The influence of sexual dimorphism on kleptoparasitism of Blue-footed Boobies by Brown Boobies

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In the Canal de Ballenas, Gulf of California, Mexico, we observed Brown Boobies (*Sula leucogaster*) steal food from Blue-footed Boobies (*Sula nebouxii*), a previously undescribed kleptoparasitic interaction. Brown Boobies were the primary kleptoparasite of Blue-footed Boobies. Of the 28 attacks recorded we determined the sex of the Brown Boobie 16 times, and in all cases the Brown Boobies were females, the larger of the two sexes. Kleptoparasitism may be facilitated by the juxtaposition of these two species, with slightly different foraging strategies, in mixed-species feeding flocks.

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Dans le canal de Ballenas, golfe de Californie, Mexique, nous avons vu des Fous bruns (*Sula leucogaster*) voler de la nourriture à des Fous à pattes bleues (*Sula nebouxii*), un comportement de cleptoparasitisme inconnu à ce jour. Les Fous bruns sont les principaux cleptoparasites des Fous à pattes bleues. Le sexe des Fous bruns a pu être déterminé dans 16 des 28 cas observés et il s'agissait toujours de femelles, plus grosses que les mâles. Le cleptoparasitisme est probablement favorisé par la juxtaposition, dans les colonies alimentaires mixtes, de ces deux espèces à stratégies alimentaires légèrement différentes.

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Introduction

The Brown Booby and the Blue-footed Booby are both sexually dimorphic in body size (Nelson 1978), and forage relatively close to shore (Schreiber and Clapp 1987; Anderson and Ricklefs 1987). In the Gulf of California, one of the few areas where the two species are sympatric, one would expect considerable overlap in foraging range which could lead to direct competition.

In this paper we report observations of one form of competition that to our knowledge has not been described: kleptoparasitism of Blue-footed Boobies by Brown Boobies. We then discuss the apparent influence of (*i*) reverse sexual dimorphism on the sex of the kleptoparasite and victim, and (*ii*) prey behavior and interspecific differences in foraging behavior on the occurrence of kleptoparasitism.

Methods and materials

The Canal de Ballenas, Gulf of California, Mexico (113°20'W, 29°00'N), is used by nonbreeding Brown Boobies and Blue-footed Boobies. Between April 1985 and April 1986 we censussed seabirds on 172 days when conditions were excellent to good (2 or less on the Beaufort scale). We used a consistent but nonrandom search method (Tershy et al. 1989) and counted all seabirds within a 100-m radius around our 4.5-m skiff. When possible we recorded the sex and age-class (following Harrison 1983). At the same time we recorded the participants, duration, outcome, and a description of kleptoparasitic attacks. We supplement these data with less systematic observations of kleptoparasitism, made between May 1983 and August 1984.

Results and discussion

Brown Boobies were responsible for 14 of the 20 kleptoparasitic attacks on Blue-footed Boobies recorded between April 1985 and April 1986 (Yellow-footed Gull (*Larus livens*), 4; Magnificant Frigatebird (*Fregata magnificens*), 1; South Polar Skua (*Catharacta maccormicki*), 1). During 1983 and 1984 we

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saw 14 additional kleptoparasitic attacks by Brown Boobies on Blue-footed Boobies.

We recorded the sex and age-class of the kleptoparasitic Brown Boobies in 16 of the 28 attacks, and in all cases they were adult females. This is significantly different from expected if kleptoparasitic attacks were distributed evenly amongst male, female, and immature Brown Boobies ($\chi^2 = 13.107$, $P < 0.005$; the observed sex and age ratio for 1985–1986 was 1:1.5:0.3 immature).

To our knowledge, Brown Booby kleptoparasitism of Blue-footed Boobies has not been reported. An excerpt from our field notes of 21 July 1985 describes a typical event:

09:20:14. An adult female Brown Booby sees a Blue-footed Booby ~50 m away and starts to fly towards it at increased speed (the Blue-footed is not carrying a fish in its bill). 09:20:20. She catches up with the Blue-footed and it turns and snaps at her. The Brown grabs the Blue-footed by the tail and they crash into the water. The Brown lunges at the head of the Blue-footed and the Blue-footed regurgitates a ~10 cm fish and then flies away. 09:20:51. The Brown picks up and swallows the fish.

We observed 20 kleptoparasitic attacks on Blue-footed Boobies by Brown Boobies from start to finish. Seventeen (85%) attacks resulted in body contact when the Brown Booby grabbed the Blue-footed's tail ($n = 14$) or wing ($n = 3$). This usually resulted in both birds crashing into the water ($n = 14$).

Blue-footed Boobies usually swallow their prey underwater or just after coming to the surface (personal observation). In all but one instance we did not see fish in the bills of individuals being chased by Brown Boobies.

Single Brown Boobies usually kleptoparasitized Blue-footed Boobies ($n = 21$), but occasionally as many as five individuals chased a single Blue-footed Booby. When more than one Brown Booby was involved, the Blue-footed was often grasped by the head or neck and held underwater. Brown Boobies were successful in 11 (52%) of the 21 attacks in which success was determined.

Brown Boobies have been observed stealing food directly from Masked Boobies (Simmons 1972) and beating Magnificent Frigatebirds to fish dropped by another bird (Richardson 1948; personal observation). In the Canal de Ballenas female Brown Boobies appeared to be skilled kleptoparasites. Like specialist kleptoparasites (Furness 1987) they were apparently able to assess whether or not their victims had food in their crops, then force them to regurgitate.

Their success rate (52%) is high compared with that found in skuas, jaegers, frigatebirds, and gulls (Furness 1987). One reason for this may be the frequency of body contact (85%), which Furness (1987) considers rare in seabird kleptoparasitism and which was more frequent and appeared more violent than that observed in kleptoparasitic interactions between other species in the study area (personal observation). Maxson and Bernstein (1982) found that physical contact increased the probability of South Polar Skuas being successful when kleptoparasitizing Blue-eyed Shags (*Phalacrocorax atriceps*). However, Andersson (1976) did not find this relationship significant in kleptoparasitism of Northern Gannets (*Sula bassana*) by Great Skuas (*Catharacta skua*).

Niche separation based on different foraging techniques or spatial and temporal segregation may break down when mixed-species feeding flocks form over schools of fish forced to the surface by large aquatic predators. The juxtaposition of seabirds with different foraging techniques may also increase the rates of kleptoparasitism (Brockmann and Barnard 1979).

In the Canal de Ballenas, Brown Boobies and Blue-footed Boobies form mixed-species feeding flocks with Brown Pelicans (*Pelecanus occidentalis*), Heermann's Gulls (*Larus heermanni*), and Yellow-footed Gulls. All birds in such flocks appear to be capturing the same prey. These flocks usually form over schools of Pacific sardines (*Sardinops sagax*) and thread herring (*Opisthonema libertate*), which are being forced to the surface by marine mammals and predatory fish (personal observation).

Duffy (1980, 1982) suggested that seabirds will kleptoparasitize victims that have access to prey at greater depths. In these mixed-species feeding flocks, Blue-footed Boobies dive from greater heights and presumably to greater depths than Brown Boobies (personal observation). They frequently continue diving once the bait fish are no longer being forced to the surface and the Brown Boobies have stopped diving (unpublished field notes). At such times Brown Boobies may have greater success kleptoparasitizing Blue-footed Boobies than fishing for themselves. Thus, the apparent interspecific difference in foraging technique may facilitate kleptoparasitism.

Kushlan (1978) suggested that larger species tend to kleptoparasitize smaller species. Although exceptions exist (e.g., Carroll and Cramer 1985), this may be true more often when kleptoparasitism involves frequent body contact, since larger species are usually agonistically superior to smaller ones (Brown and Maurer 1986). Although Blue-footed Boobies are larger than Brown Boobies, both species show considerable reverse sexual dimorphism: female Brown Boobies are about 7% heavier than male Blue-footed Boobies (Nelson 1978; E. Cardiff, unpublished data). Furthermore, unlike frigatebirds, which dive on their victims from high altitudes (Pennycuick 1987), female Brown Boobies were always observed to overtake Blue-footed Boobies in level flight. Based on the positive correlation between wing loading and flying speed (Pennycuick 1987) and their relative wing loadings (Nelson 1978), female Brown Boobies should be able to fly faster than male, but not female, Blue-footed Boobies. Relative body weight and wing loading may explain why only females were observed kleptoparasitizing, and suggests, as do our impressions of relative size, that only male Blue-footed Boobies were victims.

A better understanding of the extent to which kleptoparasitism is facilitated by differences in the foraging techniques of these two sulids, and their juxtaposition in mixed-species feeding flocks awaits more detailed at-sea observations of foraging behavior. Such observations, when combined with samples of prey regurgitated to chicks, would also be useful in examining larger-scale ecological interactions between Brown Boobies and Blue-footed Boobies.

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