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BROWN NODDY CHICK PREDATION BY GREAT FRIGATEBIRDS IN THE NORTHWESTERN HAWAIIAN ISLANDS[1]

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Abstract. Adult female Great Frigatebirds (*Fregata minor*) were responsible for 64% of the predatory behaviors on Brown Noddy (*Anous stolidus*) chicks on Tern Island, French Frigate Shoals, Hawaii. Subadults with red orbital rings (presumably females) also preyed on Brown Noddy chicks, although they were observed hunting less frequently than adult females. No adult male frigatebirds were observed hunting in 118.3 hours of observation. Frigatebird predation likely accounted for 95% of mortality observed in Brown Noddy chicks less than 24 days of age. Chicks were as likely to survive to fledging regardless of nest location or down coloration; however, more chicks survived to fledging if hatched between mid-February and mid-May. Unequal sex ratios, sexual size dimorphism, resource partitioning, and breeding strategies of frigatebirds were evaluated to explain why sex differences in frigatebird predation behaviors were observed on Tern Island.

Key words: Fregata minor; Anous stolidus; *predation; kleptoparasitism; seabirds; sex-specific behavior.*

INTRODUCTION

Frigatebirds feed on fish and squid seized at the ocean's surface and commonly kleptoparasitize seabirds. Also, three of the five species are known to prey on seabird chicks (Diamond 1975, Nelson 1976). Several authors have reported frigatebird predation of seabird chicks (Beard 1939, Sprunt 1948, Shea and Mahoney 1983, Ashmole 1963, Schreiber and Ashmole 1970), but whether this behavior occurs at all frigatebird colonies is unknown. Descriptions of the age and sex of frigatebirds observed preying on seabird chicks are not discussed in most of these studies. Here we report age- and sex-specific predation behaviors of Great Frigatebirds and the effect of frigatebird predation on Brown Noddy reproductive success on Tern Island, French Frigate Shoals, Hawaii.

STUDY AREA AND METHODS

French Frigate Shoals is a crescent-shaped atoll situated approximately midway in the Hawaiian Archipelago (23° 45′ N, 166° 17′ W). Tern Island (15.0 ha), located near the northwestern tip of the atoll, is the largest of ten permanent islands and is the only human-made island at French Frigate Shoals. An active coralline rubble runway extends the length of the island, while approximately 4 ha of the island is vegetated. Thirty-seven vascular plant species have been described (Amerson 1971), though vegetation is dominated presently by ten species (Megyesi, pers. observ.). The north and southeastern ends of the island are densely covered with *Tournefortia argentea* and *Scaevola taccada* bushes that are between 1.0–5.0 m in height and 1.0–4.0 m in diameter, while the remainder of the island is dominated by coralline rubble and clumps of vascular plants ≤1.0 m in height, including *Lepturus repens, Chenopodium oahuense, Boerhavia repens, Ipomoea pes-caprae,* and *Portulaca* spp.

Approximately 1,700–2,500 pairs of Brown Noddies nest on Tern Island, with fewer pairs on East and Whale-Skate islands (Megyesi, pers. observ.). Excluding the runway, noddies nest on the ground over the entire island in areas where vegetation is ≤1.0 m in height, though approximately 2% of the Brown Noddies nest ≤1.0 m above the ground in *Chenopodium oahuense* shrubs.

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Although Great Frigatebirds formerly nested on East, Whaleskate and La Perouse islands, by 1990 all 550 pairs had moved to Tern Island (Megyesi 1995). Nesting frigatebirds are concentrated at the north- and southeastern ends of Tern Island in *Tournefortia argentea* and *Scaevola taccada*. There are no ground-nesting frigatebirds on Tern Island.

Four areas on the island were observed during 1980–1982 and 1988–1992. Individual nests in each of the study areas were observed to determine reproductive success. Seventy-two nests in 1980–1981 and 101 nests in 1989–1991 containing eggs or newly hatched chicks were individually numbered and checked daily to determine the age at which nestlings were found missing. Brown Noddy chicks are either white or dark, slate-colored. In 1980–1981 and 1989, the down color of each of the chicks at hatching was recorded as either dark or light.

One of the study areas was used to record seasonal variation in Great Frigatebird predation on Brown Noddy chicks between 21 December 1989 and 12 November 1992. The number of new eggs laid, eggs lost, and newly-hatched chicks within this area were recorded every other day. Noddy chicks that reached 21 d of age within this plot were banded and considered fledged while missing chicks were considered preyed upon by Great Frigatebirds; dead chicks found in the plot were recorded and considered unrelated to frigatebird predation.

During 1989–1991, we made continuous observations of frigatebirds hunting with observation days based on peak Brown Noddy hatching. No observations were made when noddies were incubating eggs or when fewer than five to ten chicks were available, hence the lack of observations during mid-January and mid-July. Observations began at about 06:00 hr and ceased at about 20:00 hr from atop a utility shed 25 m to the south of the study plot. For each Great Frigatebird observed hunting within the plot, age, sex and outcome of each hunting event were recorded. Age of each individual was recorded as adult, subadult or juvenile (<1 year of age) according to plumage. It was not possible to determine the breeding status of adults observed hunting. Sex was recorded as male or female according to plumage. Sex of all subadults and juveniles was recorded as unknown although orbital ring color of subadults was recorded, as Diamond (1975) and Nelson (1976) attribute this characteristic to female Great Frigatebirds. Using plumage coloration and feather wear to identify individuals, we could estimate the minimum number of individuals hunting on each observation day. Hunting events within the study plot were recorded as failures when the frigatebird actively swooped down on a nest without successfully securing prey and as takes when prey was obtained.

RESULTS

Of 2,139 Brown Noddy chicks hatched in 1980–1981 and 1989–1991, 3% (n = 73) were found dead in the nest, 59% (n = 1,256) disappeared before 24 days of age, and 36% (n = 810) fledged. Mean (±SD) age at disappearance from the nest was 9.0 ± 5.6 d (n = 173, range = 0–24 days). Most chicks (86%) disappeared between 0 and 15 days of age.

Ninety-three percent of the Brown Noddy chicks of above-ground nests and 82% of ground nests survived to fledging (n = 87 and 44, respectively, Fisher exact test, P = 0.11). Light-colored chicks fledged at the same rate as dark-colored chicks, regardless of nest location (Fisher exact test, P = 0.27). In all years, chicks that hatched between mid-February and mid-May were more likely to survive to fledging than those hatching after this date (Fisher exact test, n = 754, $P < 0.001$).

We recorded 126 Great Frigatebird predation events on nesting Brown Noddies in 118.3 hr of observation during ten days from 1989–1991 (Table 1). Predation occurred throughout the day but was greatest during 08:01–10:00 and 16:01–20:00 hr (χ^2 = 15.70, df = 6, P = 0.02). Adult females were responsible for 64% of the events; subadults were recorded during the remaining events; and no adult males were seen hunting. There were a minimum of two subadults and ten adult females identified during 118.3 observation hours, and some individuals were observed as many as seven times in one day. All subadults observed hunting in the plot had red orbital rings. Though subadults were observed hunting less frequently, they were successful in obtaining prey 37.8% of the time, whereas adult females were successful during 37.0% of the events (Pearson χ^2 = 0.007, df = 1, P = 0.93).

We observed no predation by Great Frigatebirds as a result of researchers entering the study area to record Brown Noddy nest status. Nesting Brown Noddies did not leave the nesting area

TABLE 1. Great Frigatebird predation of Brown Noddy chicks on Tern Island, French Frigate Shoals, Hawaii, 1989–1991.

Date	Hours of observation	No. potential prey[a] available	No. of failures[b]		No. of takes[b]	
			Female	Subadult[c]	Female	Subadult[c]
12/23/89	11.7	5–10	0	2	0	0
12/24/89	11.5	5–10	0	0	0	0
01/13/90	8.8	25–30	0	0	0	0
01/20/90	4.0	40–50	0	0	0	0
07/16/90	14.0	50–100	9	0	7	0
07/17/90	14.0	50–100	9	9	4	2
08/02/90	13.3	50–100	11	6	7	3
08/04/90	13.0	50–100	4	1	7	1
07/01/91	14.0	50–100	11	7	3	7
07/02/91	14.0	50–100	7	3	2	4

[a] Numbers of Brown Noddy chicks in study plot at the beginning of each observation period.
[b] Predation event according to behavior observed; attempts refer to individuals attempting unsuccessfully to take chicks; takes refer to individuals successfully capturing chicks.
[c] Subadult, presumably females (see Diamond 1975, Nelson 1976).

when the researcher passed through the colony, but remained hovering above or diving at the intruder. Frigatebirds were not observed keying into or following in the wake of the observer.

DISCUSSION

PREDATION EFFECTS ON BROWN NODDY REPRODUCTIVE SUCCESS

There are no mammalian land predators within French Frigate Shoals, and the only resident predator of tern chicks on Tern Island is the Great Frigatebird (USFWS personnel, unpubl. observ., Honolulu HI 1979–1988; Megyesi, pers. observ. 1989–1992).

Ruddy Turnstones (*Arenaria interpres*) and Bristle-thighed Curlews (*Numenius tahitiensis*) are winter migrants at French Frigate Shoals and were observed preying on Sooty Tern, Brown Noddy, White Tern (*Gygis alba*) and Gray-backed Tern (*Sterna lunata*) eggs, but they are not known to prey on seabird chicks here or at other seabird colonies (Crossin and Huber 1970, Loftin and Sutton 1979, Morris and Wiggins 1986, Marks and Hall 1992). We also observed ghost crabs (*Ocypode laevis* and *O. ceratophthalma*) preying on dead and dying Pacific Golden Plovers (*Pluvialis fulva*) and a Wedge-tailed Shearwater chick (*Puffinus pacificus*); however, no ghost crabs occur near the Brown Noddy study areas, and no ghost crab predation of tern species on Tern Island was documented during 1979–1992 (M. Rauzon, B. Flint, P. Sievert, K. Niethammer, pers. comm.). From 21 December 1989 to 12 November 1992 no Brown Noddy chicks were rediscovered in new locations after they had been recorded as missing. Chicks were not able to burrow under coralline rubble, and there was no vegetation in the study area suitable for chicks to hide and go unnoticed. We are confident that 1,256 chicks could not have been missed by researchers and conclude that they were taken from the study area by Great Frigatebirds.

We suggest that Great Frigatebirds were responsible for 95% (n = 1,329) of mortality observed in Brown Noddy chicks less than 24 days of age on Tern Island. The size of the chick and wing growth may preclude frigatebirds from swallowing noddy chicks older than 21 days in fact, the five cases of predation that occurred after 21 days were subadults that were unsuccessful in swallowing the chicks. Predation occurred throughout each of the observation days, but may have been greater between 08:00–10:00 hr and 16:00–20:00 hr as a result of roosting frigatebirds leaving or returning to roost on the island, respectively (see also Cummins 1995).

Given the extensive period that our study spans, Great Frigatebird predation is probably an annual occurrence on Tern Island and a limiting factor of Brown Noddy reproductive success. Most noddy chicks were taken after they were exposed by brooding noddies flying up to defend against the attacker, although some frigatebirds were observed grabbing the tails of brooding adults, lifting them from the nest into the air and swooping back to the ground to retrieve the exposed chick. Both females and subadults persisted in preying on Brown Noddy chicks despite a success rate of just 37.0% and 37.8%, respectively. The persistency of brooding noddy adults in protecting their chick, and the

difficulty frigatebirds had locating exposed prey, may explain these low success rates. In contrast, Cummins (1995) and Osorno et al. (1992) found success rates of 4.0% and 5.8%, respectively for kleptoparasitic behaviors.

Although the rate of disappearance from the nest did not differ with respect to down coloration or nest location, Brown Noddy chicks may have higher survival prior to mid-May when more abundant and easily obtained Sooty Tern chicks are available (Megyesi and Griffin, in press). Between 55,000 and 100,000 pairs of Sooty Terns breed on Tern Island (B. Flint, pers. comm.; Megyesi pers. observ.). We frequently observed female adult and subadult frigatebirds taking Sooty Tern chicks from all parts of the island between April and July, though these observations were not quantified. Beard (1939) noted that Magnificent Frigatebirds preyed on Sooty Tern chicks on the Dry Tortugas, although he found no evidence that Brown Noddy chicks were taken. He attributed this to the more tenacious behavior of brooding noddy adults. Indeed, Brown Noddy adults on Tern Island will dive aggressively at all intruders to the colony, while Sooty Terns will stand and defend the nest, usually pecking at a human intruder's hands and feet or scurrying away when approached (Megyesi, pers. observ.). Brown (1973) also noted that Sooty Tern chicks took significantly longer to gain mobility than did Brown Noddy chicks. Both of these behavioral differences may make Sooty Tern chicks more vulnerable than Brown Noddy chicks to frigatebird predation and may explain why Brown Noddy chicks hatched by mid-May were more likely to survive to fledging.

SEX-SPECIFIC AND AGE-RELATED DIFFERENCES IN FRIGATEBIRD PREDATION BEHAVIOR

Our results show that seabird chick predation by frigatebirds on Tern Island was sex-specific to females only. Though no comparative frigatebird predation studies exist, a number of works have examined age-related and sex-specific differences in frigatebird kleptoparasitic behaviors (Diamond 1972, Gochfeld and Burger 1981, Osorno et al. 1992, Gilardi 1994, Cummins 1995). We considered the potential effects of unequal sex ratios, differences in wing-loading, resource partitioning, parental investment, and age-related foraging ability to explain our findings.

Although roosting females outnumber males on Tern Island, over 550 pairs of frigatebirds nest on the island. Thus, males are abundant and it is unlikely that unequal sex ratios alone can explain why adult males were never observed preying on Brown Noddy chicks.

Gibbs and Gibbs (1987) suggested that male frigatebirds may be able to pursue prey more easily because of their lower wing-loading. Nelson (1976), Fairchild et al. (1985) and Jehl and Murray (1986) reported that a male frigatebird's smaller size allows greater agility in collecting nest material and in perching atop potential nest sites to display to females flying overhead. Our observations of female adults and subadults taking Brown Noddy chicks did not suggest that this type of predatory behavior requires much agility. Additionally, the weight of 1–15 day old Brown Noddy chick (average 28–125 g, Megyesi, pers. observ.) is less than a typical fish and squid prey (average 122–180 g, Diamond 1975) suggesting that prey size and wing-loading ability are not effecting this behavior.

Asymmetrical parental investment in chick rearing could motivate female frigatebirds to forage closer to the breeding colony (Osorno et al. 1992, Gochfeld and Burger 1981, Gibbs and Gibbs 1987). Diamond (1972) and Trivelpiece and Ferraris (1987) documented differences in parental investment in Magnificent Frigatebirds, whereby females provided post-fledgling care, and annual breeding was precluded. On Midway Atoll, Gilardi (1994) observed annual breeding in male Great Frigatebirds, and year-old chicks were fed exclusively by females. In contrast, Nelson (1976) and de Vries (1984) observed both Great Frigatebird parents feeding their chicks for up to 16 months on Tower Island, Galapagos. Coello et al. (1977) observed that male and female Great Frigatebirds shared chick rearing on Genovesa Island, Galapagos, though males provided more nocturnal feedings than females. We, too, observed that both sexes feed young during all stages of development on Tern Island during 1989–1992. Resource partitioning may help to explain the sex-specificity of predatory behaviors observed on Tern Island, but it does not explain why only a few adult females and subadults exhibit this behavior rather than all females, as our data suggest.

Both Gilardi (1994) and Cummins (1995) proposed a correlation between the size of the frigatebird and the host's size, where the smaller males kleptoparasitized noddies and Wedge-

tailed Shearwaters, and the larger females preferred Masked Boobies (*Sula dactylatra*) and Red-tailed Tropicbirds (*Phaethon rubricauda*). Our observations of females foraging for Brown Noddy chicks at the colony suggest that feeding areas and energy requirements rather than prey size could partition the sexes.

We found no differences in foraging success between adult female and subadult Great Frigatebirds, though we only observed subadults during 36% of the events. In contrast to our results, Gilardi (1994) found that success of Great Frigatebird kleptoparasites improved with age on Midway Atoll, and Ashmole (1963) suggested that subadult frigatebirds on Ascension Island were less efficient in capturing Sooty Tern chicks than were adults, although differences were not significant. The subadults we observed may have been specialists who were highly proficient in hunting noddy chicks.

Given the relatively small proportion of frigatebirds that hunt seabird chicks on the island, we suspect that this behavior is not widespread throughout the Tern Island frigatebird colony. Thus, only a limited number of frigatebirds practice this foraging behavior. Resource partitioning and differences in energy requirements may in part explain why this behavior is sex-specific to females, but studies of marked individuals are needed to understand what motivates these few female adults and subadults to prey on seabird chicks on Tern Island. It is clear, however, that the impact of these individuals is substantial on reproductive success of Brown Noddies breeding between mid-May and mid-February.

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