The Condor 96:331-340

THE KLEPTOPARASITIC INTERACTIONS BETWEEN GREAT FRIGATEBIRDS AND MASKED BOOBIES ON HENDERSON ISLAND, SOUTH PACIFIC[1]

J. A. VICKERY[2]
University of East Anglia, School of Biological Sciences, Norwich, NR4 7TJ, U.K.

M. DE L. BROOKE
Department of Zoology, Cambridge University, Downing Street, Cambridge, CB2 3EJ, U.K.

Abstract. Kleptoparasitic activities by Great Frigatebirds (*Fregata minor*) on Masked Boobies (*Sula dactylatra*) were quantified on Henderson Island in the South Pacific. The frequency of kleptoparasitic attacks increased towards dusk, the time when most Masked Boobies returned to the roost site. Masked Boobies returning to the roost low (<30 m) over the water were significantly more likely to be chased than those returning at a higher altitude. Single boobies were also significantly more likely to be attacked than boobies returning as one of a group of birds. However, group size and height were positively correlated. There was no effect of group size on the likelihood of attack. Sixteen percent of chases were successful and the success rate was not influenced by either the height or the distance of the target from the roost. The duration of the chase was, however, influenced by the position of the target: chases on distant or high targets lasted significantly longer than chases on targets that were low or close to the roost. In addition successful chases were significantly longer than unsuccessful ones. We discuss these results in relation to the chase tactics of frigatebirds, the avoidance tactics of boobies and the energetic costs and benefits of kleptoparasitism. Approximately 40% of daily energy expenditure of some individual Great Frigatebirds may be secured through kleptoparasitism. However, on average, frigatebirds may be meeting under five percent of their daily energy demands by this feeding method.

Key words: Boobies; chase duration; energetics; frigatebirds; kleptoparasitism; Pacific Ocean.

INTRODUCTION

Kleptoparasitism, the stealing by one animal of food which has already been caught by another, occurs widely throughout the animal kingdom in a range of taxonomic groups including insects, fish, reptiles, birds and mammals (Thompson 1986). Although kleptoparasitism may reduce the costs of foraging, by using the time and energy investment of others, it involves a high degree of specialization and is likely to be profitable only under certain ecological conditions, for example, where numerous potential hosts carry large quantities of food and behave in a predictable way (Brockmann and Barnard 1979).

Kleptoparasitism is an important feeding method in four seabird families; Fregatidae (frigatebirds), Chionididae (sheathbills), Stercorariidae (skuas) and Laridae (gulls and terns) and has been well studied in the latter three (e.g., Dunn 1973, Anderson 1976, Verbeek 1977, Burger 1981, Furness and Hislop 1981, Birt and Cairns 1987). However, despite the fact that frigatebirds are considered among the most specialized kleptoparasites (Furness 1987), few detailed studies of the interactions between frigatebirds and their hosts exist (Furness 1987, Osorno et al. 1992).

The aims of this study were to carry out a detailed study of the kleptoparasitic behavior of the Great Frigatebird (*Fregata minor*) on one of its main target species, the Masked Booby (*Sula dactylatra*) and to evaluate the importance of this feeding method in satisfying the energy needs of the frigatebirds. Data are presented on the daily activity pattern of Great Frigatebirds and Masked Boobies over inshore waters around Henderson Island, South Pacific; the nature of the flight paths adopted by Masked Boobies as they return to their roost site; the location, duration and outcome of kleptoparasitic attacks; and the number, size, and species of fish that may be obtained from a successful attack. This information is then used, in conjunction with published figures for

[1] Received 1 September 1993. Accepted 10 January 1994.

[2] Present address: Division of Biological Sciences, University of Edinburgh, Ashworth Laboratories, King's Buildings, West Mains Road, Edinburgh EH9 3JT.

metabolic costs of flight and energy values of fish, to assess the proportion of the daily energy requirements of Great Frigatebirds that may be obtained from kleptoparasitism.

STUDY AREA AND METHODS

The study was carried from April to June 1991, on Henderson Island (24°22'S, 128°20'W), one of the Pitcairn Islands in the South Pacific. Henderson is a raised coral atoll with limestone cliffs reaching 34 m above sea level, a fringing reef 50–100 m wide and three beaches; one on each of the north, west and east coasts (Fig. 1). The East Beach was approximately 2 km long with a 20–30 m wide strip of vegetation, primarily *Pandanus tectorius* and *Argusia argentea,* between the beach and the base of the cliffs. During the study period, 70 to 80 Masked Boobies roosted at the base of the cliffs on East Beach. The roost site was located in a natural clearing on the seaward edge of the beach vegetation. All observations of frigatebirds and boobies were made from a position on the edge of the vegetation 150 m south of the roost.

A maximum of 126 Great Frigatebirds was recorded over East Beach during the study period (pers. observ.). Frigatebirds on Henderson nested and roosted in the forest of the interior plateau. Following laying in June, the number of frigatebirds continued low, probably under 100 pairs.

DAILY ACTIVITY PATTERN OF GREAT FRIGATEBIRDS AND MASKED BOOBIES

The numbers of Masked Boobies returning to roost and the activity of frigatebirds were recorded during five watches from 06:00 to 18:00 hr and five additional 2-hr watches from 16:00–18:00 hr (local time = GMT less 8.5 hr). Individual frigatebirds were followed using 10 × 40 binoculars and the total time spent perching, gliding (slow, often circling flight with few or no wing beats) and chasing (rapid, flapping flight) was recorded during each 2-hr observation period. Individual birds were selected at random and followed constantly until they were lost from view as they flew either out to sea, around the cliffs to the north or south of the beach, or overhead and into the interior of the island. The time at which a bird was lost from view was recorded and observations were switched to another randomly selected individual. This switch was made immediately or as soon as another individual came into view. Any time during which no individuals were present was recorded.

FLIGHT PATHS OF MASKED BOOBIES RETURNING TO THE ROOST SITE

Detailed observations were made of the flight paths of Masked Boobies returning to the roost site during ten 2-hr watches at dusk (16:00 to 18:00 hr). Individual Masked Boobies were sighted up to 600 m offshore and followed until they had either landed at the roost site or were lost from view out to sea. For each individual bird the following information was recorded: (i) whether the booby was single or one of a group and the size of the group, (ii) the height at which the booby crossed the reef (estimated to the nearest 5 m in relation to the height of the cliff) and (iii) whether it was chased and, if so, whether the chase was successful (a chase was considered successful if the booby was forced to regurgitate and the frigatebird obtained the food). The same information was recorded for the small number of Red-footed Boobies (*Sula sula*) that were also seen crossing East Beach to roost further inland.

KLEPTOPARASITIC BEHAVIOR OF GREAT FRIGATEBIRDS

Individual frigatebirds were followed during ten 2-hr watches at dusk (16:00 to 18:00 hr). For each kleptoparasitic attack the following information was recorded: (i) the time at the start of the chase (taken as the moment the frigatebird switched from gliding to direct flapping flight towards the booby, (ii) the distance or initial location of the target booby from the roost site (identified as being in one of three zones: over the beach, between the reef and the beach or beyond the reef), (iii) the height of the target above the sea or beach, (iv) whether the target was single or one of a group, (v) the duration of the chase, (vi) the outcome of the chase and, if successful, (vii) the number of fish the frigatebird obtained.

Information on species and mass of fish that were carried by boobies to the roost was obtained from regurgitates which usually comprised easily separated, barely digested fish. Masked Boobies will readily regurgitate food if disturbed by people. Fish were obtained from this source and also as a result of chases where the frigatebird either missed or dropped the regurgitated food. The fish were identified to family and weighed to the nearest 0.5 g using a 0–100 g Pesola spring balance.

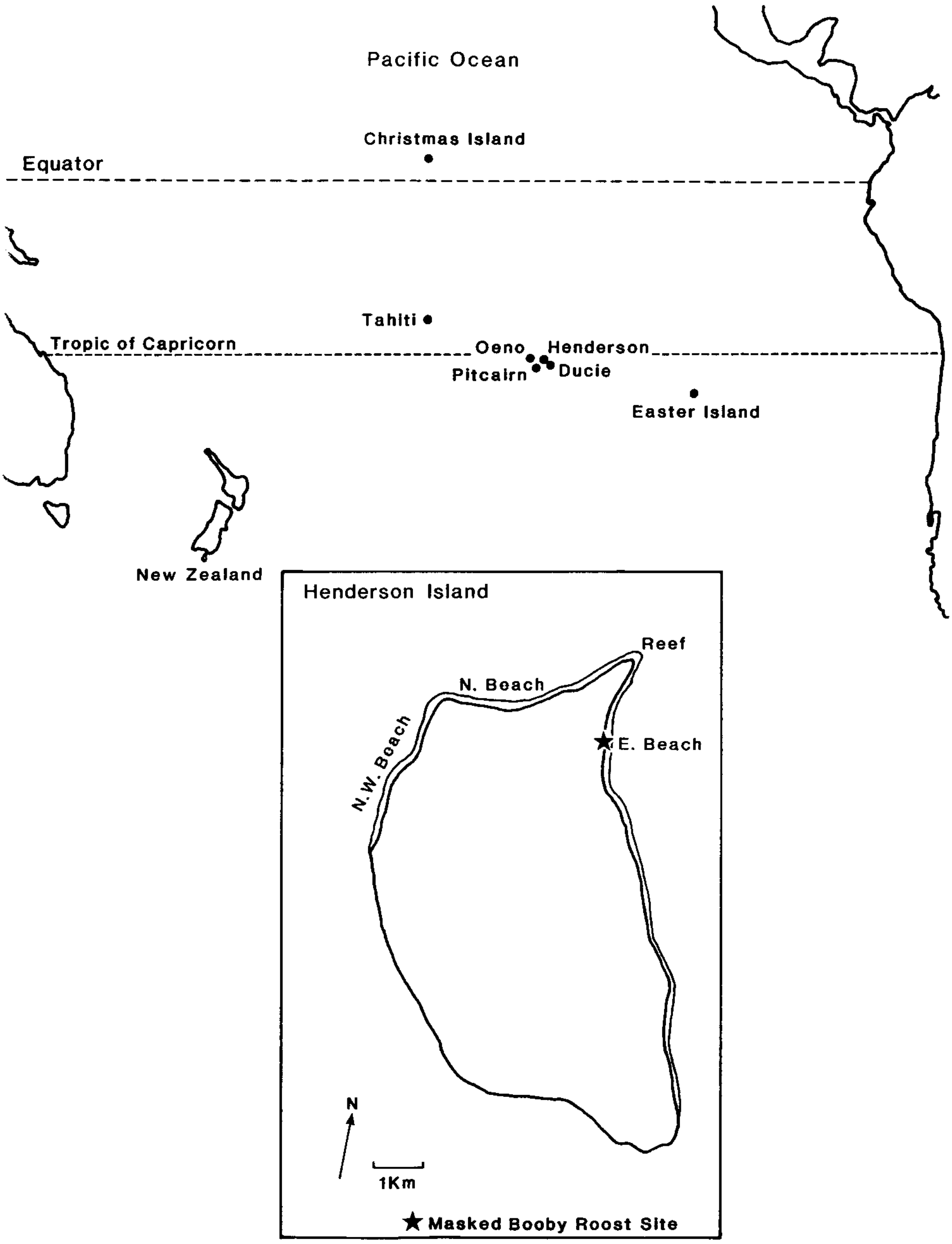

FIGURE 1. The study site.

RESULTS

DAILY ACTIVITY PATTERN OF MASKED BOOBIES AND GREAT FRIGATEBIRDS

Throughout the day (06:00 to 18:00 hr) one or more frigatebirds were visible in the air over inshore waters for approximately half of the time (mean = 51.0%, 95% Confidence Intervals [CI] = 39.1–62.8%, $n = 30$ 2-hr periods; arcsine transformations). When visible over these inshore waters frigatebirds spent 16.9% (95% CI = 11.0–23.9%) of their time perched, 82.0% (95% CI =

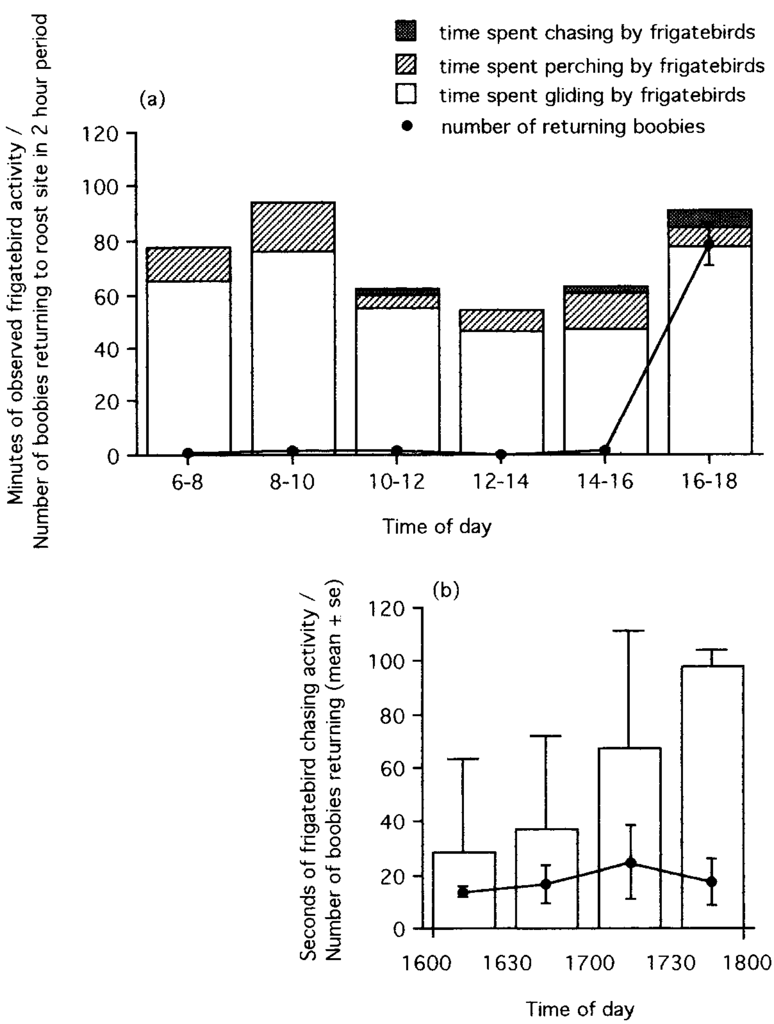

FIGURE 2. (a) Daily activity pattern of Great Frigatebirds over the inshore waters of Henderson Island and the number of Masked Boobies arriving at the roost site throughout the day. Columns show the mean time spent by frigatebirds gliding, perching and chasing from 06:00–18:00 hr (n = 5 observation periods). Continuous black line shows the number (mean ± SE) of boobies returning to roost in each 2-hr period. (b) The duration of Great Frigatebird chasing activity (columns ± SE) and number of returning boobies (mean ± SE) per half-hour period, 16:00–18:00 hr (n = 5 observation periods).

76.0–87.3%) of the time gliding and only 0.5% (95% CI = 0.1–2.3%) of their time actively engaged in chases (Fig. 2a). The proportion of time spent in these three activities did not differ between the five 2-hr observation periods from 06:00 to 16:00 hr (one-way ANOVA; time perching, $F_{4,20}$ = 0.49 ns; gliding, $F_{4,20}$ = 0.52 ns; chasing $F_{4,20}$ = 0.55 ns). However, in the 2-hr period before dusk (16:00–18:00 hr) frigatebirds spent significantly more of their time (3.1%, 95% CI = 1.9–4.5%) engaged in chases (t = 13.56, P < 0.0001; df = 33 arcsine transformations), and correspondingly less time (7.4%, 95% CI = 6.3–8.6%) perching (t = 7.98, P < 0.0001; df = 33) than during the rest of the day. There was no difference in the time spent gliding (t = 0.166, ns; df = 33). The number of boobies returning to the roost site was also greatest during the 2-hr period before dusk. Approximately 79 birds (78.6 ± 7.7, n = 5, mean ± SD) returned between

TABLE 1. The effect of height and group size on the likelihood that an individual Masked Booby will be attacked by a Greater Frigatebird as it returns to roost.

The position of the target	Number of birds Chased	Unchased	Effect on the likelihood of attack
(1) The effect of height of the Booby			
(a) All chased vs. all unchased birds			
(i) Birds returning high	14	173	high birds less likely to be chased than low
(ii) Birds returning low	37	41	birds ($G = 52.14$, $P < 0.001$)
(b) Single chased vs. singled unchased birds			
(i) Birds returning high	9	120	high birds less likely to be chased than low
(ii) Birds returning low	33	34	birds ($G = 45.52$, $P < 0.001$)
(c) Group chased vs. group unchased birds			
(i) Birds returning high	5	53	high birds less likely to be chased than low
(ii) Birds returning low	4	7	birds ($G = 4.95$, $P < 0.05$)
(2) The effect of group size (single birds vs. birds in groups >1)			
(a) All chased vs. all unchased birds			
(i) Birds returning single	41	104	group birds less likely to be chased than single birds ($G = 3.89$, $P < 0.05$)
(ii) Birds returning in a group	12	61	
(b) Chased vs. unchased birds at <30 m			
(i) Birds returning single	34	30	no significant difference ($G = 0.21$, ns)
(ii) Birds returning in a group	6	7	
(c) Chased vs. unchased birds at >30 m			
(i) Birds returning single	7	74	no significant difference ($G = 0.08$, ns)
(ii) Birds returning in a group	6	54	

16:00 and 18:00 hr compared with only one every two hours throughout the rest of the day (Figs. 2a, b).

FLIGHT PATHS OF MASKED BOOBIES RETURNING TO ROOST

The flight paths of 265 individual Masked Boobies were followed as they returned to roost. Two distinct flight paths were apparent: (i) boobies returned high in the sky, frequently circling above the roost, and then plummeted to the beach; or (ii) boobies returned low and flew directly to the roost site. The latter flight path was generally adopted by boobies that crossed the reef at a height of less 30 m. Most birds in this latter group crossed the reef within 10 m of the sea. However, most boobies returned at heights above 30 m (187 birds, 70.6%) and 89% of these plummeted to the roost site rather than slowly losing height. Thus, a booby was considered to return high if it crossed the reef above a height of 30 m and low if it crossed at a height of less than 30 m.

Fifty-one returning boobies (19.2%) were chased by frigatebirds as they returned to roost. Significantly more of the boobies (47.4%) returning at heights below 30 m were attacked than among those birds (7.5%) that returned at heights above 30 m ($G = 52.14$, $P < 0.001$; df = 1). This was also true when single birds ($G = 45.52$, $P < 0.001$; df = 1) and birds in a group ($G = 4.95$, $P < 0.05$; df = 1), were considered separately (Table 1).

The size of the group in which the boobies returned to roost was recorded for 218 boobies of which 145 (66.5%) returned as single birds. More single birds (28.3%) were attacked than individuals that returned as one of a group (16.4%; $G = 3.89$, $P < 0.05$; df = 1). However a bird's group size and return height were positively correlated ($r = 0.43$, $P < 0.001$; df = 216). Thus birds in larger groups tended to return higher than single birds and there was no effect of group size when chases launched on birds above ($n = 141$) and below ($n = 77$) 30 m were considered separately ($G = 0.08$, ns; df = 1 and $G = 0.21$, ns; df = 1 respectively, Table 1).

Twenty-five Red-footed Boobies (*Sula sula*) were also watched crossing the reef and beach en route to inland roosts; only two were attacked. Moreover, despite the fact that most of these birds (24 birds, 96%) flew low across the reef, they were significantly less likely to be attacked

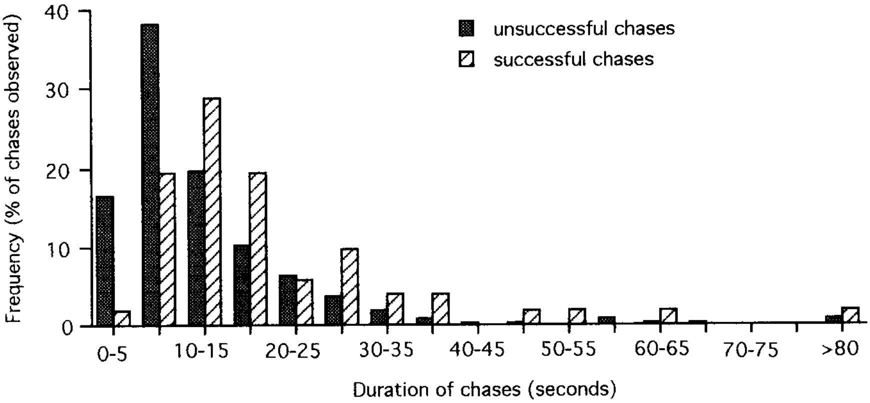

FIGURE 3. Frequency of successful and unsuccessful chases of different durations made by Great Frigatebirds on Henderson Island.

than Masked Boobies flying low over the reef ($G = 438.13$, $P < 0.001$; df = 1).

THE KLEPTOPARASITIC BEHAVIOR OF GREAT FRIGATEBIRDS

The position of the target. Of 325 chases on Masked Boobies, 52 (16%) were successful and resulted in the frigatebird obtaining food. The majority of the remaining chases were unsuccessful because the booby landed before regurgitating food, flying either to the sand (51%) or the water (13%). The remaining chases (20%) were terminated by the frigatebird itself before the booby landed.

Most chases (254 or 78.2%) were launched on boobies that returned low (<30 m) but the ratio of successful to unsuccessful chases within the two height classes (<30 m or >30 m) did not differ ($G = 0.18$, ns; df = 1). Similarly, most chases (273, 84.0%) were on boobies either over the reef or over the beach, with few on more distant targets (i.e., beyond the reef at 110 m). The proportion of chases that were successful within each distance class (<110 m or >110 m) was not significantly different ($G = 3.14$, ns; df = 1). These results suggest that the likelihood of a chase being successful was not influenced by either the height of the target or its distance from the roost.

The duration of chases. Of 325 chases recorded, mean time for successful chases (median = 15.0 sec, $n = 52$) was significantly longer than that of unsuccessful chases (median = 9 sec, $n = 273$; Mann-Whitney test, $Z = -3.84$, $P < 0.0001$, Fig. 3). However, the duration of a chase was influenced by both the height of the target and its distance from the roost at the time of initial attack (Table 2). Chases launched on targets returning to the roost at heights of greater than 30 m were significantly longer (median = 16.2 sec, $n = 71$) than those launched on low targets (median = 10.0 sec, $n = 254$). This was also true when successful and unsuccessful chases were considered separately (Table 2). In addition chases launched on targets beyond the reef were significantly longer (median = 19.0 sec, $n = 41$) than those launched on targets over the reef or the beach (median = 10.5 sec, $n = 284$). This was also the case when unsuccessful, but not successful, chases were considered separately (Table 2).

However, the fact that within all four categories (distant, near, >30 m, <30 m) successful chases lasted longer than unsuccessful ones confirms the initial result that successful chases are longer than unsuccessful ones. In addition, within unsuccessful chases there was no difference in chase duration between those terminated by the frigatebird (abandoning the chase) and those terminated by the booby (landing before regurgitating food; Mann-Whitney test, $Z = -1.59$, ns; df = 171). Thus unsuccessful chases were not shorter for the simple reason that the boobies being chased reached the roost, beach or water quickly.

The energetics of kleptoparasitism. Almost all (96%) kleptoparasitic activity recorded on Henderson Island was during the 2-hr period before dusk. In addition, successful chases were recorded only during the dusk watches (16:00–18:00

TABLE 2. The effect of target height and distance on duration of the chases by Great Frigatebirds on Masked Boobies. Adjacent values that are significantly different are indicated by the same superscript letter.

	Duration of chase seconds median (n)	
	Distant (>110 m)	Near (<110 m)
(1) The distance of the target from the roost		
(a) All chases	19.0 (41)[a]	10.5 (284)[a]
(b) Unsuccessful chases	17.5 (38)[b]	9.0 (235)[bc]
(c) Successful chases	63.0 (3)*	15.0 (49)[c]
(2) The height of the target	High (>30 m)	Low (<30 m)
(a) All chases	16.2 (71)[d]	10.0 (254)[d]
(b) Unsuccessful chases	14.0 (60)[eg]	9.0 (213)[eh]
(c) Successful chases	20.5 (11)[fg]	14.0 (41)[fh]

Significance values: a, $Z_{41,284} = -2.82$, $P < 0.01$; b, $Z_{38,235} = -3.03$, $P < 0.01$; c, $Z_{49,235} = -4.80$, $P < 0.001$; d, $Z_{71,254} = -2.87$, $P < 0.01$; e, $Z_{60,213} = -3.63$, $P < 0.001$; f, $Z_{11,41} = -2.58$, $P < 0.01$, g, $Z_{11,60} = -2.26$, $P < 0.05$; h, $Z_{41,213} = -4.22$, $P < 0.001$; *, insufficient data available.

hr). Thus, we assume that food secured through kleptoparasitic attacks during this 2-hr period represents the total food gained through kleptoparasitism in one day. We also assume in the calculations below that kleptoparasitism does not occur well away from the land. This may be justified because potential victims are generally dispersed at sea, which would militate against kleptoparasitism. However, where boobies congregate at surface driven prey, there may be opportunities for frigatebirds either to kleptoparasitize boobies or catch prey themselves.

Thus, the daily maximum number N_{max} of chases made by one bird was calculated using the formula:

$$N_{max} = (N_{chases}/N_{mins}) \times 120$$

where N_{chases} is the average total number of chases undertaken by the focal bird within a 16:00–18:00 hr observation period (usually several birds were observed sequentially during the period) and N_{mins} is the average number of minutes during which frigatebirds were actually observed during the same observation period ($n = 10$). This gives a value of a maximum of 14.3 chases in one day.

The reward for kleptoparasitism to an individual frigatebird depends on the number of chases made, the likelihood that a chase will be successful and the number and energetic content of fish obtained as a result of a successful chase. Assuming a success rate of 16%, we estimate that Great Frigatebirds may achieve 2.29 successful chases per day.

The mean number of fish regurgitated, by an individual booby, in response to our disturbance was 5.4 (±3.9, mean = SD, $n = 14$). However, fewer fish were regurgitated by boobies when chased by frigatebirds; a mean of 2.4 (±1.6, $n = 17$; $t = 3.09$, $p < 0.005$, df = 29) of which only one was usually secured by the frigatebird. On average, a frigatebird obtained 1.14 fish as a result of successful chase on a Masked Booby (Table 3). To estimate energetic content of the fish, we collected 19 regurgitates (a total of 73 fish): 14 from boobies at roost and five single fish from kleptoparasitic attacks where the frigatebird missed the fish. The majority of fish that were regurgitated by boobies were flying fish (family: Exocoetidae, 90.4%) the remainder being needle fish (family: Belonidae, 6.8%) and garfish (family: Belonidae, 2.7%). The mean mass of a fish was 50.3 ± 11.2 g (mean ± SD). Assuming an energy content of 5 kJ g^{-1} wet mass (Harris and Hislop 1978) and a digestive efficiency of 85% (Dunn 1975), a frigatebird may secure 558.1 kJ day^{-1} through kleptoparasitism (Table 3).

The basal metabolic rate of Great Frigatebirds was estimated from Lasiewski and Dawson's (1967) equation for non-passerines

$$M = 328W^{0.723}$$

where W is mass (kg) and M is expressed in kJ $days^{-1}$. The mass of a Great Frigatebird was taken as 1.3 kg (mean mass for males = 1.2 kg, mean mass for females = 1.4 kg; Brown et al. 1982), giving a basal metabolic rate of 396.5 kJ day^{-1}. Since there are no published figures for the met-

TABLE 3. The energetic costs and benefits of kleptoparasitic behavior of Great Frigatebirds on Henderson Island.

Parameter	Value
(a) Maximum daily energy gained from kleptoparasitism	
DEE of Great Frigatebirds (BMR × 3.0)[1]	1189 kJ
Number of successful chases in one day (14.3 × 0.16, $n = 10$)[2]	2.29 ± 0.2
Number of fish obtained from a successful chase ($n = 17$)	1.14 ± 0.09
Mean mass of fish ($n = 19$ regurgitates)	50.3 ± 11.2 g
Energy content of fish (g^{-1} wet weight)[3]	5 kJ
Digestive efficiency[4]	85%
Daily energetic gain from kleptoparasitism (2.29 × 1.14 × 50.3 × 5 × 0.85)	558.1 kJ
Percentage of DEE gained from kleptoparasitism	47%
(b) Average daily energy gained from kleptoparasitism	
Number of Masked Boobies using Henderson	200
Number of successful chases in one day (200 × 0.03)[5]	6
Mass of fish obtained from all successful chases (6 × 50.3 × 1.14)	344.1 g
Energetic yield of all chases (344.1 × 5 × 0.85)	1,462.4 kJ
Number of Frigatebirds on Henderson	100
Average energetic gain from kleptoparasitism (yield/frigatebird)	14.6 kJ
Percentage of DEE gained from kleptoparasitism	1.2%

[1] Drent and Daan 1980, Wijnandts 1984, Bryant and Tatner 1988.
[2] Average number of successful chases seen during watches from 16:00–18:00 (no successful chases were seen at any other time of the day, $n = 5$ all-day watches).
[3] Harris and Hislop 1978.
[4] Dunn 1975.
[5] Assumes each individual booby is only at risk once a day.

abolic costs of flapping or gliding in this species, we assume a daily energy expenditure (DEE) of 3.0 × basal metabolic rate (Drent and Daan 1980, Wijnandts 1984, Bryant and Tatner 1988), giving a value of 1,189 kJ day^{-1}. Thus the energy gained from kleptoparasitism equals a maximum of 47% of the daily energy expenditure.

We emphasize this percentage represents a maximum figure that applies only to those birds that actually kleptoparasitize Masked Boobies. An alternative calculation suggests that the "average" frigatebird on Henderson Island may secure a considerably lower proportion of its daily energy expenditure from inshore kleptoparasitism. The total number of Masked Boobies using Henderson Island at the time of the study was approximately 200 birds (80 birds roosting on East Beach, 20 roosting on North Beach and 50 breeding pairs). The probability (P) of an individual booby losing food to a frigatebird was calculated using the formula

$$P = P_a \times P_s$$

where P_a is the probability of being attacked and P_s is the probability of that attack being successful, giving a value of 0.03 (0.19 × 0.16). Assuming each booby is at risk once a day as it returns to Henderson Island at dusk, then over the island as a whole there will be a total of eight successful chases in one day (200 × 0.03) and the overall yield of these chases is 1,462.2 kJ (number of chases × energy value of fish obtained after digestion; 6 × 243.7 kJ, Table 3). Thus, given that there were approximately 100 Great Frigatebirds on Henderson Island the average frigatebird gains only 14.6 kJ day^{-1} from kleptoparasitism or 1.2% of its daily energy expenditure. Clearly, this is an underestimate if boobies are vulnerable to attack more than once a day. A small number of boobies did take off and circle from the roost after returning to the site.

The discrepancy between the two energetic calculations in Table 3 arises for the following reasons. When individual frigatebirds were watched patrolling over East Beach, they obtained food from boobies relatively frequently, about once an hour (2.3 successful chases in 2 hr) during the pre-dusk period. Extrapolating this value to all frigatebirds leads to the higher 47% value. However, the extrapolation is probably not justified because only a small proportion of the island's frigatebird population was patrolling the beach at any one time and it is unlikely that the frigatebirds were engaged in kleptoparasitism elsewhere on Henderson Island. In the absence of individually-recognizable frigatebirds, we were unable to assess whether a minority of frigatebirds were specialist kleptoparasites or whether all birds engaged in kleptoparisitism as opportunities arose.

DISCUSSION

When Masked Boobies return to roost, on Henderson Island, they follow a diurnal pattern that creates ideal conditions for kleptoparasitism to occur, as outlined by Brockmann and Barnard (1979). The boobies return in large numbers to a predictable roost site, at a predictable time (dusk) and often carrying large quantities of prey. The ease with which suitable targets can be found under these conditions is likely to reduce the cost of kleptoparasitism (Osorno et al. 1992). In fact, 96% of the kleptoparasitic activity recorded on Henderson Island occurred in the two-hour period before dusk when Masked Boobies returned to roost.

In the present study the likelihood of an individual booby losing food to a frigatebird was low; a probability of only 0.03 per return to roost. Despite this apparently low risk of losing food, the cost may be considerable and Masked Boobies followed flight paths that seemed to reduce the likelihood of attack. Boobies that returned high were less likely to be attacked than those returning low, and the majority of boobies did indeed return high, often increasing the height of the flight path as they approached the island. The majority of attacks were launched on low targets, despite their relative scarcity, suggesting these birds were actively selected by Great Frigatebirds. Thus, the strategy of returning to roost high may be one adopted by the booby to reduce the vulnerability to attack (Nelson 1978). The energy costs of gaining altitude are considerably greater than those of sustained horizontal flight (Kendeigh et al. 1977) and thus the adoption of a high flight path is likely to be more costly than a low one. Furthermore, the cost of gaining altitude is likely to increase with the weight of the food carried and boobies may, according to their load, balance the energetic costs of their ascent against the advantages of a lower risk of kleptoparasitism when returning at altitude.

Although on a worldwide scale Red-footed Boobies may be kleptoparasitized by frigatebirds more frequently than Masked Boobies (Nelson 1978), this was not the case during our study. Only eight percent of Red-footed Boobies were attacked. Red-footed Boobies were not feeding young at this time and this may have contributed to the reduced attack rate. That 96% of Red-footed Boobies flew low across the reef supports the view that the Masked Booby tactic of crossing the reef high and diving to the roost may be related to the threat of kleptoparasitism.

Frigatebirds selected targets that were low and close to the roost rather than high and distant. Although the position of the target did not affect the likelihood that a chase would be successful it did affect the duration and therefore the energetic cost of a chase. Chases launched on high or distant targets were longer than those launched on low and close birds. Since rapid flapping flight is energetically very costly (Tucker 1969, 1972) any reduction in the time spent in this activity is likely to result in considerable reduction, in energy expenditure. By selecting targets that were low and close to the roost, frigatebirds would reduce the cost of kleptoparasitic attacks and maximize energy gain. The profitability of chasing lower targets may be further increased if the prey loads carried by low birds were greater than those carried by birds flying high, but we have no data on this.

Evaluating the profitability of targets that carry food in the gut, such as boobies, is extremely difficult. Although the presence of food in the gut may affect flight and allow the kleptoparasite to discriminate between targets with and without food, it is unlikely to allow the evaluation of the relative profitability of prey-carrying hosts at a distance (Furness 1987). Under these conditions, the frigatebirds could employ either a "giving-up-time rule" (chase for a fixed time, then give up if no food is obtained) or an "assessment strategy." Under the latter (Osorno et al. 1992), the frigatebird would chase for a fixed time to obtain information about the profitability of the target and therefore of continuing the chase. The use of such a strategy will result in successful chases being longer than unsuccessful ones as was the case in our study. In addition it has been suggested that such a strategy is also most likely to be employed if the success rate of chasing is low; prior assessment reduces the chance of a long and potentially unprofitable chase (Osorno et al. 1992). The success rate of kleptoparasitic attacks of Great Frigatebirds on Henderson Island was, indeed, relatively low (16%) compared with other species of kleptoparasitic birds (Furness 1987) but in agreement with success rates recorded elsewhere for Great Frigatebirds of 18%

(Aldabra), 12% (Galapagos), and 63% (Christmas Island, Pacific; Nelson 1976).

It is interesting to consider whether a food-carrying booby should regurgitate immediately, saving itself further harassment, or continue evasion with the possibility of eventual escape? Assessing the cost of these alternatives is beyond the scope of this paper. However, we would note that the number of fish regurgitated by Masked Boobies in response to our disturbance was considerably less than the number of fish regurgitated by boobies when chased (see Results). Do Masked Boobies have the ability to regurgitate a partial load to, literally, "get the frigatebirds off their tails"?

No other studies have attempted to determine the proportion of energy requirements secured by kleptoparasitism in frigatebirds, but estimates have suggested that it is less than 20%. This study suggests that frigatebirds on Henderson Island may secure a minimum of only 1.2% of their daily energy expenditure through kleptoparasitism on Masked Boobies. However, some individuals could obtain as much as 47% of the DEE through kleptoparasitism, a proportion that is much higher than previously suggested (Furness 1987). Without marked frigatebirds, we could not determine whether a few frigatebirds were specialist kleptoparasites, leaving the rest to secure fish themselves, or whether all birds engaged in kleptoparsitism as opportunities arose. Further work is required to distinguish between these two strategies.

ACKNOWLEDGMENTS

The work was funded by the Association for the Study of Animal Behaviour, the British Ecological Society, Jarroulds Department Store, the National Westminster Bank and P. J. Salter, all of whom we thank for their support. We also thank N. Davies, P. Jones, R. Furness, D.B.A. Thompson and S. Wanless for advice and helpful comments on the manuscript. The project was undertaken as part of the Sir Peter Scott Commemorative Expedition to the Pitcairn Islands and thanks are also due to numerous organizations and individuals who generously supported this expedition, particularly the British Ornithologists' Union, the International Council for Bird Preservation (British Section), UNESCO, the Royal Society, the Foreign and Commonwealth Office, London and J. Shirley. This paper is number 6 of the Pitcairn Islands Scientific Expedition.

LITERATURE CITED

ANDERSON, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. Ibis 118: 208–217.

BIRT, V. L., AND D. K. CAIRNS. 1987. Kleptoparasitic interactions of Arctic Skuas *Stercorarius parasiticus* and Black Guillemots *Cepphus grylle* in northeastern Hudson Bay, Canada. Ibis 129:190–196.

BROCKMANN, H. J., AND C. J. BARNARD. 1979. Kleptoparasitism in birds. Anim. Behav. 27:487–514.

BROWN, L. H., E. K. URBAN, AND K. NEWMAN. 1982. Birds of Africa Vol. 1. Academic Press, London.

BRYANT, D. M., AND P. TATNER. 1988. Energetics of the annual cycle of Dippers *Cinclus cinclus*. Ibis 130:17–38.

BURGER, A. E. 1981. Time budgets, energy needs and kleptoparasitism in breeding lesser sheathbills *Chionis minor*. Condor 83:106–112.

DRENT, R., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding biology. Ardea 68:225–252.

DUNN, E. H. 1975. Caloric intake of nestling Double Crested Cormorants. Auk 92:553–565.

DUNN, E. K. 1973. Robbing behaviour of Roseate Terns. Auk 90:641–651.

FURNESS, R. W. 1987. Kleptoparasitism in seabirds, p. 77–100. *In* J. P. Croxall [ed.], Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge.

FURNESS, R. W., AND J.R.G. HISLOP. 1981. Diets and feeding ecology of Great Skuas during the breeding season in Shetland. J. Zool. Lond. 195:1–23.

HARRIS, M. P., AND J.R.G. HISLOP. 1978. The food of young puffins, *Fratercula arctica*. J. Zool. Lond. 185:213–236.

KENDEIGH, S. C., V. R. DOL'NIK, AND V. M. GAVRILOV. 1977. Avian energetics, p. 127–204. *In* J. Pinowski and S. C. Kendeigh [eds.], Granivorous birds in ecosystems. Cambridge Univ. Press, Cambridge.

LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 13–23.

NELSON, J. B. 1976. The breeding biology of frigatebirds—a comparative review. Living Bird 14:113–155.

NELSON, J. B. 1978. The Sulidae, gannets and boobies. Oxford Univ. Press, Oxford.

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

THOMPSON, D.B.A. 1986. The economics of kleptoparasitism: optimal foraging, host and prey selection by gulls. Anim. Behav. 34:1189–1205.

TUCKER, V. A. 1969. The energetics of bird flight. Sci. Am. 220:70–78.

TUCKER, V.A. 1972. Metabolism during flight in the Laughing Gull *Larus atricilla*. Amer. J. Physiol. 222:237–245.

VERBEEK, N.A.M. 1977. Interactions between Herring and Lesser Black-backed Gulls feeding on refuse. Auk 94:726–735.

WIJNANDTS, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). Ardea 72:1–92.