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KLEPTOPARASITISM IN TROPICAL SEABIRDS: VULNERABILITY AND AVOIDANCE RESPONSES OF A HOST SPECIES, THE RED-FOOTED BOOBY[1]

MATTHIEU LE CORRE AND PIERRE JOUVENTIN
CEBC - CNRS - Villiers en Bois, F - 79360 Beauvoir sur Niort, France

Abstract. We investigated the importance of kleptoparasitism in a population of Red-footed Boobies (*Sula sula*) sympatric with frigatebirds (Great and Lesser Frigatebird *Fregata minor* and *F. ariel*) and identified the responses adopted by boobies. Less than 1% of the boobies lost their food by kleptoparasitism. Birds flying in a group >50 m high or after dusk were less likely to be chased than others. We compared the way boobies returned to land and the rate of successful chases in this population with another population of Red-footed Boobies where kleptoparasitic attempts were rare. Birds were more nocturnal in the former population and were better able to resist chases. These observations suggest that the coexistence of boobies with frigatebirds may have led to avoidance responses. Comparison of the behavior of the Masked Booby (*Sula dactylatra*) to that of the Red-footed Booby showed that the former should be more vulnerable when returning to land than the latter. Further investigations are needed on the way Masked Boobies interact with frigatebirds in a place where both coexist in large numbers and to determine if this species has adopted other avoidance tactics.

Key words: Red-footed Booby, Masked Booby, kleptoparasitism, Great Frigatebird, chase frequency, avoidance responses.

INTRODUCTION

The stealing of food, or kleptoparasitism, is widespread among seabirds, and is an important feeding strategy for several species of three families: frigatebirds (*Fregatidae*), skuas (*Stercorariidae*) and sheathbills (*Chionididae*) (Brockmann and Barnard 1979, Furness 1987). Unlike predation, kleptoparasitism does not cause the death of the victim and seldom results in injuries (but see Gilardi 1994). However, several studies on seabirds suggested that kleptoparasitism may have led to avoidance responses. The synchronization of targets returning to colonies (Grant 1971, Rice 1985, Birt and Cairns 1987), the ability to assess the risk and modify the flight path (Grant 1971, Emms and Verbeek 1991), and nocturnality (Watanuki 1990) are the main avoidance responses used by host species.

In tropical areas, frigatebirds chase a great variety of species, especially boobies, tropicbirds, and terns (Furness 1987, Gilardi 1994). These aerial chases are particularly conspicuous in the vicinity of the islands where the hosts roost or breed. Most studies on kleptoparasitism by frigatebirds have focused on the importance of this strategy from the point of view of the kleptoparasite (Osorno et al. 1992, Gilardi 1994, Vickery and Brooke 1994), but the impact on the host remains poorly known (Furness 1987, but see Vickery and Brooke 1994). The Red-footed Booby (*Sula sula*) is sympatric with frigatebirds over most of its range (Nelson 1978) and is very commonly chased (Nelson 1978, Brockmann and Barnard 1979, Furness 1987). However, there has been no study of the impact of kleptoparasitism on Red-footed Booby (RFB) and on the way this species avoids kleptoparasitism.

Our aim was to determine whether RFB would acquire avoidance responses when living with frigatebirds. We quantified kleptoparasitism on Europa Island where RFB and frigatebirds (Great and Lesser Frigatebirds, *Fregata minor* and *F. ariel*, respectively) breed in large numbers, and identified the factors influencing the risk of a booby being chased. We compared the pattern of returns and resistance to chases on Europa to that of Tromelin Island where no frigatebirds breed. Finally, we compared this species with the Masked Booby (*Sula dactylatra*) in the way both species interact with frig-

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TABLE 1. Status, numbers and body weight of the seabirds involved in kleptoparasitic interactions on Europa and Tromelin Islands during the study.

Species (body weight)	Europa	Tromelin
Great Frigatebirds (m: 1,240 g, f: 1,630 g)	2,500 to 3,000 B	<10 NB[1]
Lesser Frigatebirds (m: 754 g, f: 860 g)	3,000 to 5,000 B	<10 NB[1]
Red-footed Boobies (940 to 1,070 g)	8,000 to 10,000 B	400 B
Masked Boobies (1,630 to 1,880 g)		600 B
Brown Skuas (m: 1,536 g, f: 1,735 g)	?(<50) NB	?(<50) NB
Kleptoparasite/Host Ratio[2]	0.25 to 0.37	RFB: 0.025; MB: 0.016

B: Breeding, NB: Nonbreeding.
[1] Number of roosting frigatebirds present during the study.
[2] The K/H ratio is calculated using only Great Frigatebird numbers as kleptoparasite, as Lesser Frigatebird has never been observed chasing a Booby on Europa, and only once on Tromelin (unpubl. data on population sizes from Le Corre).

atebirds, to determinate if both are equally vulnerable to kleptoparasitism.

METHODS

Europa (22°S, 40°E) and Tromelin Islands (15°S, 54°E), are two small and flat coralline islands of the western Indian Ocean. Data on the seabirds of these islands involved in kleptoparasitic interactions during the study are summarized in Table 1. On Tromelin, field work was carried out from 8 to 28 June 1994, as most Masked Boobies (MB) and RFB were incubating or rearing a chick. During that period, a frigatebird roost of 12 to 18 nonbreeding birds gathered each evening. Brown Skuas (*Catharacta skua*), wintering from subantarctic islands, were present in low numbers. On Europa, the study was conducted from 26 April to 2 June 1994 when RFB were not breeding and from 28 November 1994 to 11 January 1995 when most RFB were rearing a chick. Both frigatebird species were breeding during the two visits to Europa, whereas wintering skuas were present during the first visit only. The two islands are similar in their flat topography (highest point at 6–8 meters asl). RFB roost and breed communally on bushes or trees and MB roost on the ground. Observations were made from the top of a coastal dune as birds were returning to land. The distance between the observation point and the colonies was about 300 m on Europa and 50 m on Tromelin. Observations began 3 hr before sunset and stopped 30 min after sunset (15 sessions on Tromelin during the breeding season, 24 sessions on Europa, of which six were during the breeding season and 18 during the nonbreeding season).

Each booby or group of boobies was observed until it disappeared behind the coastal vegetation or was chased by a frigatebird or skua. Local time (GMT + 1 hr on Europa, GMT + 2 hr on Tromelin), flock size, flight height (low = <50 m and high = >50 m), and chases were noted for each return. As the fieldwork was conducted at two different localities and at two different seasons of the year for Europa, we transformed the local time to "solar times" fixing the hour of sunset at 18:00. The terms diurnal and crepuscular refer to events that happened before or after 18:15, respectively. When a chase occurred, the species of kleptoparasite, the number of kleptoparasites involved and the outcome of the chase were noted. As we focused on the cost of kleptoparasitism for boobies and not on the benefits of chasing for frigatebirds, a chase was considered as successful when the booby regurgitated, regardless of the success of the kleptoparasite in obtaining food. Thus, we calculated the success rate of the chases (SR) by dividing the number of successful chases by the total number of chases. The chase frequency (CF) was calculated by dividing the number of chases by the number of returns (single boobies or groups of boobies). The individual risk (IR) for one booby was calculated by dividing the number of chases by the total number of returning boobies.

The Typical Flock Size (TFS, Jarman 1974) was calculated as follows:

$$TFS = (\Sigma n_i^2)/N$$

where n_i is the number of birds of the ith observation, and N the total number of birds. The TFS is the size of the group where an average individual is a member and gives a better estimate of gregariousness than the mean group size (Jarman 1974).

Data on the effect of season, flock size (single or group), and height of the flight on chase frequency on Europa were analyzed using log-

TABLE 2. Chase frequency (%) on returning Red-footed Boobies in relation to season, gregariousness and flight height on Europa Island (crepuscular observations are excluded from the data set, number of observations in parentheses).

Season	Gregariousness	Chase frequency <50 m	Chase frequency >50 m
Breeding	single	15.5 (787)	11.8 (51)
	group	18.4 (1,261)	10.9 (201)
Nonbreeding	single	29.3 (549)	25 (48)
	group	27.2 (707)	18 (177)

For statistical treatment, see text.

linear models of the CATMOD procedure (SAS Institute 1988), in which parameters are estimated using the maximum-likelihood method. The complete log-linear model (e.g., with all the interactions between variables) was tested first, then we selected the best fitting model by deletion of the nonsignificant variables and interactions.

RESULTS

PATTERN OF RETURN AND RISK OF BEING CHASED ON EUROPA

On Europa, from 79 to 82% of the population of RFB returned to land between 17:00 and 18:30 (Fig. 1a) during both seasons. Most chases (65%) occurred during that period (Fig. 1b). The chases were initiated by Great Frigatebirds (97.4% vs. 2.6% initiated by skuas, n = 531 chases for which the kleptoparasite had been identified), and particularly by adult females (91.6%, n = 464 chases for which the sex and age of the bird had been determined). Lesser Frigatebirds were never observed chasing boobies on Europa. Frigatebirds were less active after 18:15 (Fig. 1b), which resulted in a reduction in chase frequency (20.7% vs. 6.2% for diurnal and crepuscular observations, respectively, $\chi^2_1 = 55.2$, $n = 4{,}242$, $P < 0.001$).

We tested the effect of flight height, season and gregariousness on diurnal chase frequency. The best fitting log-linear model indicated that the occurrence of a diurnal chase was influenced by flight height and season and the interaction of gregariousness and season. Chase frequency was higher for birds flying low than for birds flying high (Table 2) and it was lower during the breeding season than during the nonbreeding season (Table 2). Single birds were more often chased than groups during the nonbreeding season. However, for both seasons, the risk of an individual bird being chased (IR) decreased proportionally as the size of the group to which it belonged increased (Fig. 2).

COMPARISONS OF RETURNS, INDIVIDUAL RISK AND SUCCESS OF CHASES

Breeding RFB tended to return later, in larger flocks and at lower altitude on Europa than on Tromelin (Table 3). The success rate of the chases on breeding RFB was higher on Tromelin than on Europa (Table 4). On Tromelin, RFB came back later (Fig. 3), more synchronously and at greater height (Table 3) than MB. However, there was no difference in the individual risk of being chased for either host species (48 birds chased/2,073 birds observed [2.3%] versus 30/2,029 [1.5%] for RFB and MB, respectively; $\chi^2_1 = 3.4$). Skuas chased RFB almost exclusively (19/2,073 vs. 2/2,029 for RFB and MB, respectively; G-test = 13.5, df = 1, $P < 0.001$), while frigatebirds chased both host species equally (29/2,073 vs. 28/2,029 for RFB and MB, respectively; $\chi^2_1 = 0.003$). The success of chases was high and did not differ between host species (Table 4).

Knowing the individual risk of being chased (IR) and the success rate of a chase (SR), we calculated the risk (RK) for a given individual returning to land of losing its food to a kleptoparasite: RK = IR × SR (Vickery and Brooke

TABLE 3. Paired comparisons of the pattern of the returns of the two host species (breeding period only).

	Crepuscular flights	Daily TSF m ± SE (n)	Single birds	High flights
Interspecific comparison[1]				
MB on Tromelin	0.01%	3.4 ± 1.0 (15)	28.6%	10.9%
RFB on Tromelin	4.3%	5.8 ± 1.5 (15)	10.7%	37.9%
Intraspecific comparison[1]				
RFB on Tromelin	4.3%	5.8 ± 1.5 (15)	10.7%	37.9%
RFB on Europa	15.3%	12.3 ± 3.3 (6)	7.7%	22.5%

[1] Tests are χ^2 for comparisons of two proportions and t-test for comparison of two means. All pair-wise comparisons, $P < 0.001$.

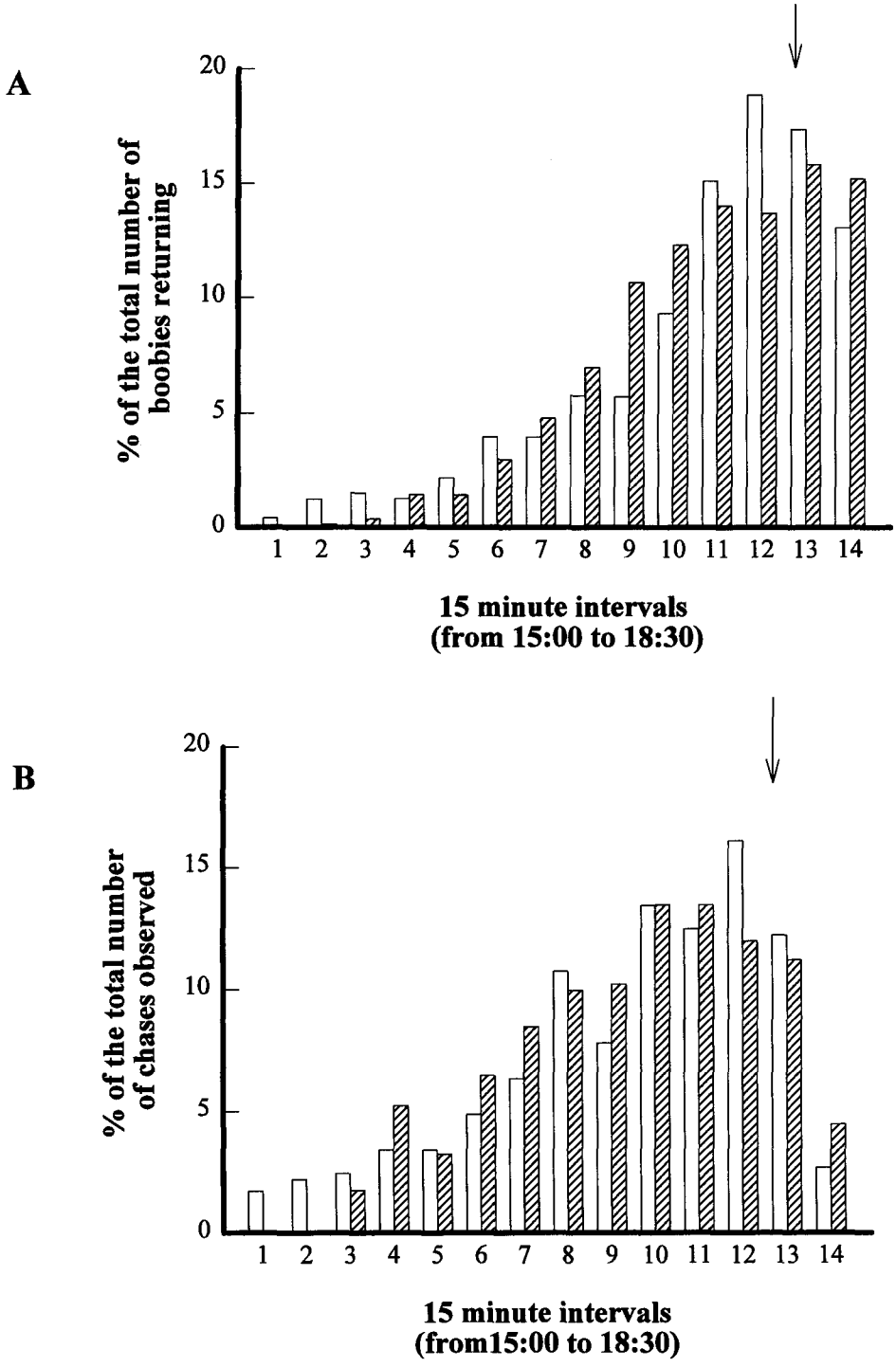

FIGURE 1. Pattern of the return of the Red-footed Boobies (A) and kleptoparasitic activity of the frigatebirds and skuas (B) on Europa Island (hatched bars: breeding season, open bars: nonbreeding season, the arrow indicates time of sunset). Data are percentages of the cumulative number of boobies or chases observed during the observation sessions.

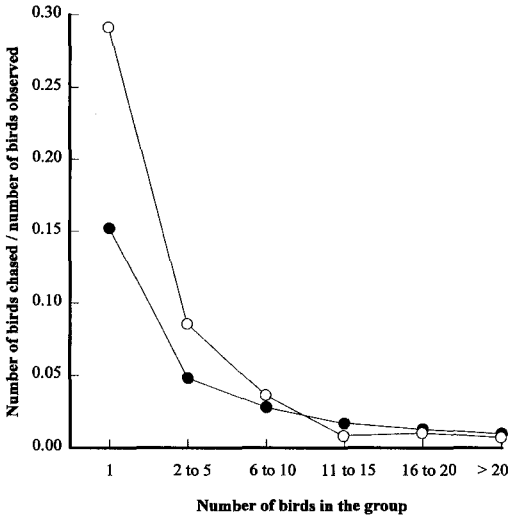

FIGURE 2. Individual chase frequency of the Red-footed Booby according to the group size on Europa Island (open circle = nonbreeding period, solid circle = breeding period).

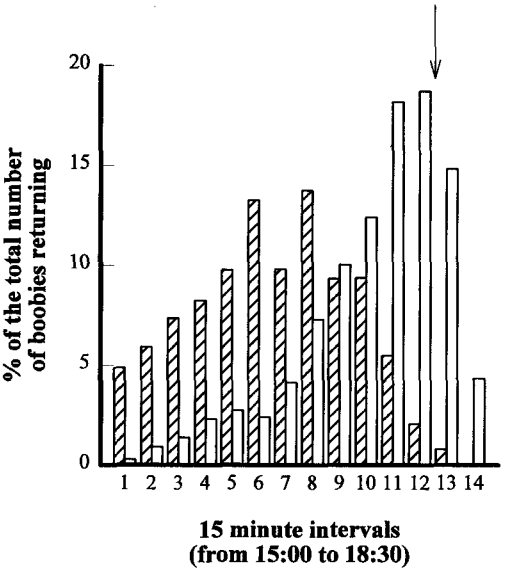

FIGURE 3. Pattern of the return of the Masked Booby (hatched bars) and Red-footed Booby (open bars) on Tromelin Island (the arrow indicates the time of the sunset). Data are percentages of the cumulative number of boobies observed during the observation sessions.

1994). On Europa, this risk was very low (3.8% × 11% = 0.4% during the breeding season, 5.4% × 19% = 1% during the nonbreeding season). On Tromelin, RK was 0.7% and 0.45% for RFB and MB, respectively.

DISCUSSION

IMPORTANCE OF KLEPTOPARASITISM AT THE HOST POPULATION LEVEL

Our results indicate that on both islands and for both host species, the risk of being chased successfully was low for any given booby, suggesting the overall impact of kleptoparasitism on populations may be low. On Henderson Island (South Pacific Ocean), the probability of a MB being chased successfully was 3% (Vickery and Brooke 1994). Furness (1987) found that the proportion of birds successfully chased by skuas is always less than 5%, whatever the host species. He suggested that this low impact is the condition for the kleptoparasite/host interaction to be evolutionarily stable. Our results from interactions between Red-footed Boobies and Great Frigatebirds on Europa, where both host and kleptoparasites coexist in large numbers, are consistent with this hypothesis.

TABLE 4. Paired comparisons of the success rate of the chases (%, number of observations in brackets, breeding period only).

	All chases	Solitary GF	Solitary BS	Collective GF
Interspecific comparisons[1]				
MB on Tromelin	30.0 (30)	32.1 (28)	0 (2)	not observed
RFB on Tromelin	32.6 (46)	22.2 (27)	47.4 (19)	not observed
Intraspecific comparisons[1]				
RFB on Tromelin	32.6 (46) A	22.2 (27) A	47.4 (19)	not observed
RFB on Europa	11.1 (379) B	4.2 (281) B	not observed	30.6 (98)

[1] Tests are χ^2 for comparisons of proportions; GF: Great Frigatebird, BS: Brown Skua, RFB: Red-footed Booby; MB: Masked Booby. Values with different letters within a column are significantly different from each other at $P < 0.01$.

AVOIDANCE TACTICS OF THE RED-FOOTED BOOBY

The low proportion of birds which lost food through kleptoparasitism on Europa may be the consequence of a strategy adopted by boobies. Three factors are associated with an individual's risk of being chased: the time of return, the flock size and the flight height. The strategy adopted by a booby may be a trade-off between the costs and benefits associated with flying in groups, flying high or flying at night. These three tactics reduce the risk of being chased, but each of them may have specific costs. Nocturnal flight may increase the risk of striking obstacles and may reduce the possibility of reaching the exact place of the nest. Flying in groups may require more time and energy to gather with other boobies unless they stay in groups during foraging trips. Flying high also may require more energy to gain altitude during the trip back to the island. It is worth noting that some birds in flocks returned to land from a very high altitude (maybe more than 300 m).

On Europa, birds tended to return later than on Tromelin, suggesting that the nocturnal flight strategy may be advantageous on this island because of the high risk of being chased. The flocks were larger on Europa than on Tromelin. However, the size of the two populations are very different so we cannot discriminate between a simple population size effect and an avoidance tactic to decrease the individual risk of being chased. High flights were more frequent on Tromelin than on Europa, even though the number of frigatebirds was higher on Europa than on Tromelin. This is contrary to expectation, and one might conclude that flying high is not an avoidance tactic, but is affected by other factors such as distance to foraging areas or wind speed.

Breeding RFB were less able to resist chases on Tromelin than on Europa, as the success of chases was three to five times higher on the former than on the latter. The ability to resist a chase may be related to individual experience and to characteristics like flight agility and speed, vigilance and control of regurgitation. It is worth noting that while collecting food samples from RFB colonies on the two islands, we observed that on Tromelin boobies generally regurgitated spontaneously, whereas on Europa they often regurgitated only if handled. The strong pressure of kleptoparasitism which exists on Europa may have selected birds with a greater ability to resist chases.

DIFFERENCES IN THE VULNERABILITY OF THE TWO HOST SPECIES

Both Red-footed and Masked Boobies have biological characteristics that make them important targets of frigatebirds: colonial habits and spontaneous regurgitation if stressed. Our results showed that both species are chased by frigatebirds. Furthermore, chases on MB and RFB had the same success, suggesting that they were equally sensitive to chases. We therefore expect that both have evolved avoidance responses when sympatric with frigatebirds. Our study showed significant differences in the way the two species returned to land. Masked Boobies returned in the afternoon, in small groups or singly. Only 10.9% were flying higher than 50 m. This pattern contrasts sharply with that of the RFB which returned at dusk, in larger groups and often at high altitude. These differences should lead to higher vulnerability of MB compared to that of RFB. Both were equally chased by frigatebirds but the skua seemed to select RFB. The difference in body size between the two boobies may explain the skuas' apparent preference for the smaller of the two species.

The kleptoparasitism pressure on MB may be too low on Tromelin to have led to avoidance strategies. On Henderson, where the kleptoparasitism pressure on nonbreeding MB is high, most boobies fly at high altitude (Vickery and Brooke 1994). As boobies are less often chased if flying high, the authors suggested that MB returned high to avoid kleptoparasitism. The fact that MB on Tromelin (where frigatebirds are rare) do not fly high is consistent with this hypothesis.

However, MB seem less gregarious than RFB when returning to land: the TFS of MB on Tromelin was half that of RFB in spite of a higher population size of MB. Furthermore, the proportion of single birds was high even on Henderson (Vickery and Brooke 1994). This low gregariousness may be explained by a tendency to forage in pairs or singly (Anderson 1954), contrasting with the mostly collective foraging behavior of RFB (Nelson 1978). In a locality where both species coexist with frigatebirds, MB may be more at risk when returning to land than RFB, as the risk of being chased decreases proportionally with an increase in

group size. Both boobies also differ in their nocturnality. Masked Boobies returned to land well before sunset while RFB returned at dusk. The nocturnality of RFB, both at sea and at colonies has already been noted (Murphy 1936 in Brooke and Prince 1992), and this species is regarded as the most nocturnal of the sulids (Nelson 1978). Nocturnal behaviors of seabirds in colonies, especially among the smallest-bodied species, has often been interpreted as an adaptation to avoid predation (Watanuki 1986, Brooke and Prince 1992, MacNeil et al. 1993). However, Rhinoceros Auklets (*Cerorhinca monocerata*) return to colonies at night to avoid kleptoparasitism by gulls (Watanuki 1990) and nocturnality of the Swallow-tailed Gull (*Larus furcatus*) of Galapagos may have been selected to avoid frigatebirds (Hailman 1964, Snow and Nelson 1984).

It would be of interest to investigate how frigatebirds interact with other tropical seabirds, especially other boobies, and to focus on the avoidance strategies developed by these species. The RFB is gregarious and nocturnal, which reduces the individual risk of being chased. Nocturnality and the ability to resist chases may have been selected by kleptoparasitism in heavily kleptoparasitized populations. If such selection occurs, it means that kleptoparasitism might reduce the fitness of the birds exploited. The mechanisms of this reduction (effect on the reproductive success, or on the survival of the birds chased), although suspected (Gilardi 1994), still remains to be determined.

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