SHORT COMMUNICATIONS

The Condor 97:811–814
© The Cooper Ornithological Society 1995

SEX-BIASED HOST SELECTION AND SUCCESS OF KLEPTOPARASITIC BEHAVIOR OF THE GREAT FRIGATEBIRD IN THE NORTHWESTERN HAWAIIAN ISLANDS[1]

ROBERT E. CUMMINS
National Biological Survey, Hawaii Field Station, Box 44, Hawaii Volcano National Park, HI 96718

Key words: Fregata minor; Sula dactylatra; Puffinus pacificus; *Kleptoparasitism; sex bias.*

Food stolen from one individual by another, or kleptoparasitism, is known for a variety of bird species and is common in Fregatidae, Laridae, and Stercorariidae (Brockman and Barnard 1979, Furness 1987). Many observations of kleptoparasitism have been made near nesting colonies (Verner 1965, Amerson 1971, Diamond 1975, Nelson 1975, Brockman and Barnard 1979, Gochfeld and Burger 1983, Furness 1987, Osorno et al. 1992, Gilardi 1994, Vickery and Brooke 1994). Nelson (1975) showed for Great Frigatebirds in the Galapagos, Christmas Island, and elsewhere (Vickery and Brooke 1994, Gilardi 1994), that chases occurred close to seabird colonies when victims returned to their roosting sites with full crops. In Hawaii, female and juvenile Great Frigatebirds capture most of their food directly from the ocean and limited kleptoparasitism is generally thought to be a supplement to their diet (Harrison 1990).

In this and other species of frigatebirds, success of kleptoparasitic robberies by adults and subadults is ambiguous. Some suggest the juvenile success rates have been lower or equivalent (Gochfeld and Burger 1983), no different (Osorno et al. 1992), or significantly different from that of the adults (Gilardi 1994). When kleptoparasitic behavior was examined by sex of adult frigatebirds, one sex overwhelmingly performed the attacks (Verner 1965, Nelson 1968, Diamond 1975, Gibbs and Gibbs 1987, Osorno et al. 1992).

I examined sex bias of host selection and rates of success in kleptoparasitic robberies by Great Frigatebirds of Wedge-tailed Shearwaters (*Puffinus pacificus*) and Masked Boobies (*Sula dactylatra*). I also compared success rates between individual and group robberies.

METHODS

I observed foraging frigatebirds between 1 June 1991 and 16 August 1991 on East Island, a sand islet in the French Frigate Shoals (23°47′5″ N, 166°12′40″ W). Because of a concurrent study, observations could only be made 1 hr before dusk, when the frequency of victims returning to roost seemed greatest.

An observation station with a viewing area extending outward approximately 150 m. from shore between 130° ESE and 250° WSW was set up on the southwestern end of the island, 20 m. inland. I observed attacks through 10 × 50 binoculars and timed the duration of chases with a stopwatch. Following Osorno et al. (1992), I recorded the age, sex, and numbers of pirates, the species and age of the victim, duration of chases, and regurgitation of food by the hosts. Duration of chases began when a parasite initially was on a direct path to intercept the host and ended when the host regurgitated or when the parasite maneuvered itself away from the host, thus ending the chase. Regurgitation of food items from hosts was recorded only if the pirate could be seen obtaining the regurgitated food in flight or suddenly stopping the chase and dipping to the water to obtain the food. If the chase resumed after this, it was considered a separate event.

Great Frigatebirds attempting to rob their hosts could not be identified individually, therefore, each incident was treated independently. When making comparisons between kleptoparasitic events, the likelihood ratio test (G-test) was used to analyze the data. Duration of chases were analyzed using student's t-test.

RESULTS

There were no nesting Great Frigatebirds on East Island, although, the only island that did was Tern Island, 9.6 Km to the NNW with 536 nesting pairs on 2 July 1991 (USFWS unpubl. data). I recorded 472 kleptoparasitic attempts (Table 1) by Great Frigatebirds. Of 99 successful robberies 98 were of shearwaters or boobies and one was of a Red-tailed Tropicbird. Shearwaters were the most frequently chased species (n = 414).

Kleptoparasitic attempts of adult (n = 40) and juvenile (n = 9) boobies elicited the same regurgitation rates (10.3%, 11.2%, respectively; $G = 0.10$, $P = 1.000$), whereas the rate of shearwaters was 22.7%. When there was only one parasite, adult Masked Boobies (n = 97)

[1] Received 6 December 1994. Accepted 22 March 1995.

TABLE 1. Six species of birds robbed by Great Frigatebirds (*Fregata minor*) and numbers of nests of these species at East Island, French Frigate Shoals, during July 1991.[1]

Species[2]		Number attacked	Number of nests	Census date
Wedge-tailed Shearwater (*Puffinus pacificus*)		414	271	07 July[2]
Masked Booby (*Sula dactylatra*)	Adult	40	28	
	Juvenile	9		18 July[2]
Sooty Tern (*Sterna fuscata*)		5	0	1991[2]
Red-footed Booby (*Sula sula*)	Adult	2	0	
	Juvenile	0		1991[2]
Red-tailed Tropicbird (*Phaethon rubricauda*)		1	9	04 July[3]
Brown Noddy (*Anous stolidus*)		1	18	26 July[3]

[1] Species arranged according to the number of chases by *Fregata minor*.
[2] U. S. Fish and Wildife, unpubl. data.
[3] Personal observation.

were chased predominately by female Great Frigatebirds (Table 2) whereas Wedge-tailed Shearwaters were chased primarily by male Great Frigatebirds ($n = 277$; $G = 59.5$, $P < 0.001$; Table 3)

When chasing Wedge-tailed Shearwaters single, male frigatebirds were successful 20.0% of the time ($n = 275$), females 20.8% ($n = 72$), and juveniles 0% ($n = 4$). The percentage of successful robberies was higher by groups of robbers ($n = 68$, 33.8%) than by single male or female robbers ($n = 347$, 20.2%; $G = 5.64$, $P = 0.0251$; Table 3). The success rate was not different between mixed sex-groups ($n = 30$, 43.3%) and single-sex groups of frigatebirds ($n = 24$, 37.5%; $G = 0.188$, $P = 0.783$). When juveniles paired with a male(s), the success rate was ($n = 12$) 16.7%. In contrast, group attacks, excluding juveniles, were ($n = 53$) 39.6% successful ($G = 2.49$, $P = 0.19$).

Twenty-five of 28 robberies by solitary frigatebirds of adult boobies were by females. Only one attack was successful (4.0%). No solitary frigatebirds were successful in robbing juvenile boobies (Table 2). The success rate of chases by more than one aggressor of adult boobies did not differ between male/female combinations ($n = 4$, 25.0%) and female combinations ($n = 9$, 11.1%; $G = 0.385$, $P = 0.535$). There was no difference in success of robberies of adult boobies by individuals ($n = 28$) or groups ($n = 12$; $G = 1.59$, $P = 0.21$).

Chase times for male ($n = 139$; 19.8 ± 1.1 sec) and female ($n = 72$; 20.6 ± 2.9 sec) frigatebirds robbing shearwaters were similar ($t = 0.28$, df = 164, $P = 0.78$). Successful mean duration of chases of shearwaters was longer than unsuccessful chases (longer: $n = 42$; 25.13 ± 2.9 sec; range = 2.5–93.7 sec; shorter: $n = 124$; 18.22 ± 2.9 sec; range = 1.2–52.4 sec; $t = 2.99$, df = 164, $P = 0.003$).

Group chases ($n = 26$; 26.9 ± 2.2 sec; range = 8.2–54.3 sec) were longer than individual chases ($n = 166$; 20.0 ± 1.0 sec; range = 1.2–93.7 sec; $t = 2.4$, df = 190, $P = 0.02$). Shearwater regurgitation because of robberies was equal if being chased by a group or individual (group: $n = 10$; 29.3 ± 2.8 sec; range = 16.4–45.5 sec; individual: $n = 42$; 25.1 ± 2.9 sec; range = 2.5–93.7 sec; $t = 0.67$, df = 50, $P = 0.50$). When female frigatebirds chased adult boobies, chase times for lone attackers ($n = 11$; 15.1 ± 5.3 sec; range = 1.5–55.8 sec) were shorter than group chases ($n = 6$; 43.1 ± 15.5 sec; range = 8.5–94.0; $t = 2.1$, df = 15, $P = 0.05$). Chase times of solitary male aggressors were not recorded.

DISCUSSION

Female Great Frigatebirds persisted in chasing Masked Boobies even though they had a success rate of only 4.0%. This is lower than Osorno et al. (1992) found among *F. magnificens* attacking Blue-footed Boobies (5.8%), lower also than attacks by *F. minor* on Red-footed Boobies in the Galapagos (12%), Aldabra Atoll (18%), and on Christmas Island in the Pacific (63%) (Diamond 1975). Previous reports suggests that female frigates perform most kleptoparasitic attacks near their hosts' colonies. Since Masked Booby and Wedge-tailed Shearwater colonies are on East Island, it might be expected for females to do most of the parasitizing. Gilardi (1994) showed that the size of the parasite influences host selection which suggests males chase smaller hosts and female chase larger hosts. The data herein support this by showing that males preferentially chase shearwaters whereas Masked Boobies were chased almost exclusively by females.

One possible reason why the females continue to chase the boobies, even with such a low success rate, is that they may be feeding on a variable ratio schedule (Ferster and Skinner 1957), similar to the interaction when Great Skuas (*Catharacta skua*) parasitize murres (*Uria* sp.) and puffins (*Fratercula arctica*) (Furness 1987). A variable ratio schedule is when the aggressor does not know on which particular chase the host will regurgitate, but will continue to chase even without a previous success. Success may come on the first chase or a later chase. When regurgitation does occur, the reward for the aggressors is sufficient to reinforce the behavior. The variable ratio schedule is response-based not time-based. Masked Boobies carry the largest prey items (> 20 cm) of any pelicaniformes in Hawaii (Har-

TABLE 2. Robberies of adult and juvenile Masked Boobies (*Sula dactylatra*) by single and multiple Great Frigatebird (*Fregata minor*) aggressors at East Island, French Frigate Shoals, 1991.

Combinations of attackers[1]	Adult Masked Boobies			Juvenile Masked Boobies		
	Number of attacks	Number of success	% success	Number of attacks	Number of success	% success
M	2	0	0	1	0	0
F	25	1	4.0	4	0	0
J	1	0	0	0	0	0
MM	0	0	0	0	0	0
MF	4	1	25.0	1	1	100
MJ	0	0	0	0	0	0
FF	8	1	12.5	1	0	0
FJ	0	0	0	2	0	0
JJ	0	0	0	0	0	0
MFJ	0	0	0	0	0	0

[1] M = Male, F = Female, J = Juvenile.

TABLE 3. Robberies of Wedge-tailed Shearwaters (*Puffinus pacificus*) by single and multiple Great Frigatebird (*Fregata minor*) aggressors at East Island, French Frigate Shoals, 1991.

Combinations of attackers[1]	Number of attacks	Number successful	% success
M	275	55	20.0
F	72	15	20.8
J	4	0	0.0
MM	23	8	34.8
MF	30	13	43.3
MJ	12	2	16.7
FF	1	1	100.0
FJ	0	0	0
JJ	1	0	0
MFJ	1	0	0

[1] M = Male, F = Female, J = Juvenile.

rison et al. 1983). Therefore, the parasite might gain as much as 47% of its daily energetic expenditure from kleptoparasitizing the boobies which may be more than if they had to forage daily for prey in the open ocean (Vickery and Brooke 1994).

The data show that successful mean chase times were longer than unsuccessful ones supporting Vickery and Brooke (1994). Group chases by Great Frigatebirds of Wedge-tailed Shearwaters were longer than chases by individual robbers. Osorno et al. (1992), noted that a group of frigates averaging three members would be needed for each in the group to obtain the same amount of food that would be obtained by a single bird. In support of that finding, attacks by groups of frigates on shearwaters and boobies (one group of four, 11 groups of three, and 72 groups of two) decreased in number as group size increased. It appears that it would not be beneficial to participate in groups with more than two members, because the odds of obtaining food with each additional member are reduced (see also Furness 1987).

Male Great Frigatebirds feed free-flying young for several months after fledgling but soon abandon them leaving the females to continue to feed the juveniles (Diamond 1975, Nelson 1975). When group chases occurred of shearwaters, juvenile frigatebirds predominately paired with males rather than females (Table 3). Juveniles that acted alone or in groups played a minor part in the interactions and were not successful in obtaining any of the food regurgitated by the hosts. Even if the juveniles were not related to the males they were in direct competition for food. They also appeared to be learning skills to be used later in life by watching and joining the males.

The larger number of shearwaters robbed compared to boobies is consistent with the greater number of shearwaters nesting on East Island (Table 1). There were no nesting Red-footed Boobies or Sooty Terns on East Island, and the numbers of nesting Brown Noddies and Masked Boobies were low. This suggests host selection against Brown Noddies on East Island, although frigatebirds do parasitize Brown Noddies elsewhere (Brockman and Barnard 1979, Gilardi 1994).

Gilardi (1994) showed that Great Frigatebirds kleptoparasitize and partition host selection according to size of parasite and host. At East Island, adult Masked Boobies were attacked almost exclusively by female Great Frigatebirds whereas Wedge-tailed Shearwaters were primarily chased by male Great Frigatebirds. These results support Gilardi's (1994) findings that sex bias for host selection occurs in *Fregata minor*.

I thank Ken McDermond of the U.S. Fish and Wildlife Service in Honolulu and Jennifer Megyesi currently at the Petit Manan NWR for allowing this study to be conducted in the Northwestern Hawaiian Island NWR; Paul Seivert for his guidance and suggestions in the initial stages of data collection; Thane K. Pratt, Scott A. Hatch, Darcy Hu and two anonymous reviewers for their many suggestions and comments on previous drafts of the manuscript; Steven G. Fancy for help with the statistical analysis; and Leona P. Laniawe for her guidance and support throughout the study.

LITERATURE CITED

AMERSON, A. B., JR. 1971. Atoll research bulletin. The natural history of French Frigate Shoals northwestern Hawaiian Islands. No. 150. The Smithsonian Institution, Washington, DC.

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

DIAMOND, A. W. 1975. Biology and behavior of frigatebirds *Fregata spp.* on Aldabra atoll. Ibis 117: 302–323.

FERSTER, C. B., AND B. F. SKINNER. 1957. Schedules of reinforcement. Prentice-Hall, New York.

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

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

GILARDI, JAMES D. 1994. Great Frigatebird kleptoparasitism: sex-specific host choice and age related proficiency. Condor 96:987–993.

GOCHFELD, M., AND J. BURGER. 1983. Age related differences in piracy in frigatebirds from Laughing Gulls. Condor 83:79–82.

HARRISON, C. S. 1990. Seabirds of Hawaii, natural history and conservation. Cornell Univ. Press, Ithaca, NY.

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

NELSON, J. B. 1968. Galapagos, islands of birds. Longmans, London.

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

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

VERNER, JARED. 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.

The Condor 97:814–815
© The Cooper Ornithological Society 1995

UNUSUAL PARASITISM BY THE BRONZED COWBIRD[1]

ETHAN D. CLOTFELTER
Department of Zoology, University of Wisconsin, Madison, WI 53706

TIMOTHY BRUSH
Department of Biology, University of Texas, Pan American, Edinburg, TX 78539

Key words: Molothrus aeneus; *brood parasitism;* Coccyzus americanus; Tyrannus verticalis; Tyrannus couchii; Cyanocorax yncas.

We report four unusual incidences of brood parasitism by the Bronzed Cowbird (*Molothrus aeneus*) in south Texas during July 1993 and June–July 1994: (1) the first reported use of the Yellow-billed Cuckoo (*Coccyzus americanus*) as a host; (2) the first reported use of the Western Kingbird (*Tyrannus verticalis*) as a host; (3) the second reported raising of Bronzed Cowbirds to fledging age by a Couch's Kingbird (*Tyrannus couchii*), a known rejector of cowbird eggs; and (4) a record number of parasitic eggs laid in a single host's nest and still incubated by the host, in this case a Green Jay (*Cyanocorax yncas*).

The Bronzed Cowbird is a generalist brood parasite, known to parasitize nearly 80 species of birds (Friedmann 1929, 1963, 1971; Friedmann et al. 1977; Carter 1984). Bronzed Cowbirds range from Colombia into the extreme southwestern United States, and are common in the Lower Rio Grande Valley region of southern Texas, particularly in the Santa Ana National Wildlife Refuge (SANWR). As part of a larger study of Bronzed Cowbird social behavior (E.D.C.) and a breeding bird study (T.B.) in the SANWR, we examined host nests whenever they were found and made observations of parental behavior.

Although the Yellow-billed Cuckoo is common in the Lower Rio Grande Valley, there are no records of brood parasitism of this species by Bronzed Cowbirds (Friedmann 1929, 1963; Friedmann et al. 1977; Carter 1986). This lack of records is surprising because Yellow-billed Cuckoos are known to be occasional hosts of Brown-headed Cowbirds (*Molothrus ater*; Friedmann 1971), and because they are relatively large-bodied (28–33 cm long) and insectivorous, two characteristics common to many Bronzed Cowbird hosts. There is no evidence that Yellow-billed Cuckoos reject Bronzed Cowbird eggs, either by ejection or by desertion (Carter 1986; Clotfelter, unpubl. data). On 7 June 1994, we found a cuckoo nest in the SANWR, one that previously contained three cuckoo eggs, with one cuckoo egg and one Bronzed Cowbird egg. Both eggs were punctured, presumably by a Bronzed Cowbird. This is consistent with Carter's (1986) observation that Bronzed Cowbirds puncture both host eggs and other cowbird eggs. Brown-headed Cowbirds are not known to puncture host eggs (Scott et al. 1992). On 12 July 1994, we found another nest in the SANWR containing only one punctured cuckoo egg, also presumably punctured by a Bronzed Cowbird.

Bronzed Cowbirds have approximately 11-day nestling periods, typical for a brood parasite (Payne 1977, Carter 1986). Yellow-billed Cuckoos, however, have accelerated nestling periods for their body size (9–11 days; Nolan and Thompson 1975, Potter 1980). As most brood parasites select hosts with developmental periods longer than their own (Payne 1977), it is unlikely that Bronzed Cowbirds can successfully fledge from cuckoo nests. It is possible that parasitism and

[1] Received 13 September 1994. Accepted 1 February 1995.