GREAT FRIGATEBIRD KLEPTOPARASITISM: SEX-SPECIFIC HOST CHOICE AND AGE-RELATED PROFICIENCY[1]

JAMES D. GILARDI

Section of Evolution and Ecology, University of California, Davis, CA 95616

Abstract. Avian kleptoparasitism is a specialized foraging behavior requiring rapid flight speeds and extreme agility. As such, it is expected that proficiency will correlate with experience and that the size of the kleptoparasite will influence its choice of host species. I investigated age- and sex-differences in the kleptoparasitic behavior of Great Frigatebirds (*Fregata minor*) on Midway Atoll. The results indicate that chases by more than one frigatebird are more successful than solitary ones, and that success rates vary with the host pursued. In contrast with previous work, success improved with age and sub-adults were more likely to chase as part of a group than were adults. Adults showed striking sex-differences in their selection of host species, females preferring large species such as boobies and tropicbirds while males preferred the smaller noddies and terns. The role of these sex-differences in the evolution of sexual size dimorphism is discussed. Finally, since marked breeding individuals were not observed in kleptoparasitic events near the colony, this foraging mode is apparently not important to breeding birds in this population. However, in some cases the frigatebird kleptoparasitism may directly influence the behavioral patterns and the survival of host individuals.

Key words: Great Frigatebird; Fregata minor; *kleptoparasitism; age effects; sex-differences; sexual dimorphism.*

INTRODUCTION

The acquisition of previously caught prey, or kleptoparasitism, is particularly common in the Fregatidae, Laridae, and Stercorariidae (Brockmann and Barnard 1979, Furness 1987). Near many tropical seabird colonies, frigatebirds pursue a variety of species (hosts), frequently catching them by the wing or tail, encouraging them to regurgitate prey items. In this specialized foraging mode, many factors potentially effect the success of such attempts: i.e., the frigatebird's assessment of a host's alertness, fullness of crop, agility, location relative to land, as well as its own capabilities of speed and agility, and the presence of potentially competing frigatebirds.

In species with such highly skilled foraging techniques, performance typically improves with age and experience (Orians 1969, Carroll and Cramer 1985). Moreover, aerodynamic theory predicts that physical parameters such as mass wing-loading constrain both agility and peak dive velocity in birds (Andersson and Norberg 1981). For frigatebirds then, it is expected that success of kleptoparasitic events should improve with age and that success will vary with the size of

both the parasite and host. As frigatebirds show delayed plumage maturation and are sexually dimorphic in size and plumage (*Fregata minor*: Females 1,800 g, males 1,000 g, Schreiber and Schreiber 1988), predictions of age- and size/sex-differences are readily testable.

In studies that have looked for age-differences in the success of kleptoparasitism by Magnificent Frigatebirds (*Fregata magnificens*), results were either equivocal or no differences in success were detected (Gochfeld and Burger 1981, Gibbs and Gibbs 1987, Osorno et al. 1992). These findings contradict a wealth of evidence on avian foraging behavior demonstrating that proficiency improves with age (Recher and Recher 1969, Orians 1969, Morrison et al. 1978, Carroll and Cramer 1985, Weathers and Sullivan 1989).

Sex-differences in kleptoparasitic behavior have been observed in several frigatebird species (Verner 1965, Diamond 1975, Gochfeld and Burger 1981, Gibbs and Gibbs 1987, Osorno et al. 1992). In general, one sex performs virtually all of the kleptoparasitic behavior although this varies with the colony and species of frigatebird. For instance, in Magnificent Frigatebirds females were more likely to chase boobies in Belize (Verner 1965), while in the Galápagos males were the more common kleptoparasites (Gibbs and Gibbs 1987).

TABLE 1. Breeding populations, frequency of attack, and mass of potential host species on Midway Atoll, 1989–1991.

Species	Number of indiv.	Frequency of attack[+]	Mass g (range)*
Black Noddy		rare	
(*Naous tenurostris*)	3,000*		108 (85–133)
Brown Noddy		frequent	
(*Anous stolidus*)	5,000*		205 (153–275)
Grey-backed Tern		infrequent	
(*Sterna lunata*)	1,000†		146 (115–177)
Laysan Albatross		very rare	
(*Diomedea immutabilis*)	500,000*		2,400 (1,900–3,075)
Red-footed Booby		frequent	
(*Sula sula*)	1,000*		1,110 (905–1,400)
Red-tailed Tropicbird		very freq.	
(*Phaethon rubricauda*)	30,000†		624 (540–750)
Sooty Tern		very freq.	
(*Sterna fuscata*)	100,000†		198 (153–320)
Wedge-tailed Shearwater		rare	
(*Puffinus pacificus*)	400†		388 (320–510)
White Tern		rare	
(*Gygis alba*)	20,000†		111 (92–139)

[+] A rough indicator of how often this type of chase is observed.
* Data from Harrison et al. (1983).
† Personal observation, 1989–1991.

In contrast, on Midway Atoll, all sexes and ages of Great Frigatebird commonly kleptoparasitize a great diversity of host species varying in size from Grey-backed Terns (100 g) to Laysan Albatross (2,400 g; Table 1). This study focuses on the four most commonly chased species: Brown Noddies, Sooty Terns, Red-tailed Tropicbirds, and Red-footed Boobies. During the frigatebirds' breeding seasons of 1989–1991, I evaluated age and sex-related differences in kleptoparasitic behavior and explored the importance of this behavior to breeding individuals.

STUDY AREA AND METHODS

Midway Atoll (28° N, 178° W) is near the northwest end of the Hawaiian leeward chain and is comprised of a fringing reef 8–10 km in diameter surrounding a shallow lagoon and three small islands. The Great Frigatebird population numbers 500–900 non-breeders and a colony of 50–80 breeding pairs (pers. observ. 1989–1991). Midway Atoll is also the breeding site for a large and diverse community of potential kleptoparasitic hosts (Table 1).

I observed kleptoparasitic events from several locations on the three islands, from June–August 1989, May–July 1990, and June–August 1991, using 9× binoculars to age and sex individuals based on plumage characters (Harrison 1985). For each kleptoparasitic event the following data were collected: number of individuals involved, their sexes and ages, individual marks (see below), success of the event, and the host species. As the plumage of young frigatebirds is highly variable, I disregarded distinctions between sub-adult, immature, and juvenile birds, considering them all 'sub-adults' for the purposes of this study. Kleptoparasitic attempts lasting longer than one second were deemed chase events and I considered events successful when the frigatebird retrieved prey either in flight or from the water. For group events, only frigatebirds that clearly acquired prey were considered successful.

In 1990, to determine whether breeding adults were responsible for a significant portion of the kleptoparasitism, 53 breeders were individually marked with coded notches in the outer rectrices. These marks were observable when the birds were in flight, and allowed determination of both breeding status and individual recognition. Although at times these birds represented ≈5% of both roosting and breeding frigatebirds, the fluctuating size of the roosting population and accumulation of the marked group over time prevent knowing the exact proportion of marked individuals. These observations therefore were not treated statistically.

TABLE 2. Success of Great Frigatebird kleptoparasitic events by all ages and sexes, success/total (%).

	Brown Noddies	Sooty Terns	Red-tailed Tropicbirds	Red-footed Boobies
Females				
Solitary	†	4/14 (28.6)	16/95 (16.8)	2/10 (20.0)
Group	†	17/25 (68.0)	47/92 (51.1)	4/8 (50.0)
Males				
Solitary	2/12 (16.7)	15/32 (46.9)	8/60 (13.3)	†
Group	17/19 (89.5)	24/39 (61.5)	2/13 (15.4)	†
Sub-adults				
Solitary	†	2/10 (20.0)	0/21 (0.0)	0/2 (0.0)
Group	5/6 (83.3)	9/28 (32.1)	7/24 (29.2)	†

† Not observed.

As the frigatebirds involved in kleptoparasitic events were from a large pool of individuals commuting to or from the colony, I assume that few events involved the same individual (parasite or host). All variables used in the analysis were categorical in nature: [A] age/adult-sex (sub-adult, male, female), [G] association with other frigatebirds in a chase (solitary, group), [H] host species (the four most common were analyzed, BRNO, SOTE, RTRR, RFBO, see Table 1), and [S] success of the events (+ or −).

I analyzed the data with log-linear models using the BMDP 4F procedure (Dixon 1990) and selected the best model with a combination of forward selection and backward deletion (Agresti 1990). Similar to other stepwise methods, the forward selection procedure adds terms to the model starting with the most statistically significant and stopping at a selected level of significance ($P = 0.05$). The first model includes all the data to consider general effects. To look specifically at age and sex effects, I ran two subsequent models, an age model comparing sub-adults and adults, and a gender model which explores sex-differences comparing only males and females. For each model, the significance of each term and the selected model is presented, and to facilitate interpretation, I also present some of the data in graphical form, collapsing across one or more variables.

RESULTS

Frigatebirds pursued a number of host species, the ages and sexes showing considerable variation in proficiency, selection of host species, and whether to chase as part of a group or solitarily (Tables 1, 2). In general sub-adults were less successful than adults and chased more often as part

of a group. Females clearly preferred the larger host species, whereas males preferred smaller hosts.

In the general effects model, forward selection indicated that all two-way interactions were significant and backward deletion included an additional three-way interaction [SHG] (Table 3A). This suggests that the success of kleptoparasitic events was affected by both the host species pursued and whether the frigatebird chased solitarily or with others (Fig. 1). Group events were more successful than solitary ones, although as the three way interaction suggests, this varied as a function of host species. As both age and gender effects were significant ([SA] [HA] [GA]), they were explored directly in the two subsequent models.

In the age model both selection procedures yielded the same result: all but one two-way interaction were significant ([AS] [AG] [AH] [SH] [SG], Table 3B). Sub-adults differed from adults in three ways: the success of their attempts, the frequency with which they chased as part of a group, and the host species they selected (Table 2). Sub-adults were less successful than adults in both solitary and group events and were also more likely to chase as part of a group. In comparison with adults, they also pursued tropicbirds and noddies somewhat more often than the other species.

In the gender analysis, both selection procedures converged on the same model which included all but one two-way interaction: [SH] [SG] [HG] [HA] [GA] (Table 3C). Female and male Great Frigatebirds showed dramatic differences in the species they chose to parasitize (Fig. 2), females preferring the larger boobies and tropicbirds while males selected terns and noddies

TABLE 3. Analysis of log-linear models of Great Frigatebird kleptoparasitism on Midway Atoll. [S] = success, [H] = host species, [G] = group vs. solitary, [A] = age or adult gender.

A. GENERAL MODEL

Effect	df	Partial association	
		χ^2	P
[SH]	3	25.16	0.0000
[SG]	1	47.84	0.0000
[SA]	2	14.23	0.0008
[HG]	3	14.55	0.0022
[HA]	6	121.69	0.0000
[GA]	2	25.73	0.0000
[SHG]	3	7.04	0.0705
[SHA]	6	4.63	0.5920
[SGA]	2	2.21	0.3318
[HGA]	6	6.05	0.4176
[SHGA]	6	5.31	0.5041

forward selection [SH] [SG] [SA] [HG] [HA] [GA]
backward deletion [SHG] [SA] [HA] [GA]

B. AGE MODEL

Effect	df	Partial association	
		χ^2	P
[SH]	3	25.39	0.0000
[SG]	1	52.66	0.0000
[SA]	1	12.86	0.0003
[HG]	3	5.89	0.1169
[HA]	3	8.72	0.0332
[GA]	1	11.22	0.0008
[SHG]	3	7.37	0.0609
[SHA]	3	1.08	0.7828
[SGA]	1	0.02	0.8949
[HGA]	3	2.29	0.5137
[SHGA]	3	2.01	0.5702

model selected by both methods: [SH] [SG] [SA] [HA] [GA]

C. GENDER MODEL

Effect	df	Partial association	
		χ^2	P
[SH]	3	20.29	0.0001
[SG]	1	41.62	0.0000
[SA]	1	1.01	0.3160
[HG]	3	10.31	0.0161
[HA]	3	111.54	0.0000
[GA]	1	13.20	0.0003
[SHG]	3	7.72	0.0521
[SHA]	3	3.97	0.2653
[SGA]	1	3.29	0.0698
[HGA]	3	4.94	0.1765
[SHGA]	3	2.04	0.5644

model selected by both methods: [SH] [SG] [HG] [HA] [GA]

more frequently. Also, males pursued hosts solitarily more often than females (Table 2).

By the end of the 1990 season, individually marked birds comprised roughly five percent of all frigatebirds and 30–50% of the breeding birds on Midway. While the marked breeders were frequently observed, they were never seen in kleptoparasitic events.

DISCUSSION

These results provide insight into the types of decisions made by the various ages and sexes of Great Frigatebirds participating in kleptoparasitic behavior. Independent of the age and sex of the frigatebirds, the success of kleptoparasitic events was affected by both the host species pursued and whether the frigatebird chased solitarily or with other conspecifics. In general group chases were more successful than solitary ones and smaller hosts were more easily kleptoparasitized than larger ones. The frequency of the less successful chase events (i.e., solitary attempts or large hosts) may be maintained by trade-offs in the benefits of a given chase type. That is, chasing as part of a group yields a partial reward on average, and second, higher probability of success on smaller hosts may be countered with larger rewards from large hosts. As both host availability and potential competitors/conspirators are spatially and temporally variable, the most effective pursuit strategy is likely to vary accordingly.

Adults were more often successful than sub-adults in both group and solitary chase events, supporting the hypothesis of age-related foraging proficiency. Given the delayed breeding and an unpredictable food supply in this species (Nelson 1975), this age difference is predicted by both theoretical and empirical work (Recher and Recher 1969, Orians 1969, Morrison et al. 1978, Gochfeld and Burger 1981, Carroll and Cramer 1985, Hesp and Barnard 1989, Tuljapurkar 1990). It is surprising that other studies of frigatebird kleptoparasitism have not found such differences (Gochfeld and Burger 1981, Gibbs and Gibbs 1987, Osorno et al. 1992), and it remains to be seen whether more extensive work on Magnificent Frigatebirds will concur with the present study.

The age × group interaction suggests that by chasing more often in groups, sub-adults may compensate for their inferior foraging ability. Many chases are of sufficient duration that the sub-adults might assess the likelihood of success, and then join the event or not. Brown Noddies often tagged along on such longer chases as 'secondary kleptoparasites' with surprisingly fre-
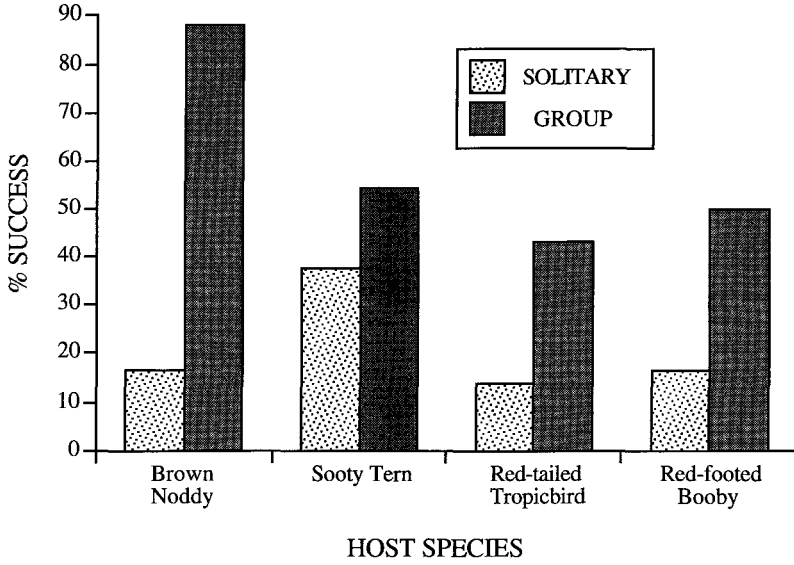
FIGURE 1. The effects of host species and group size on the success of kleptoparasitic attempts by Great Frigatebirds at Midway Atoll.

quent success. Further studies on the age variation in the sequence of frigatebirds joining the group might shed light on this question.

The striking sex-difference in host choice suggests a correlation between the size of the frigatebird and the size of the preferred host species. The fact that the smaller males selected the smaller hosts and the larger females selected correspondingly larger hosts is consistent with other work on kleptoparasitism (Kushlan 1978, Tershey and Breese 1990, but see Duffy 1980). It is tempting to consider this trend in host size selection as a contributing factor to the reversed-size sexual dimorphism in Fregatidae, the origin
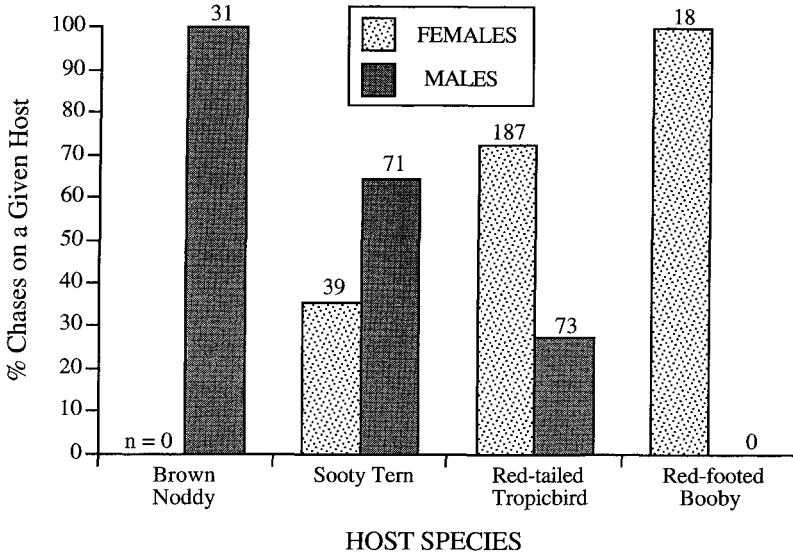

FIGURE 2. Sex-differences in host choice by adult Great Frigatebirds at Midway Atoll.

of which remains an open question (Pennycuick
1983, Schreiber and Schreiber 1988, Gilardi
1992). Since frigatebirds interact with hosts of
varying body-sizes both at sea and near the col-
ony, the sexes could potentially partition the host
community, each specializing on a different size
range thereby reducing intrapair competition.
However, the colonial nature of both frigatebirds
and their victims undermine the benefits of this
type of niche partitioning which has been ap-
plied, albeit inconclusively, to terrestrial raptors
which are generally territorial (cf. Andersson and
Norberg 1981).

Rather than causing the size-dimorphism, sex-
differences in host choice may themselves be the
result of a dimorphism resulting from other caus-
es. Possibly more important to the evolution of
dimorphism are the unusual sex-differences in
chick provisioning shown by Great and Magnif-
icent Frigatebirds and that males may be annual
breeders and females biennial (Diamond 1972,
pers. observ.).

Finally, the relationship between host size
preference and the size of the frigatebird is not
perfect. Despite the similarity in mass of the Sooty
Terns and Brown Noddies, females frequently
chased the former but never the latter. This may
result from differences in wing-loading as the terns
soar almost exclusively whereas noddies rarely
do so (pers. obsver.). As wing-loading affects both
agility and dive velocity (Andersson and Norberg
1981), analysis of this character in both frigate-
birds and their hosts may yield additional under-
standing of the observed sex differences in host
choice.

Observations of marked individuals suggest
that kleptoparasitism near the colony is not an
important source of nutrition for breeding frig-
atebirds at Midway Atoll. Although frigatebird
kleptoparasitism behavior is not often observed
at sea (pers. observ.), these data do not address
its importance away from the colony. Also, klep-
toparasitism may be important to a small num-
ber of specialist individuals, breeding or other-
wise, which this study might very well have
missed. In fact, Vickery and Brooke (1994) sug-
gest that kleptoparasitism in this species could
theoretically account for as much as 40% of the
daily energy expenditure of some individuals.

From the hosts' perspective however, klepto-
parasitism may cause the loss of a prey load,
changes in diurnal behavior patterns (cf. Emms
and Verbeek 1991), and even fatal injuries. Al-
though the loss of an occasional meal seems un-
likely to reduce reproductive success, it has been
suggested that kleptoparasitism by frigatebirds is
responsible for the nocturnality of Swallow-tailed
Gulls (Creagrus furcatus, Hailman 1964, Snow
and Snow 1968). Indeed, Sooty Terns and Brown
Noddies which are preferred hosts on Midway
also feed their chicks predominantly at night
(Brown 1975). Although suggestive, this pattern
would require extensive investigation before
drawing conclusions on causal links. Finally, I
encountered numerous Sooty Terns and a trop-
icbird with broken or severed wings which could
only have been caused by frigatebirds. Clearly,
kleptoparasite-induced mortality would have
major fitness consequences for hosts, particularly
in tropical seabirds where adult survival is an
important life history character.

ACKNOWLEDGMENTS

LITERATURE CITED

AGRESTI, A. 1990. Categorical data analysis. John
Wiley and Sons, New York.
ANDERSSON, M., AND R. A. NORBERG. 1981. Evo-
lution of reversed sexual size dimorphism and role
partitioning among predatory birds, with a size
scaling of flight performance. Biol. J. Linnean Soc.,
Lond. 15:105–130.
BROCKMANN, H. J. AND C. J., BARNARD. 1979. Klep-
toparasitism in birds. Anim. Behav. 27:487–514.
BROWN, W. Y. 1975. Parental feeding of young Sooty
Terns (Sterna fuscata) and Brown Noddies (Anous
stolidus) in Hawaii. J. Anim. Ecol. 44:731–742.
CARROLL S. P., AND K. L. CRAMER. 1985. Age dif-
ferences in kleptoparasitism by Laughing Gulls
(Larus atricilla) on Brown Pelicans (Pelicanus oc-
cidentalis). Anim. Behav. 33:201–205.
DIAMOND, A. W. 1972. Sexual dimorphism in breed-
ing cycles and unequal sex ratio in Magnificent
Frigatebirds. Ibis 114:395–398.
DIAMOND, A. W. 1975. Biology and behaviour of
frigatebirds Fregata spp. on Aldabra atoll. Ibis 117:
302–323.
DIXON, W. J. 1990. BMDP statistical software man-
ual. Univ. of California Press, Berkeley.
DUFFY, D. C. 1980. Patterns of piracy by Peruvian
seabirds: a depth hypothesis. Ibis 122:521–525.

EMMS, S. K., AND N.A.M. VERBEEK. 1991. Klepto-parasite avoidance tactics of pigeon guillemots, *Cepphus columba*. Anim. Behav. 41:907–909.

FURNESS, R. W. 1987. Kleptoparasitism in seabirds, p. 71–100. *In* Croxall, J. P. [ed.], Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge.

GIBBS, H. L., AND J. P. GIBBS. 1987. Prey robbery by non-breeding Magnificent Frigatebirds (*Fregata magnificens*). Wilson Bull. 99:101–104.

GILARDI, J. D. 1992. Sex-specific foraging distributions of Brown Boobies in the eastern tropical Pacific. Colonial Waterbirds 15:148–151.

GOCHFELD, M., AND J. BURGER. 1981. Age-related differences in piracy of frigatebirds from laughing gulls. Condor 83:79–82.

HAILMAN, J. P. 1964. The Galápagos Swallow-tailed Gull is nocturnal. Wilson Bull. 76:347–254.

HARRISON, C. S., T. S. HIDA, AND M. P. SEKI. 1983. Hawaiian seabird feeding ecology. Wildl. Monogr. 85:1–71.

HARRISON, P. 1985. Seabirds, an identification guide. Houghton Mifflin, Boston.

HESP, L. S., AND C. J. BARNARD. 1989. Gulls and plovers: age-related differences in kleptoparasi-tism among Black-headed Gulls (*Larus ridibun-dus*). Behav. Ecol. Sociobiol. 24:197–304.

KUSHLAN, J. A. 1978. Nonrigorous foraging by robbing egrets. Ecology 59:649–653.

MORRISON, M. L., R. D. SLACK, AND E. SHANLEY, JR. 1978. Age and foraging ability relationships of Olivaceous Cormorants. Wilson Bull. 90:414–422.

NELSON, J. B. 1975. The breeding biology of frigate-birds—a comparative review. Living Bird 14:113–155.

ORIANS, G. H. 1969. Age and hunting success in the Brown Pelican (*Pelicanus occidentalis*). Anim. Behav. 17:316–319.

OSORNO, J. L., R. TORRES, AND C. MACIAS-GARCIA. 1992. Kleptoparasitic behavior of the Magnificent Frigatebird: sex bias and success. Condor 94:692–698.

PENNYCUICK, C. J. 1983. Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens, Pelicanus occidentalis,* and *Coragyps atratus.* J. Exp. Biol. 102:307–325.

RECHER, H. F., AND J. A. RECHER. 1969. Comparative foraging efficiency in adult and immature Little Blue Herons. Anim. Behav. 17:320–322.

SCHREIBER, E. A., AND R. W. SCHREIBER. 1988. Great frigatebird size dimorphism on two central Pacific atolls. Condor 90:90–99.

SNOW, B. K., AND D. W. SNOW. 1968. Behavior of the Swallow-tailed Gull of the Galápagos. Condor 70:252-264.

TERSHEY, B. R., AND BREESE, D. 1990. The influence of sexual dimorphism on kleptoparasitism of Blue-footed Boobies by Brown Boobies. Can. J. Zool. 68:197–199.

TULJAPURKAR, S. 1990. Delayed reproduction and fitness in variable environments. Proc. Natl. Acad. Sci. USA 87:1139–1143.

VERNER, J. 1965. Flight behavior of the Red-footed Booby. Wilson Bull. 77:229–234.

VICKERY, J. A., AND M. DE L. BROOKE. 1994. The kleptoparasitic interactions between Great Frigatebirds and Masked Boobies on Henderson Island, south Pacific. Condor 96:331–340.

WEATHERS, W. W., AND K. A. SULLIVAN. 1989. Juvenile foraging proficiency, parental effort and avian reproductive success. Ecol. Monogr. 59:223–246.