

The Auk 116(2):545–548, 1999

Kleptoparasitism by Brown Skuas on albatrosses and giant-petrels in the Indian Ocean

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The behavior of skuas and jaegers (subfamily Stercorarinae) when kleptoparasitizing other seabirds has been studied in detail at breeding colonies (Furness 1987a, b; Maxson and Bernstein 1982; Le Corre and Jouventin 1997), at a coastal estuary along a migration route in Britain (Taylor 1979), in boundary currents off Peru and south Africa (Duffy 1982), and in pelagic waters of the Eastern Tropical Pacific (Spear and Ainley 1993). The size of the host is usually smaller than that of the kleptoparasite. Indeed, only 9 of the 40 host species recorded had a mean body mass greater than that of the parasite (mean body mass of the host was 1.1 to 2.4 times greater than that of the kleptoparasite; Table 1).

Attacks by skuas on giant-petrels and albatrosses have not been described. Therefore, we were surprised to see attempted kleptoparasitism by Brown Skuas (form from the Crozet and Kerguelen archipelagoes = *Catharacta antarctica lonnbergi* sensu Devillers 1978, Malling-Olsen and Larsson 1997; but see Peter et al. 1994) on a Wandering Albatross (*Diomedea exulans*) and a Northern Giant-Petrel (*Macronectes halli*), because these hosts are 5.9 and 2.6 times larger, respectively, than the skuas (Table 1). We also report an attempted kleptoparasitism by a Brown Skua on a Light-mantled Albatross (*Phoebastria palpebrata*) in the Kerguelen Archipelago, and four attempts by Brown Skuas (the Amsterdam Island [Indian Ocean] form, which is similar in size to the Tristan Brown Skua [*C. a. hamiltoni*]) on Yellow-nosed Albatrosses (*Thalassarche chlororhynchos bassi*) adjacent to the primary breeding colony of the latter at Amsterdam Island.

The kleptoparasitism attempts on the Wandering Albatross and Northern Giant-Petrel were observed while we surveyed seabirds from the R/V *Marion Dufrenoy* in the southwestern Indian Ocean. The incident involving the albatross happened on 9 November 1997 at 44°09'S, 51°26'E (238 km from the Crozet Islands), and that involving the giant-petrel occurred on 14 November 1997 at 49°21'S, 66°43'E (147 km from the Kerguelen Islands). LBS, CSO, and SNGH saw both attempts from the flying bridge; DL saw the first attempt from the bridge.

The Brown Skua that attacked the albatross was in

its first year, based on uniform dull-brown feather color, no dorsal flecking or hackle sheen on the neck feathers, and a bicolored bill. The skua making the attempt on the giant-petrel was a subadult (i.e. older than one year but not an adult) based on presence of light flecking on the dorsal surface but absence of prominent hackles. Based on plumage, both the albatross and the giant-petrel were subadults or adults.

The attack on the Wandering Albatross was initiated from 20 m above sea level (asl). Using continuous flapping flight, the skua descended at an angle of about 35° directly toward and from behind the albatross, which was gliding 2 to 3 m asl. The skua did not strike the albatross, although the latter began continuous flapping flight, increased its speed, and initiated evasive maneuvers using an irregular flight path, including a 160° change in course. The skua usually remained 0.5 to 2 m behind the albatross, but several times it grabbed the rectrices or inner secondaries of the albatross. The most aggressive contacts occurred on the two occasions that the albatross tried to increase its altitude. The chase ended unsuccessfully (i.e. the skua obtained no food) after a chase of 1 to 1.5 min, just after the skua had pulled vigorously on the tail of the albatross for 2 to 3 s.

The attack on the Northern Giant-Petrel also was unsuccessful and was initiated from 30 m asl at an angle of descent of about 45°. The giant-petrel was gliding with periodic wing beats at 2 to 3 m asl. The skua did not strike the petrel but came within 0.5 m as it swooped over and past it. The skua then increased its altitude steeply to 10 m above and beyond the petrel, reversed direction, increased its speed with strong flapping, and descended again. Upon reaching the petrel, the skua grabbed its scapulars or inner secondaries as the petrel tried to increase its altitude. Upon being grabbed, the petrel dropped to the water from 3 m asl. The skua hovered for several seconds 2 m above the petrel and then departed.

On 29 December 1993, JB observed a probable attempted kleptoparasitism by an adult Brown Skua on a Light-mantled Albatross at Mayes Island (49°28'S, 69°57'E) in the Kerguelen Islands. The skua stooped on the albatross from 60 m asl at an angle of about 40° as the albatross was flying 25 to 30 m asl along an island ledge 300 m inland from the sea.

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TABLE 1. Prior records of kleptoparasitism in which skuas and jaegers were smaller than their hosts, and new records of Brown Skuas attacking large procellariiforms. Body mass was averaged between the sexes for all species except Yellow-nosed Albatross, White-chinned Petrel, Razorbill, and Common Murre. "Difference" is the mean mass of the host divided by that of the kleptoparasite.

Kleptoparasite	\bar{x} Mass (g)	Host	\bar{x} Mass (g)	Difference	Source ^a
Prior records					
Parasitic Jaeger	418	Common Murre	990	2.4	1, 2, 3
Pomarine Jaeger	654	Blue-footed Booby (<i>Sula nebouxii</i>)	1,542	2.4	4, 5, 6
Great Skua	1,410	Northern Gannet	3,080	2.2	1, 2, 3
South Polar Skua	1,350	Imperial Shag	2,799	2.1	7, 8, 9
Pomarine Jaeger	695	White-chinned Petrel	1,134	1.6	4, 2, 10
Parasitic Jaeger	418	Razorbill	620	1.5	1, 2, 11
Pomarine Jaeger	654	Sooty Shearwater (<i>Puffinus griseus</i>)	799	1.2	12, 5, 5
Parasitic Jaeger	405	Juan Fernandez Petrel	428	1.1	12, 13, 14
Brown Skua	1,635	Masked Booby	1,750	1.1	15, 5, 15
New records					
Brown Skua	1,635	Wandering Albatross	9,580	5.9	21, 2, 16
Brown Skua	1,635	Northern Giant-Petrel	4,250	2.6	21, 2, 17
Brown Skua	1,635	Light-mantled Albatross	3,150	1.9	21, 2, 18
Brown Skua	1,450	Yellow-nosed Albatross	2,070	1.4	21; 19, 20; 10

^a Numbers refer to source of observation, source of kleptoparasite mass, and source of host mass, respectively. 1, Furness (1978); 2, Furness (1987a); 3, Birkhead and Harris (1985); 4, Duffy (1982); 5, Spear and Ainley (1997); 6, Nelson (1978); 7, Maxson and Bernstein (1982); 8, Ainley et al. (1985); 9, Bernstein and Maxson (1984); 10, Warham (1977); 11, Lloyd (1976); 12, Spear and Ainley (1993); 13, Spear and Ainley (unpubl. data); 14, Spear et al. (1992); 15, Le Corre and Jouventin (1997); 16, Voisin (1969); 17, Voisin (1968); 18, Weimerskirch et al. (1986); 19, Malling-Olsen and Larsson (1997); 20, Stahl et al. (1996); 21, this paper.

When the skua tried to grab the nape of the albatross, the albatross began evasive flight and uttered a shrill call but did not regurgitate any food. Upon completing the attack, the skua returned to its territory on an adjacent slope. The attack may have been an act of territory defense, but this was unlikely because skuas at Mayes Island were not seen attacking albatrosses during frequent flights of the latter over the skuas' territories.

On 23 and 24 November 1997, SNGH saw four kleptoparasitism attempts by Brown Skuas on Yellow-nosed Albatrosses. Three of the attempts occurred while the ship was anchored 1 km from Amsterdam Island (37°50'S, 77°33'E); fishing activity by the ship's crew had attracted about 50 Yellow-nosed Albatrosses, 2 Shy Albatrosses (*Thalassarche cauta*), about 20 White-chinned Petrels (*Procellaria aequinoctialis*), and 3 Brown Skuas (*C. a. hamiltoni*). A successful attempt occurred when a subadult Brown Skua descended at an angle of 30° from 30 m above and behind an adult Yellow-nosed Albatross that was gliding (with occasional flapping) 1 m asl and carrying a piece of offal in its bill. The skua did not strike the albatross but caused it to adopt an erratic course and increase its speed using continuous flapping. The skua pulled up to 10 m and made a second stoop, causing the albatross to drop the offal, which the skua caught and swallowed in flight. The second and third attempts occurred 20 min later when an adult Brown Skua briefly chased two different adult Yellow-nosed Albatrosses that were carrying offal. In both cases, up to eight other Yellow-nosed Albatross-

es followed behind the skua and the birds with the offal. When the latter landed on the water, surrounded by squabbling albatrosses, the skua was reluctant to approach and discontinued the chase. The fourth attempt occurred at St. Paul Island (38°43'S, 77°32'E), 95 km from Amsterdam Island, on 24 November 1997. SNGH and JB saw a Brown Skua stoop on an adult Yellow-nosed Albatross from about 350 m asl at an angle of 30° as the albatross was gliding along the island's crater rim. The albatross, which was not carrying prey, took evasive action (increased flapping with erratic course) as the skua pulled up to make a second stoop before departing.

The size ratios of the Brown Skuas and their "small" albatross hosts that we observed at Amsterdam, St. Paul, and Mayes islands (host:skua = 1.4:1 and 1.9:1; Table 1) were similar to those of prior observations where the hosts were larger than the parasites (range 1.1:1 to 2.4:1). Our observations of kleptoparasitism by Brown Skuas on small albatrosses were also similar to those of skuas chasing Northern Gannets (*Morus bassanus*), Masked Boobies (*Sula dactylatra*), Imperial Shags (*Phalacrocorax atriceps*), Common Murres (*Uria aalge*), and Razorbills (*Alca torda*) because in each case (i.e. 6 of the 13 parasite-host relationships; Table 1), the skuas operated near breeding colonies of their hosts. This facilitated frequent attempts, thus increasing the odds for success with minimal energy expenditure when searching for potential hosts.

Although three of the five attempts by Brown Skuas on albatrosses were in an unnatural context (hu-

man fishing activities), the occasional use of this behavior in a natural context suggests that attempted kleptoparasitism on species of smaller albatrosses is not unusual. This conclusion is consistent with observations elsewhere (Table 1), in which host species weighing up to 2.4 times more than skuas were kleptoparasitized occasionally (but see below). However, even when considering the aggressiveness, strength, and tenacity of skuas, the attacks on the Wandering Albatross and the Northern Giant-Petrel were unexpected because the Crozet-Kerguelen form of Brown Skua averages six times smaller than the albatross, and the formidability of giant-petrels is well known. For example, during land-based confrontations over carrion, giant-petrels dominate all other avian species, including skuas (L. Spear, S. Howell, and J. Bried pers. obs.). Similarly, during confrontations over dead prey at sea, the giant-petrel was the only species (others involved were Black-browed [*Thalassarche melanophris*], Gray-headed [*T. chrysostoma*], and Sooty [*Phoebastria fusca*] albatross) able to exclude the Wandering Albatross (Weimerskirch et al. 1986), which averages 2.3 times larger than the petrel (Table 1).

The form of Brown Skua breeding on the Crozet and Kerguelen archipelagos is the largest, most tenacious *Catharacta* (Furness 1987a, Malling-Olsen and Larsson 1997), and conceivably it could succeed at kleptoparasitizing the less-mobile giant-petrel and "great" albatross. An analysis of the expected success rate of skuas as a function of the parasite-host mass differential (Fig. 1), however, revealed a significant negative relationship, indicating that, on average, the success rate of kleptoparasites should become zero as the mass of the host approaches 1.4 times that of kleptoparasite. Thus, it is unlikely that the behavior of the skuas that attacked the Northern Giant-Petrel and Wandering Albatross was adaptive. We suspect that because the two skuas were young and less experienced, they overestimated their capabilities.

The greatest deviation from the predicted success rate shown in Figure 1 was the relationship reported by Furness (1978), in which Great Skuas (*Catharacta skua*) achieved a much higher success rate than expected (success rate = 0.30 from hosts 2.2 times larger) when attacking Northern Gannets returning to a breeding colony. In his study, gannets were regular victims of skuas. The higher success rate occurred mainly because (1) several skuas often attacked a single gannet simultaneously, and (2) the gannets fed locally in waters that were highly productive. As a result, the gannets could find additional food relatively easily so that the occasional loss of food to skuas was of low cost. In this context, the relationships among Brown Skuas and albatrosses may be different. Albatrosses are probably less likely to be attacked by groups of Brown Skuas because colonies of the latter tend to be small (Stahl et al. 1996) com-

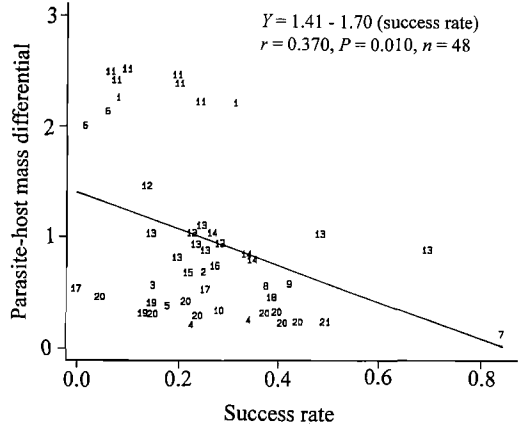


FIG. 1. Relationship between success rate of kleptoparasitism by skuas and jaegers and parasite-host mass differential (host mass divided by kleptoparasite mass). Mass of hosts and kleptoparasites are from this paper and Spear and Ainley (1997). Success rate is the number of successful attacks divided by the number of attacks. Data are from Furness (1987b: table 5.1) and Spear and Ainley (1993). Only parasite-host relationships with 10 or more observations were used in the analysis. Data points were "jittered" to prevent overlap. Numbers denote different host-kleptoparasite combinations: 1, Great Skua vs. Northern Gannet; 2, Great Skua vs. Common Murre; 3, Great Skua vs. Razorbill; 4, Great Skua vs. Atlantic Puffin (*Fratercula arctica*); 5, Great Skua vs. Black-legged Kittiwake (*Rissa tridactyla*); 6, South Polar Skua (*Catharacta maccormicki*) vs. Imperial Shag; 7, South Polar Skua vs. Wedge-tailed Shearwater (*Puffinus pacificus*); 8, Pomarine Jaeger (*Stercorarius pomarinus*) vs. Juan Fernandez Petrel (*Pterodroma externa*); 9, Pomarine Jaeger vs. Wedge-tailed Shearwater; 10, Pomarine Jaeger vs. Sooty Tern (*Sterna fuscata*); 11, Parasitic Jaeger (*Stercorarius parasiticus*) vs. Common Murre; 12, Parasitic Jaeger vs. Razorbill; 13, Parasitic Jaeger vs. Atlantic Puffin; 14, Parasitic Jaeger vs. Black-legged Kittiwake; 15, Parasitic Jaeger vs. Hartlaub's Gull (*Larus hartlaubii*); 16, Parasitic Jaeger vs. Sabine's Gull (*Xema sabini*); 17, Parasitic Jaeger vs. Sandwich Tern (*Sterna sandvicensis*); 18, Parasitic Jaeger vs. Sooty Tern; 19, Parasitic Jaeger vs. Common Tern (*Sterna hirundo*); 20, Parasitic Jaeger vs. Arctic Tern (*Sterna paradisaea*); 21, Long-tailed Jaeger (*Stercorarius longicaudus*) vs. Leach's Storm-Petrel (*Oceanodroma leucorhoa*).

pared with those of Great Skuas (Klomp and Furness 1992). Furthermore, the duration of foraging trips of albatrosses is much longer than that of other seabirds (Weimerskirch et al. 1988, Jouventin and Weimerskirch 1990, Prince et al. 1992). Therefore, giving up food to skuas is of higher cost, and albatrosses would probably be less likely to do so compared with

Northern Gannets. These differences might help to explain the paucity of reports of attempted kleptoparasitism by skuas on large procellariiforms.

Acknowledgments.—We thank the officers and crew of R/V *Marion Dufresne* for cooperation and great food. We are especially grateful to Pierre Jouventin for inviting us. We thank David Ainley, Lisa Ballance, Stephen Maxson, Jeff Marks, and an anonymous reviewer for helpful comments on the manuscript. Funding to LBS, SNGH, and CSO was by the U.S. National Science Foundation supplement to grant OPP95-26865 to David Ainley and LBS; support to JB and DL was provided by the Institut Francais pour la Recherche et al Technologie Polaires.

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Received 1 May 1998, accepted 29 July 1998.

Associate Editor: J. S. Marks