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KLEPTOPARASITIC BEHAVIOR OF THE MAGNIFICENT FRIGATEBIRD: SEX BIAS AND SUCCESS[1]

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Abstract. Kleptoparasitism (the stealing of food) by the Magnificent Frigatebird (*Fregata magnificens*) was recorded over three breeding seasons at Isla Isabel, Nayarit, México. Observation of chases on the principal target, the Blue-footed Booby (*Sula nebouxii*) were made in front of their joint breeding colonies. Most attacks were conducted by female and juvenile frigatebirds; male frigatebirds were not kleptoparasitic near their breeding colony. The proportion of chases provoking the target to regurgitate (success rate) was low (0.059) and only on 67% of those cases did the frigatebird get any food. Attacks were more frequent in the afternoon, when the boobies were returning to their breeding colony and were likely to be transporting food. In addition, frigatebirds may be evaluating the target's profitability in short chases, since longer chases provided a proportionately higher success. If so, the success reported above underestimates the profitability of these behaviors because it considers all chases equally. Group pursuits were three times more successful than those performed by single individuals. We did not find differences in the success and sexual bias in the kleptoparasitic tendencies between winter (frigatebirds' courtship and laying season) and spring (frigatebirds' feeding season) observations.

Key words: Kleptoparasitism; frigatebirds; foraging success; foraging sexual bias; seabirds' diet.

INTRODUCTION

Kleptoparasitism, or piracy, is defined as the stealing of food (Curio 1976, Brockmann and Barnard 1979, Barnard 1984). This is a foraging pattern which reduces the cost (energy and risks) associated with direct foraging, but requires that the pirates successfully out-maneuver their victims (hereafter referred to as targets; Gochfeld and Burger 1983, Barnard 1984). If kleptoparasitism produces a greater return or a lower cost than direct foraging, natural selection should favor such specialization (Barnard 1984, Vollrath 1984). Brockmann and Barnard (1979) concluded that kleptoparasitism may be profitable when several ethological and ecological factors exist: (1) the pirates need to be opportunistic feeders with aerobatic flying capabilities, (2) large host concentrations in open habitats must occur (also Paulson 1985), and (3) hosts must predictably transport large quantities of food to a fixed place. In addition, the incidence of kleptoparasitism in seabirds seems to be more frequent in surface-feeding seabirds than in species that dive or plunge to get their food (depth hypothesis; Duffy 1980, 1982).

For some species of birds, piracy contributes significantly to an individual's diet (Brockmann and Barnard 1979, Furness 1987, Thompson 1986). Piracy seems to disproportionately occur in raptors and marine birds (Brockmann and Barnard 1979). In frigatebirds (*Fregata* spp.) kleptoparasitism is mainly performed on boobies (*Sula* spp.). It has often been reported as an important alternative to direct fishing by frigatebirds (Nelson 1975). In fact, the highly aerobatic capabilities of these seabirds have been interpreted as an adaptation to kleptoparasitism (Nelson 1975, Brockmann and Barnard 1979, Furness 1987). However, the scanty evidence indicates poor performance of frigates in piracy. Furness (1987) found no difference in the success rate of frigatebirds, skuas, jaegers and generalist pirates such as gulls. Some incidental reports indicate low success rate as well as differences in frequency and success of piracy between males and females, and among different age classes and localities; such reports do not mention the context in which kleptoparasitism occurs.

Theory predicts that frigatebirds could reduce costs by evaluating the profitability of potential targets, and by searching for targets when and where there is a high probability of them carrying food (Furness 1987). Here we report on sexual

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bias, profitability, success rates and mechanisms to reduce costs of piracy by frigatebirds.

On Isla Isabel, kleptoparasitism by the Magnificent Frigatebird (*Fregata magnificens*) on the Blue-footed Booby (*Sula nebouxii*) combines characteristics suggested by Brockmann and Barnard (1979) as likely to promote the evolution of avian piracy. Frigatebirds harass the target by chasing closely, often pulling its tail feathers, thus unbalancing and frequently causing the victim to fall into the sea. If the target regurgitates, the pirate stops pursuit and takes the food before it falls into the sea. This style of piracy contrasts with the stealing-from-the-beak technique used by frigatebirds against other species (e.g., gulls; Gochfeld and Burger 1983).

STUDY AREA AND METHODS

We recorded the kleptoparasitic behavior of the Magnificent Frigatebird on Isla Isabel, Nayarit, México (21°51'N, 105°54'W) in three annual visits totaling 19 days (13–19 December 1985, 19–26 December 1986 and 7, 8, 10 and 11 June 1987). These birds breed on Isla Isabel together with three species of boobies and other Pelecaniform birds. The observations were made from two sites on the east side of the island: Las Monas Beach, in front of a breeding colony of Blue-footed Boobies (1985, 1986 and 1987), and the Acantilado Oriental (1985 and 1987), in front of a roosting place for Blue-footed and Brown Boobies. Pairs of observers (observer and recorder) recorded all chases that occurred over the beach and sea within 200 m of the observation points, where virtually all the interactions occur. A chase was defined as any interaction starting with a frigatebird positioning itself behind, and subsequently following closely, any flying bird. Continuous observations were made from 07:30 to 17:30 hr using 8 × 30 or 8 × 50 binoculars. Teams alternated every two hours. Distinct patterns of plumage coloration allowed us to make a reliable assessment of the age class and sex of the pirate in each chase (Nelson 1975). Regurgitation by the target was used as the criterion of success. For each chase we recorded time of day, age and sex of pirate (male, female or juvenile), species of the target (also from plumage), and success or failure of chase. In the case of successful chases, we recorded which bird(s) benefited by obtaining all or part of the pirated food. Additionally, we recorded the duration of the chase from its initiation until successful piracy or until the parasite moved out of the target's path. In some instances, the chased bird fell into the sea. When this happened, the frigatebird often circled over it for several seconds, and sometimes resumed the chase if the chased bird attempted to fly. In these cases, a chase was judged to have terminated when the frigatebird finally left the target. From 1986, we differentiated those chases performed by single birds from those carried out by groups (group size, $n \geq 2$), although we were unable to accurately assess the number of frigatebirds on a group chase.

In 1987, we also recorded the frequency of arrivals and departures of Boobies to and from their breeding area and roosting place.

TABLE 1. Absolute frequency (percent) of chases by frigatebirds on several species of seabirds found on Isla Isabel.

Identity of the targets*	Frequency	(%)
Magnificent Frigatebird (*Fregata magnificens*)	5	(0.24)
Blue-footed Booby (*Sula nebouxii*)	1,723	(84.13)
Brown Booby (*S. leucogaster*)	179	(8.74)
Heermann's Gull (*Larus heermanni*)	107	(5.22)
Brown Pelican (*Pelecanus occidentalis*)	12	(0.59)
Sooty Tern (*Anous stolidus*)	3	(0.15)
Tropic Bird (*Phaethon aethereus*)	19	(0.93)
Red-footed Booby (*S. sula*)	0	(0.00)
Total	2,048	

* Species are arranged in order of decreasing abundance on the Island. There are no reliable figures on the numbers of birds of any species on Isla Isabel, however, the first three species are counted by the thousands (the population of Magnificent Frigatebird may reach 10,000 birds), whereas less than fifty birds are found of the last two species.

RESULTS

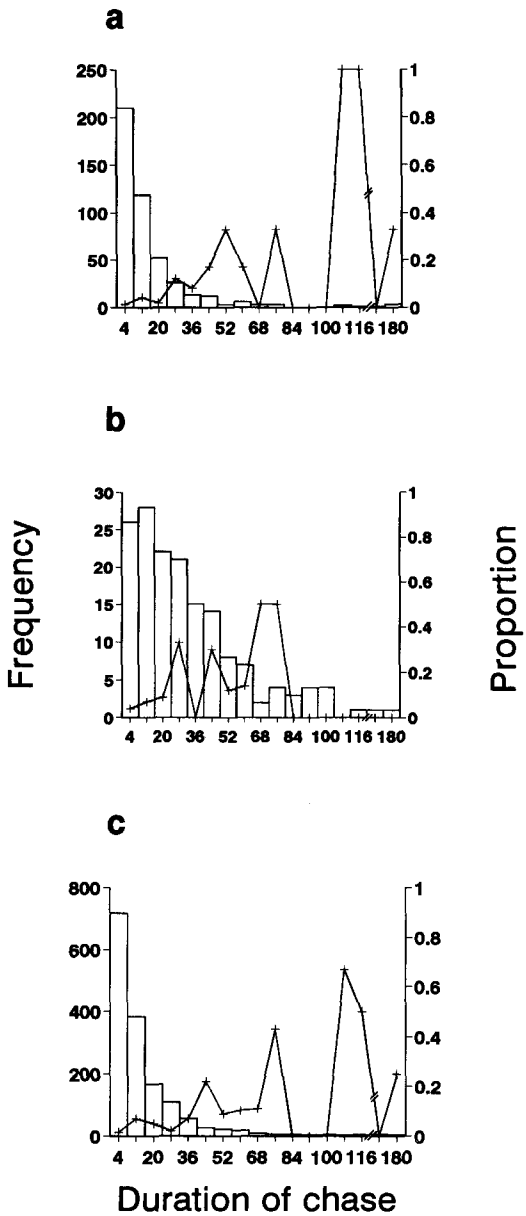
SPECIES CHASED AND SUCCESS RATE

In total we recorded 2,048 kleptoparasitic chases. The most frequent targets were sulids, mainly the Blue-footed Booby; gulls and other seabirds were attacked much less frequently (Table 1). Frigatebirds were equally successful in robbing the two most common species of sulids (Blue-footed Booby, $n = 1{,}723$, 5.6% successful; Brown Booby *S. leucogaster*, $n = 179$, 5.0% successful; G-test $= 0.1$, df $= 1$, $P > 0.05$).

Piracy near the island against Blue-footed Boo-

TABLE 2. Frequency of success (%) of chases on Blue-footed Boobies by sex and age class of the frigatebirds.

Breeding season	Year	Females		Males		Juveniles	
		Success	*n*	Success	*n*	Success	*n*
Early	1985	48 (5.1)	938	0	4	1 (1.3)	76
Early	1986	27 (7.1)	379	0	4	2 (15.3)	13
Late	1987	16 (6.7)	236	0	0	6 (3.7)	162
Both	Total	91 (5.8)	1,553	0	8	9 (3.6)	251



bies was mostly carried out by females (n = 1,553) and juveniles (n = 162). Males only rarely chased other birds near their breeding area (n = 8; Table 2). We have no data on whether some individuals had a greater tendency to engage in kleptoparasitism than others, nor the number of potential pirates simultaneously present at the observation sites.

Absolute success of kleptoparasitism was low; only 91 of the 1,553 chases initiated by females against Blue-footed Boobies resulted in regurgitation (5.8%), and only 58 of these cases resulted in gain for the pirate. There was no significant difference between the value for females and the mean value (3.7%) for juveniles (G-test = 1.28, df = 1, $P > 0.05$).

ATTACKS ON BLUE-FOOTED BOOBY

Considering only the successful chases by females on Blue-footed Boobies (n = 91), frigatebirds that joined but were not necessarily present at the onset of the chase benefited in 22 instances (24.2%). Heermann's Gull (*Larus heermanni*), reported elsewhere to be both targets and parasites of frigatebirds (Brockmann and Barnard 1979), joined the chases opportunistically at Isla Isabel, obtaining a substantial proportion of the rewards (43 of 91 successful chases, 43.3%).

Considering all the chases performed by adult females against Blue-footed Boobies (n = 1,153), frigatebirds were more successful in front of the

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FIGURE 1. Frequency of piracy (bars) and relative success (line) as a function of the duration of the chase. Chases by single birds (a) and groups (b), distinguished only in the records of 1986 and 1987, did not differ significantly in their time distributions (Kolmogorov-Smirnov test, D = 0.2353, n = 17 time-intervals, $P > 0.1$). In (c), all the data from 1985, 1986 and 1987 are plotted together; the proportion of success in long chases is higher than in short ones, but the small numbers of lengthy interactions render non-significant the correlation (Spearman's ρ = 0.158, $P > 0.1$).

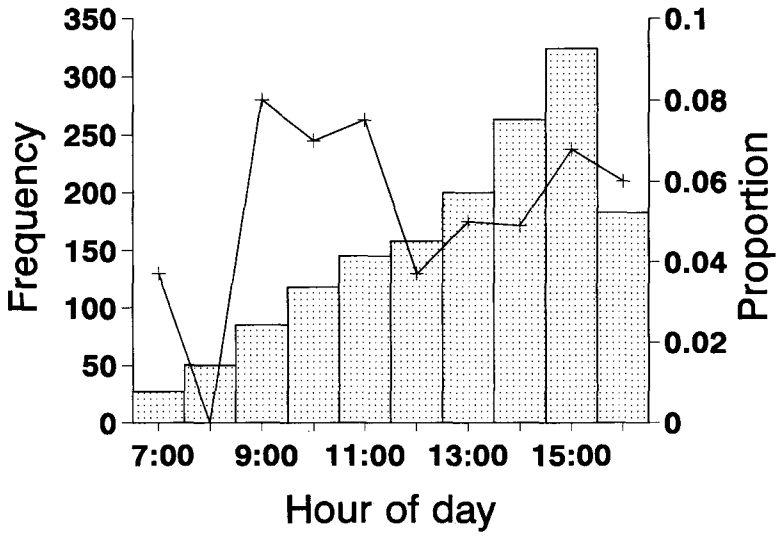

FIGURE 2. Frequency of piracy (bars) and proportion of success (line) by hour of day.

target's breeding place (7.0%, n = 1,091) than in front of the roosting place (3.0%, n = 462; G-test = 9.54, df = 1, $P < 0.01$). Additionally, group attacks were three times more successful than the ones conducted by single individuals (group 15.0%, n = 140; single 5.1%, n = 432; G-test = 12.28, df = 1, $P < 0.001$). Most chases (46.2%) between female frigatebirds and Blue-footed Boobies were of short duration (range 1–8 sec). However, relative success was greater in longer chases (Fig. 1), a pattern that was apparent for both chases made by single birds and by groups (Fig. 1a, b).

Chases were more frequent in the afternoon, but the proportion of success was independent of both frequency of chases (Spearman's $\rho = 0.15$, $P > 0.05$) and hour of occurrence ($\rho = 0.17$, $P > 0.05$; Fig. 2). Frigatebird piracy concentrated on boobies arriving at the breeding colony ($\rho = 0.71$, $P < 0.022$) rather than those departing for the sea ($\rho = -0.74$, $P < 0.015$; Fig. 3a). Boobies arriving are more likely to be returning with food (Anderson and Ricklefs 1987). At the boobies' roosting place, the activity patterns of both parasite and target were different (Fig. 3b). Here the correlations between the frequency of piracy and the frequencies of arrivals or departures of targets were not significant (arrivals: $\rho = -0.12$, $P > 0.05$; departures: $\rho = -0.27$, $P > 0.05$). The proportion of successful chases did not vary significantly between the early (6.0%, n = 1,317) and late (7.3%, n = 236; G-test = 0.42, df = 1, $P > 0.05$) part of the frigatebird breeding season.

DISCUSSION

SPECIES OF BIRD CHASED

The bias toward attacking Blue-footed Boobies is probably related to the abundance of these birds on Isla Isabel, especially near the observation sites. The Red-footed Booby (*S. sula*), the most common reported target of *F. magnificens* elsewhere (Nelson 1975, Diamond 1975), is very rarely found on Isla Isabel (10 nests in 1987, pers. observ.).

Although there are reports of differential piracy success of frigatebirds on several species of seabirds in other locations (Nelson 1975, Diamond 1975), our data show similar success rates against Blue-footed and Brown Boobies, probably suggesting that these two species pose similar robbing difficulties.

SEXUAL BIAS IN PIRACY

The sexual bias in the tendency of frigatebirds to chase sulids near Isla Isabel does not seem related to the disproportionate abundance of females in the colony. Adult males were not recorded to engage in kleptoparasitism in December when the sex ratio is nearly 1, nor in June when the sex ratio is strongly female-biased as a result of seasonal male nest-desertion (Nelson

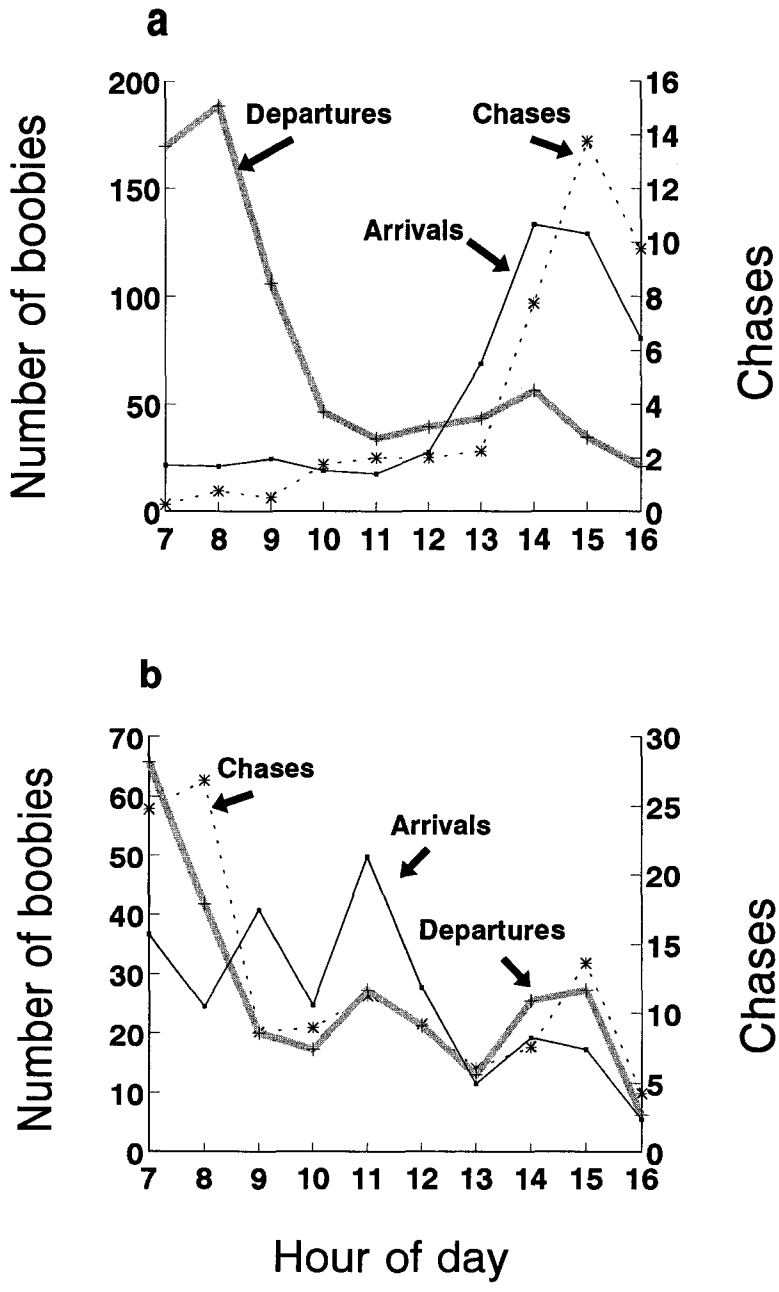

FIGURE 3. Mean frequencies of arrivals and departures of the Blue-footed Boobies to/from (a) their breeding colony, and (b) a much visited roosting site; and mean frequency of frigatebird chases over the day. Data presented are 4-day averages.

1975, Trivelpiece and Ferraris 1987). Sex bias may occur because males tend to feed far from their nesting place, while females prefer to feed close to their breeding colony (Gochfeld and Burger 1983). Since we did not observe feeding at other places, we have no data to test this idea. Females may parasitize in response to the chicks' need to be fed frequently, thus making it prof-

itable to fly a few tens of meters off the nest to chase a passing booby.

ADULTS AND JUVENILES

In contrast to evidence from other seabirds (Orians 1969, Brant 1984, Hesp and Barnard 1989) and from frigatebirds in somewhat artificial conditions (observations were helped by providing food to the birds; Gochfeld and Burger 1983), success rates of females and juveniles did not differ significantly. However, overall adult efficiency in provoking the target's regurgitation was 0.6 times higher. An inadequate sample of juvenile chases could be responsible for this result as some juveniles might have had several months of experience at attempting piracy.

GROUP CHASES

The chases performed by groups were more successful than the ones conducted by a single individual (see also Barnard 1984). However, it would require an average group size of only three individuals (which is very likely an underestimate) to make the per-capita rate of success from group chases equal to that of individual chases. The data collected do not show whether the greater success in group chases is due to an enhanced ability to harass the target or whether the group arises opportunistically when a chase seems likely to succeed. Absence of differences in time distributions between group and single chases supports the idea of enhanced harassment by groups (Fig. 1a, b).

PROFITABILITY

It is unexpected for a kleptoparasitic specialist to have such a low success rate of piracy, the lowest yet reported (5.4%), compared with 12% on Galápagos on Red-footed Booby (Nelson 1975), 18% in Aldabra on Red-footed Booby (Diamond 1975) and 63% on Christmas Island on Red-footed Booby (Nelson 1975). This low profitability seems even more striking when the frequency of theft of the regurgitated food by the opportunistic Heermann's Gull is considered; almost half of the successful chases resulted in no gain for the frigatebirds. Kleptoparasitism seems to be a poor feeding strategy at this location. However, if direct fishing is also costly or prey scarce, this strategy could make a significant contribution to their diet.

Since boobies carry their food in the gut, the frigatebird may not be able to evaluate the profitability of potential targets at a distance (Furness 1987, Thompson 1986). A pirate may reduce kleptoparasitic costs if it evaluates the profitability of targets. The low frequency of success and subsequently higher success of longer chases may suggest that in the first few seconds of pursuit the frigatebirds may obtain information about the profitability of continuing the chase. If the short chases are the local strategy to obtain information about the target's profitability as opposed to, for instance, watching the potential targets from a long distance (see Furness 1987), then the success rate of piracy reported here is an underestimate of the real profitability. In that case, our estimates of profitability cannot be directly compared with those previously reported in the literature.

The search for targets, in places and at times predictably more profitable, should enhance the probability of success of this feeding pattern by diminishing the sampling costs. The greater proportion of successful attacks and the strong positive association of piracy with the arrival of food-bringing boobies at their breeding place suggest that the approaching of the potential target to its nesting colony provides the most profitable condition.

It has been suggested that surface-fishing birds are subject to wider fluctuations in food availability and are thus more prone to engage in kleptoparasitism than plunging/diving species (Duffy 1980, 1982). This could explain why frigatebirds chase and steal for food, but data on the contribution of direct fishing to the diet of frigatebirds are needed to evaluate the real profitability of kleptoparasitism.

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