probably only an opportunistic feeding strategy for frigatebirds at Isla Isabel.

In spite of the reversed, sexual size dimorphism in the Magnificent Frigatebird, females did not capture larger prey than males, although sample sizes were small. Females did however disgorge more food than males, possibly because they are more prone to disgorge than males. They may also have greater fishing ability than males, or they may fish for longer periods of time to fill their larger crops. Greater prey loads of females are consistent with the disparate sexual roles in chick rearing reported for this species (males contribute less than 40% of the feedings to young chicks and desert when the chick is between 20 and 160 days old, whereas fledging occurs at 180 days of age on average; Durand 1992, Osorno 1996).

Differences between adults and juveniles were found in diet composition and marginally in the amount of food regurgitated, but the size of the fish families disgorged by juveniles was the same as that from adults. It is possible that flying juveniles are getting more food because they are able to capture prey by themselves at different patches as the adults do, and still complement their diet with parental feedings. This is consistent with the fact that the differences in diet composition between age classes were largely due to the disproportionately high abundance of Clupeiform fish (surface-dwelling) in juvenile crops. Age differences in foraging efficiency have been reported for this species (Gochfeld and Burger 1983) and for the Great Frigatebird (Gilardi 1994). Foraging efficiency may be claimed as responsible of the differences in diet mentioned above. However, in another study on kleptoparasitism in this population, Osorno et al. (1992) did not find foraging differences associated with age class. Greater foraging success or greater efficiency at catching prey, although expected in adults (and confirmed in some studies) under challenging conditions, may not be apparent when food is abundant. Be-

cause flying juveniles are still fed by females for more than 9 months after fledging, the expected foraging inefficiency of juveniles may not necessarily translate in their diet composition.

Although the average mass of adult regurgitations did not change through time, diet composition did. This result is not surprising, because the variety of available prey is expected to change during the breeding season, and adults may also change their foraging tactics in response to the presumably increasing demand of food from growing chicks.

ACKNOWLEDGMENTS

We thank the technical support of J. Madrid and M. E. Martínez-Delgado in prey identification. This manuscript is based on the bachelor thesis of ICA. We thank H. Drummond, J. Madrid, C. Macías-García, and F. Guillén for comments to the thesis version of this manuscript. Leticia Durand helped during the fieldwork. Fishermen from San Blas and Boca de Camichín kindly supported us in many ways. Financial support came from a grant provided by The National Geographic Society to H. Drummond. The Mexican Navy provided logistical support to the project. We thank R. Torres, C. Macías-García, and J. D. Gilardi for comments to our draft versions of this manuscript.

LITERATURE CITED

- AMEZCUA, L. F. 1985. Recursos potenciales de peces capturados con redes camarónicas en la costa del Pacífico de México, p. 39–94. *In* A. Yañez-Arancibia [ED.], Recursos pesqueros potenciales de México: la pesca acompañante del camarón. Programa Universitario de Alimentos, Inst. Cienc. del Mar y Limnol., Inst. Nal. de Pesca, UNAM, México.
- ASHMOLE, N. P. 1971. Seabird ecology and the marine environment, p. 223–286. *In* D. S. Farner and J. R. King [EDS.], Avian biology. Academic Press, New York.
- ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. *Peabody Mus. Nat. Hist. Bull.* 24:1–131.
- CRAWLEY, M. J. 1993. GLIM for ecologists. Blackwell Scientific, London.
- DIAMOND, A. W. 1973. Notes on the breeding biology and behavior of the Magnificent Frigatebird. *Condor* 75:200–209.
- DIAMOND, A. W. 1975. Biology and behaviour of frigatebirds *Fregata* spp. on Aldabra atoll. *Ibis* 117: 302–323.
- DUFFY, C. D., AND S. JACKSON. 1986. Diet studies of seabirds: review of methods. *Colonial Waterbirds* 9:1–17.
- DURAND, S. M. 1992. Dimorfismo sexual en la conducta de reproducción y la deserción del macho en *Fregata magnificens* en Isla Isabel, Nayarit. Tesis de Licenciatura, Facultad de Ciencias, UNAM, México.

- GILARDI, J. D. 1994. Great Frigatebird kleptoparasitism: sex-specific host choice and age-related proficiency. *Condor* 96:987–993.
- GOCHFELD, M., AND J. BURGER. 1983. Age-related differences in piracy of frigatebirds from Laughing Gulls. *Condor* 83:79–82.
- HARRISON, C. S., T. S. HIDA, AND M. P. SEKI. 1983. Hawaiian seabird feeding ecology. *Wildl. Monogr.* 85:1–71.
- NELSON, J. B. 1975. The breeding biology of frigatebirds—a comparative review. *Living Bird* 14:113–155.
- NELSON, J. S. 1984. *Fishes of the world*. John Wiley and Sons, New York.
- ORIAN, G. H. 1969. Age and hunting success in the Brown Pelican *Pelecanus occidentalis*. *Anim. Behav.* 17:316–319.
- OSORNO, J. L. 1996. Evolution of breeding behavior in the Magnificent Frigatebird: copulatory pattern and parental investment. Ph.D. diss., Univ. Florida, Gainesville, FL.
- OSORNO, J. L., R. TORRES, AND C. MACÍAS-GARCÍA. 1992. Kleptoparasitic behavior of the Magnificent Frigatebird: sex bias and success. *Condor* 94:692–698.
- POWER, W. H. 1980. The foraging behavior of Mountain Bluebirds with emphasis on sexual foraging differences. *Ornithol. Monogr.* 28:1–72.
- RANDALL, J. E. 1983. *Caribbean reef fishes*. T. F. H. Publications, New York.
- ROJO, A. L. 1991. *Dictionary of evolutionary fish osteology*. CRC Press, Boston.
- SAGE, B. 1995. Great Blue Herons *Ardea herodias* and Magnificent Frigatebird *Fregata magnificens* feeding on young turtles. *Bull. No. 7. Ornithol. Club* 115:68.
- SCHNEIDER, D., AND G. L. HUNT. 1984. A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska, p. 86–95. *In* D. N. Nettleship, G. A. Sanger, and P. F. Springer [EDS.], *Marine birds: their feeding ecology and commercial fisheries relationships*. Canadian Wild. Serv. Minister of Supply and Service Canada. Catalogue No. CW66-65/1984. Ottawa, Canada.
- SCHREIBER, R. W., AND R. B. CLAPP. 1987. Pelecaniform feeding ecology, p. 173–188. *In* J. P. Croxall [ED.], *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge Univ. Press, Cambridge.
- SCHREIBER, R. W., AND D. A. HENSLEY. 1976. The diets of *Sula dactylatra*, *Sula sula*, and *Fregata minor* on Christmas Island, Pacific Ocean. *Pacific Sci.* 30:241–248.
- THOMSON, D. A., L. T. FINDLEY, AND A. N. KERSTITCH. 1979. *Reef fishes of the Sea of Cortez. The rocky-shore fishes of the Gulf of California*. John Wiley and Sons, New York.
- TRIVELPIECE, W. Z., AND J. D. FERRARIS. 1987. Notes on the behavioural ecology of the Magnificent Frigatebird *Fregata magnificens*. *Ibis* 129:168–174.
- VAN DER HEIDEN, A. M. 1985. Taxonomía, biología y evaluación de la ictiofauna demersal del Golfo de California, p. 149–200. *In* A. Yañez-Arancibia [ED.], *Recursos pesqueros potenciales de México: la pesca acompañante del camarón*. Programa Universitario de Alimentos, Inst. Cienc. del Mar y Limnol., Inst. Nal. de Pesca, UNAM, México.
- WALLS, J. G. 1975. *Fishes of the Northern Gulf of Mexico*. T. F. H. Publications, New York.
- YÁÑEZ-ARANCIBIA, A. 1985. Recursos pesqueros potenciales de México: la pesca acompañante del camarón. Programa, Universitario de Alimentos, Inst. Cienc. del Mar y Limnol., Inst. Nal. de Pesca, UNAM, México.