

TRIOS OF BROWN SKUAS AT BIRD ISLAND, SOUTH GEORGIA: INCIDENCE AND COMPOSITION

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Abstract. Cooperative breeding is unusual in seabirds, but recorded in varying proportions in Brown Skuas (*Stercorarius* [= *Catharacta*] *lonnbergi*). With no evidence for kin selection or delayed dispersal, nor for any reproductive advantage, the reason for its occurrence in skuas is uncertain. This study describes the incidence, composition, and breeding characteristics of trios of Brown Skuas at Bird Island, South Georgia. Trios were recorded in nine seasons, including a polygynous and a polyandrous trio found in both 2000–2001 and 2001–2002. In some years, birds hatched three chicks from supranormal clutches, which is exceptional in skuas and jaegers, yet their overall performance was no better than monogamous pairs. I suggest that compared with closely related taxa, Brown Skuas have a slight behavioral or genetic predisposition that facilitates cooperative breeding. Cooperation conveys a minor advantage in territory acquisition, but none in terms of reproductive success (particularly for polygynous groups), and consequently has not proliferated at most colonies.

Key words: cooperative breeding, habitat saturation, polygyny, supranormal clutch.

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Resumen. La crianza cooperativa es inusual en aves marinas pero se ha reportado en diversa medida en *Stercorarius* [= *Catharacta*] *lonnbergi*. Sin ninguna evidencia sobre selección de parentesco o dispersión retrasada, ni ninguna ventaja reproductiva, se desconoce por qué sucede en los págalos. Este estudio describe la incidencia, composición y características de cría de tríos de *S. lonnbergi* en Bird Island, Georgia del Sur. Varios tríos fueron monitoreados durante nueve estaciones, incluyendo un trío polígamico y otro poliándrico encontrados en 2000–2001 y 2001–2002, respectivamente. En algunos años las aves lograron la eclosión de tres polluelos de nidadas más grandes de lo normal, lo cual es excepcional en págalos, pero su éxito no fue mayor que el de parejas monógamas. Se sugiere que en comparación con taxa estrechamente

relacionados, *S. lonnbergi* tiene una ligera predisposición de tipo comportamental o genética que facilita la cría cooperativa. La cooperación conlleva una cierta ventaja en la adquisición de territorios, pero ninguna ventaja en términos de éxito reproductivo (en particular para grupos polígamicos), y en consecuencia no ha proliferado en la mayoría de las colonias.

Cooperative breeding, where three or more adults jointly raise offspring, is rare, particularly in seabirds (Stacey and Koenig 1990). One exception is the Brown Skua (*Stercorarius* [= *Catharacta*] *lonnbergi*), in which it occurs frequently in three archipelagos in the New Zealand area, and is recorded, albeit at extremely low density, at colonies elsewhere (Hemmings 1994). These associations are unusual compared with most cooperative systems. Breeding groups in New Zealand are almost exclusively polyandrous, all males in a group copulating with one female and potentially sharing paternity both between and within years (Hemmings 1989, Millar et al. 1994), and in addition, birds are virtually always unrelated (Young 1998).

Although the behavioral ecology of these groups has been studied extensively in the Chatham Islands, New Zealand (Young 1978, 1994, 1998, Hemmings 1989, 1994), there is much less information from other sites. Here I report on the incidence and composition of Brown Skua trios present on Bird Island, South Georgia. The breeding characteristics of trios are compared with those of monogamous pairs to determine whether they experience any reproductive advantage. The results are discussed in the context of the evolution of cooperative mating systems in this and other skua species.

METHODS

In late November and December 2000, ca. 250 Brown Skua territories at Bird Island, South Georgia (54°00'S, 38°03'W), were visited, the nests located, and the presence of trios of breeding birds recorded. Clutch size and egg dimensions (length and breadth to the nearest 0.1 mm) were recorded for the trios and for 97 pairs. In addition, hatching date and hatching and fledging success were followed for trios by daily visits around the time of peak hatching and every 7–10 days thereafter. Indices of egg volume were calculated as $0.00048 \times \text{length} \times \text{breadth}^2$ (Hemmings 1989). Adults from pairs and trios were captured, banded, weighed, and measured (maximum wing chord, head

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plus bill length, bill length, bill depth, and tarsus length). A small (<200 μ L) blood sample was taken from the tarsal vein of one bird in each pair and all birds in trios, and stored in 90% ethanol. DNA was subsequently extracted from the blood samples, PCR amplification carried out with primers 2550F/2718R, PCR products visualized on a 3% agarose gel, and birds sexed as male or female according to the presence of single or double bands, respectively (Fridolfsson and Ellegren 1999). The two territories with trios were also visited in the following season (December 2001) to determine whether the same banded individuals were breeding together. In addition, information on trios at Bird Island in previous seasons was collated from unpublished British Antarctic Survey reports and published sources (Bonner 1964, Osborne 1985).

RESULTS

In the 2000–2001 season, two trios were recorded (<1% of all territories). In both trios, all adults were active in nest defense, and took turns incubating the eggs. Molecular genetic analysis of the blood samples indicated that one trio was polyandrous (two males and one female) and the other polygynous (two females and one male). Skuas show reverse sexual size dimorphism (Catty et al. 1999), and morphometry corroborated the results of the genetic sexing procedure.

The clutches of the polyandrous and polygynous trios were two and three eggs, respectively. Sixteen percent of the nests of pairs held one egg, and the remainder held two eggs ($n = 97$). The volumes of eggs laid by trios (mean \pm SD 100.9 ± 3.6 , $n = 5$) were not significantly different from those of pairs (102.2 ± 7.1 , $n = 173$, $t_{176} = 0.4$, $P > 0.5$). Neither egg hatched from the two-egg clutch of the polyandrous trio: one was added, and the other was ejected from the nest while the chick was pipping. All three eggs in the nest of the polygynous trio hatched, but none of the chicks survived to fledging. Although systematic data were not collected, it was clear that the 2000–2001 season was relatively poor overall for skuas, with only 30–40% of pairs successful in fledging a chick, compared with over 70% in the early 1980s (Osborne 1985). The first eggs from both trio clutches were recorded pipping on 31 December 2000, which coincided with the peak hatching period of pairs.

Visits to the same territories and recapture of banded birds in December 2001 revealed that the same individuals were also breeding together as trios in the 2001–2002 season. Trios have also been present on Bird Island in at least seven previous seasons. In 1961, Bonner (1964) found and shot a polygynous trio with a three-egg clutch. In 1976–1977, two trios were recorded, and in 1980–1981, a trio was recorded defending two nests, 3 cm apart, one with a single egg, and one with a two-egg clutch from which one chick hatched (British Antarctic Survey, unpubl. data). In 1983–1984, Osborne (1985) found a trio nest with two eggs. In 1986–1987, four eggs were recorded in a single trio nest, of which three hatched. In 1987–1988, four eggs were again recorded in a trio nest but hatching success was unknown; in 1988–1989, three eggs were recorded, at least two of which hatched (British Antarctic Survey, unpubl. data). The last three records

related to a territory in exactly the same location in every season, and although the adults were unbanded it was strongly suspected that the same three birds were involved.

DISCUSSION

As far as I am aware, this is the first proven instance of a polygynous and a polyandrous trio of Brown Skuas recorded at a single breeding colony. Indeed, polygynous trios of skuas or jaegers are very unusual, having been suspected in Brown Skuas on only a handful of previous occasions, including that on Bird Island in 1961 (Bonner 1964, Burton 1968, Barré 1976) and in Great Skuas (*Stercorarius skua*) only once (Furness 1987). By comparison, only polyandrous breeding associations have been confirmed in the Chatham Islands (Millar et al. 1992, Young 1998).

The presence of a supranormal clutch of three eggs, which occurs at rates of 0.1% in Great Skuas (Furness 1987) and 0.4–0.5% in Parasitic Jaegers (*Stercorarius parasiticus*; Phillips 2001), should not in itself be considered evidence for polygyny, as females are capable of replacing eggs if they are lost shortly after laying. Natural four-egg clutches are even less common, and these possibly never originate from pairs (Hemmings 1994).

That adults were able to hatch chicks from three- or four-egg clutches on three occasions on Bird Island is something of an achievement. Skuas and jaegers have two brood patches and incubate eggs on their feet, so hatching success of supranormal clutches is generally very low. At least one chick has been hatched from a three-egg clutch incubated by Great Skuas (Furness 1987), and at artificially enlarged clutches of Long-tailed Jaegers (*Stercorarius longicaudus*; Andersson 1976), but never by Brown Skuas in New Zealand (Millar et al. 1992) or Parasitic Jaegers (Phillips 2001). As far as I am aware, the instances on Bird Island are the only records of any species of skua or jaeger managing to hatch three chicks. We might therefore conclude that in general there is a distinct selective disadvantage to polygyny if both females typically lay two eggs in their common nest.

The trios at Bird Island are not transient associations, as the two trios present on Bird Island in 2000–2001 were also breeding together at the start of the 2001–2002 season, and circumstantial evidence from the late 1980s suggested strongly that a trio bred together for at least three seasons. Similarly, the composition of cooperative groups of skuas at the Chatham Islands often remained stable for many years (at least 14 seasons in one case; Hemmings 1994, Young 1988).

The overall incidence of trios in the 2000–2001 season on Bird Island was <1% of territories. With the exception of the New Zealand sites, this proportion is remarkably similar to that recorded elsewhere (<2%; Burton 1968, Barré 1976, Williams 1980, Parmelee and Pietz 1987, Peter et al. 1990, Hemmings 1994). By comparison, at the Chatham and Snares archipelagos, an average of 17–19% of territories are occupied by trios or occasionally larger breeding units (Hemmings 1994, Young 1998, Miskelly et al. 2001). In clear contrast, trios are recorded in only a tiny proportion of territories, if at all, in other skua or jaeger

species (Furness 1987, Hemmings 1994). It is instructive to consider briefly what factors might contribute to this variation.

Many explanations exist for the evolution of cooperative breeding in birds, many of which are based on the benefits of remaining on the natal territory for the first year or of associating with close kin (Stacey and Koenig 1990). However, these obviously do not apply to Brown Skuas, where recruitment does not take place until birds reach 5 years of age and individuals in breeding groups are rarely closely related (Young 1998). Another hypothesis (Hemmings 1994), that communal breeding in Brown Skuas at the Chatham and Snares archipelagos is not adaptive, but results instead from the intermittent occupancy of territories throughout the winter, cannot apply at Bird Island where skuas are completely absent during June–August. As neither this nor kin selection appear to be suitable explanations, an alternative hypothesis is that cooperating individuals experience a direct selective advantage. This does not appear to be a reproductive benefit, as Brown Skua trios either at Bird Island or elsewhere perform no better than monogamous pairs in terms of chicks fledged, even if they produce a supernormal clutch (Williams 1980, Hemmings 1989, Young 1998, this study). One other possibility is therefore that resource limitation, probably territory availability, may force birds to cooperate rather than defer breeding entirely.

The mean age of recruitment in Brown Skuas is similar to other *Stercorarius* species, implying no greater barrier to first breeding (Young 1998). In addition, Young (1994) concluded that there was no evidence for saturation of habitat in the Chatham Islands. However, this is a complex issue, as the perspective of a recruiting skua in the assessment of habitat suitability may be rather different than that of a human observer. There is a substantial pool of nonbreeding birds at most skua colonies including Bird Island (where the peak count at all roosting and bathing sites traditionally used by nonbreeders was ca. 350 birds in late December 2000). It is quite possible that although many of these are too inexperienced or physiologically unprepared, others may be outcompeted for breeding territories (Furness 1987). We should probably be cautious before asserting that nest sites can be obtained readily. The low but widespread incidence of communal breeding in Brown Skuas compared with closely related taxa implies a greater genetic or behavioral predisposition. At the Chatham Islands, disproportionately more new territories are established by breeding coalitions than by pairs (Young 1998), presumably because of strength in numbers. If this represented a tangible, albeit slight, selective advantage, traits that facilitate communal breeding could have spread, particularly as the Chatham Island population is small and highly philopatric (Young 1998). The question then arises as to why cooperative breeding is not more common at other colonies. The answer may be that ecological differences reduce or eliminate any benefits of group cooperation during territory acquisition at other sites, or alternatively, that trios, particularly those that are polygynous, simply experience no overall reproductive advantage.

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