FEEDING TERRITORIES OF BROWN SKUAS (*CATHARACTA LONNBERGI*)

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ABSTRACT.—The maintenance of feeding territories by Brown Skuas (*Catharacta lonnbergi*)[3] was observed in a pygoscelid penguin rookery on King George Island during the 1977–1978 austral summer. Brown Skuas fed exclusively on penguin eggs and chicks once they became available in late October, and skua pairs holding feeding territories in the penguin rookery defended these areas against intruders that attempted to obtain food items from these territories. These intruders included conspecifics, Southern Black-backed Gulls (*Larus dominicanus*), and American Sheathbills (*Chionis alba*). Although territorial Brown Skuas attacked and chased overflying intruder conspecifics and gulls indiscriminately, only intruding skuas elicited the long call display from the territorial pair. Male skua energy investment in hunting and territorial defense was significantly greater than that of the female.

Brown Skua territories were defined as optimal or suboptimal based on their available food resources. Analysis of skua breeding data suggests that an adaptive advantage in maintaining an optimal feeding territory appears to be increased reproductive success. Although there were no statistical differences in egg production, Brown Skuas defending optimal territories fledged significantly more chicks per pair than all other skuas [i.e. suboptimal territorial Brown Skua, nonterritorial Brown Skua, mixed Brown Skua–South Polar Skua (*C. maccormicki*), and South Polar Skua pairs]. This increased reproductive success of optimal territorial pairs may be linked to the proximity of an abundant food source. *Received 27 September 1979, accepted 6 March 1980.*

THE Brown Skua (*Catharacta lonnbergi*) is an opportunistic feeder that obtains its food through scavenging, kleptoparasitism, and predation (Burton 1968a, b; Johnston 1973). Brown Skuas have also been reported to defend feeding-breeding territories in rookeries of pygoscelid penguins (Stonehouse 1956, Sladen 1958). These territories are defended against conspecifics and contain colonies of penguins that produce eggs and chicks that are exploited as a food resource by the territorial pair. To date, the maintenance of feeding territories by Brown Skuas has not been described as completely as has been done for the congeneric South Polar Skua (*C. maccormicki*) (Young 1963a, b, 1972; Wood 1971; Trillmich 1978). The objectives of the present study were (1) to describe quantitatively the defense of feeding-breeding territories by Brown Skuas in a pygoscelid penguin rookery, and (2) to determine whether Brown Skuas with penguin nests in their territories bred more successfully than those without.

STUDY SITE AND METHODS

This study was conducted at Point Thomas, King George Island, South Shetland Islands (62°10'S, 58°30'W) from 1 November 1977 through 21 February 1978. All three pygoscelid penguins breed in two rookeries (designated East and West) at Point Thomas. The rookeries are approximately 3 km apart and

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[3] The two skuas in this paper are referred to binomially pending resolution of their biological and systematic status (Watson 1975).

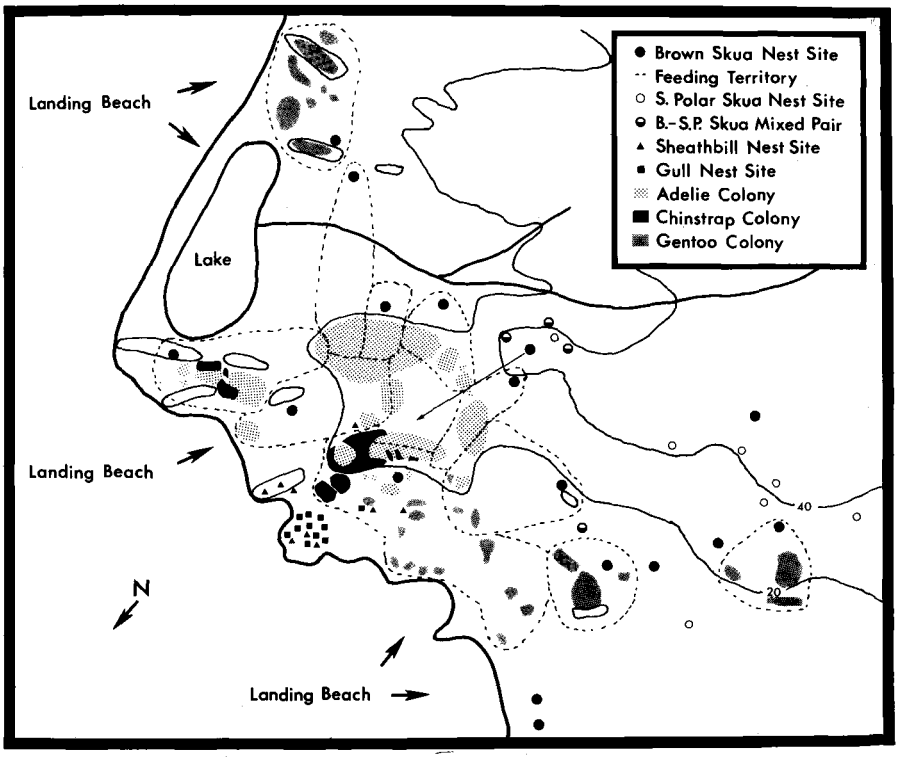

Fig. 1. Map of the West rookery at Point Thomas showing locations of feeding territories, penguin colonies, and nest sites of other seabirds.

are separated by a glacial tongue. An estimated 18,000 Adelie (*Pygoscelis adeliae*), 1,040 Chinstrap (*P. antarctica*), and 2,600 Gentoo pairs (*P. papua*) breed in the Point Thomas rookeries. In addition, 28 Brown Skua, 13 South Polar Skua, 4 mixed Brown–South Polar Skua, 12 American Sheathbill (*Chionis alba*), 13 Southern Black-backed Gull (*Larus dominicanus*), and 120 Southern Giant Fulmar (*Macronectes giganteus*) pairs nested at Point Thomas in 1977–78. The majority of data (including all behavioral data) were collected in the West rookery, which contained 16 Brown, 8 South Polar, and 4 mixed skua breeding pairs. All of the gulls, nine sheathbills, and 40 of the Southern Giant Fulmar pairs bred there also. The Polish Academy of Science's research station, Henryk Arctowski, is located 1 km south of the West rookery.

Twelve pairs of territorial skuas in the West rookery were selected for behavioral observations from 1 November 1977 through 5 January 1978. At least one member of each pair was captured and banded with USFWS bands and patagial tags (constructed of Herculite) to facilitate individual identification. Skuas were then sexed on the basis of courtship behavior and copulations. Behavioral observations (127 territory-observation h) of the hunting activities (e.g. attempts to obtain food items, successful attempts, etc.) and estimated overflight altitudes of territorial skuas and all intruding birds were recorded using binoculars, digital stopwatches, and portable cassette recorders. Behavioral data were collected from a vantage point that permitted an unobstructed view of the territory from a distance of approximately 100 m, and all responses of territorial birds to intruders were recorded. The mapping of feeding territories was based upon the agonistic interactions between territorial pairs and intruding birds over the course of the breeding season (Fig. 1). The reproductive success of 36 skua nest sites in both rookeries was monitored at weekly intervals until late February, when skua chicks began to fledge.

All nesting skuas and gulls defended breeding territories (Type B according to Hinde 1956). To facilitate discussion, however, only skuas defending feeding-breeding territories (Type A according to Hinde 1956) have been designated as "territorial" in this paper. Definitions of the terms rookery and colony are those used by Penney (1968).

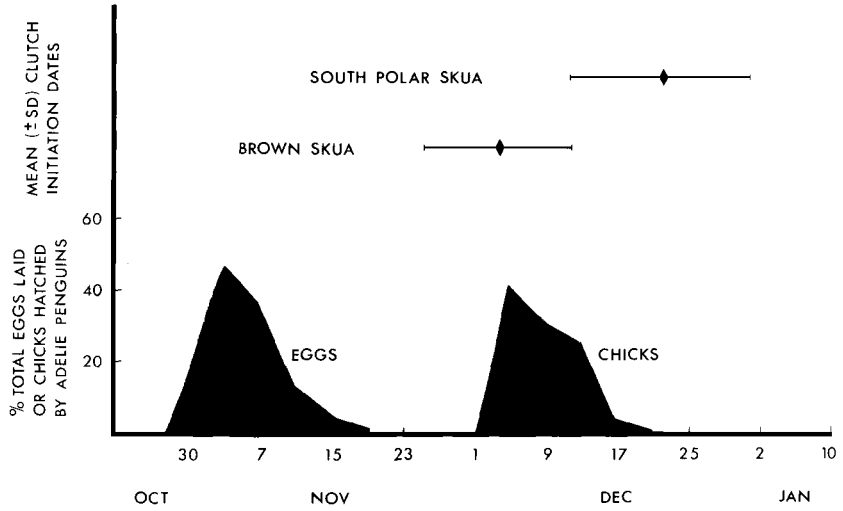

Fig. 2. The breeding chronology of the Adelie Penguin (88% of all penguin pairs) and the Brown and South Polar skuas at the Point Thomas West rookery in 1977–1978.

Statistical analysis was performed using the Kruskall-Wallis and Dunn's tests for ranked data (*H* values). Data were further analyzed with contingency tables (χ^2 values) and using the Wilcoxon two-sample test. The latter test was performed as described by Sokal and Rohlf (1969: 392) for large samples and tied values; the results appear as *t* values in the text.

Results

Characteristics of feeding territories.—Brown Skuas began arriving at Point Thomas in late October, and feeding territories (in which the skuas also nested) were established in both the East and West rookeries by early November. The 12 feeding territories selected for study encompassed all of the pygoscelid colonies in the West rookery. The breeding chronology of the Adelie Penguins (88% of all penguin pairs) and the Brown and South Polar Skuas is presented for this rookery during the 1977–1978 season in Fig. 2. Territories contained from 90 to 2,011 penguin nests ($\bar{x}$ = 1,028), and 2 territories contained 2 or more penguin species. Breeding pairs that defended feeding territories preyed and/or scavenged exclusively on penguin eggs and chicks. Territorial boundaries remained constant over the course of the reproductive cycle.

Brown Skuas hunted by flying over a colony, searching for a potential food item, hovering, and dropping to seize the food item. Most successful hunting attempts were initiated from an overflight altitude of 1–3 m. The skua generally flew back to the nest site with the egg or chick. Although both "active predation" and "scavenging" (i.e. seizure of deserted eggs or dead chicks) were recorded, it was generally not possible to distinguish between them when a bird acquired a food item. The mean (± SE) duration of 50 aerial "hunting bouts" for territorial skuas was 68.8 (± 8.0) s. Intruder skuas and gulls used a similar method, except that they flew directly out of the territory with a food item. Intruders with a food item that were sighted by a territorial skua were chased. Occasionally, the intruder was forced to drop the egg or chick, which the territorial animal then recovered. Hovers and

TABLE 1. Comparisons of rates of overflights, attempts, and egg-chicks taken by territorial skuas and intruder species (mean ± S.E.) during 127 h of territory observation.[a]

	Territorial Brown Skuas	Intruders				
		Brown Skuas	Gulls	Sheathbills	South Polar Skuas	Southern Giant Fulmars
Overflights/h	2.1 ± 0.3	11.1 ± 0.6**	4.5 ± 0.6**	0.6 ± 0.2**	0.1 ± 0.1**	0.2 ± 0.1**
Attempts to obtain eggs or chicks/h	0.7 ± 0.1	0.5 ± 0.1	0.2 ± 0.1*	—[b]	0*	0*
Eggs and chicks taken/h	0.6 ± 0.1	0.4 ± 0.1	0.2 ± 0.1*	0.1 ± 0.1*	0*	0*

[a] Comparisons analysed with Kruskall-Wallis and Dunn's tests; * = significance at the 0.01 level; ** = significance at the 0.005 level.
[b] Sheathbills were never observed making an aerial attempt to obtain a penguin egg. They usually entered the colony on foot to obtain broken or abandoned eggs.

attempts to seize prey items by intruders that were sighted also resulted in a chase and/or an attack by the territorial bird. Following a chase, the territorial animal usually flew over penguin colonies within its territory and occasionally obtained a food item in the exact area where the intruder had attempted to do so.

Brown Skuas made 2.1 (± 0.3) overflights per h of the penguin nests within their territories and acquired a mean of 0.6 (± 0.1) food items per h (Table 1). Although both intruder conspecifics and Southern Black-backed Gulls overflew Brown Skua feeding territories significantly more frequently (means = 11.1 and 4.5 overflights per h, respectively), territorial pairs acquired slightly more food items per h than did intruder skuas and significantly more than did gulls (Table 1). Of all territorial Brown Skua overflights, 82% were under 3 m in height, while only 28% of intruder skua or gull overflights were below 3 m (Table 2; $\chi^2 = 81.052$, df = 2, $P < 0.001$). The mean percentage of all overflights under 10 m that resulted in the acquisition of a food item by territorial Brown Skuas was significantly greater than that of intruding conspecifics and gulls (29.5% versus 4.3% and 3.3%; $\chi^2 = 29.810$, df = 2, $P < 0.001$). South Polar Skuas and Southern Giant Fulmars were not observed hunting within the penguin colonies during observation periods. Later in the season, however, Fulmars were observed attacking Chinstrap chicks (4–6 weeks old) on several occasions. Sheathbills generally entered penguin colonies on foot to forage.

Territorial defense consisted of a hierarchy of agonistic responses to intruders, from low level long-call displays, given from the ground by one or both members of the territorial pair, to aerial chases and/or attacks, which were generally confined within the pair's territorial boundaries. Territorial skuas had significantly more agonistic interactions with nonterritorial Brown Skuas ($t = 15.670$, df = 147, $P < 0.001$) and Southern Black-backed Gulls ($t = 3.802$, df = 140, $P < 0.001$) than with

TABLE 2. Percentage of overflights by territorial skuas and intruder species for which altitudes were estimated.

		Altitude of overflights		
	(N)[a]	0–3 m	3–10 m	10+ m
Territorial skuas[b]	(72)	82	15	3
Intruder skuas	(613)	28	51	21
Intruder gulls	(268)	27	56	17

[a] N = total number of overflights recorded.
[b] Contingency table analysis; $\chi^2 = 81.052$, $P < 0.001$.

TABLE 3. Reproductive success (mean ± SE) of Brown, South Polar, and mixed skua territorial pairs at Point Thomas in 1978.

	Pairs	Feeding territory	Eggs	Eggs/ breeding pair	Fledg- lings	Fledglings/ breeding pair[a]
Brown Skuas	13	(optimal)	24	1.85 ± 0.10	15	1.15 ± 0.19
Brown Skuas	3	(suboptimal)	4	1.33 ± 0.67	0	0***
Brown Skuas	8	No	12	1.50 ± 0.19	3	0.38 ± 0.26***
South Polar Skuas	8	No	12	1.50 ± 0.33	4	0.50 ± 0.19***
Mixed pairs	4	No	7	1.75 ± 0.25	0	0***

[a] *** $P < 0.005$ for Kruskall-Wallis and Dunn's comparison with territorial Brown Skuas.

territorial conspecifics. Both intruding Brown Skuas and gulls were attacked and chased significantly more often by territorial Brown Skuas when their overflights of penguin colonies were in the 0–3 m altitude range (Brown Skuas $\chi^2 = 37.069$, df = 2, $P < 0.001$; gulls $\chi^2 = 29.132$, df = 2, $P < 0.001$). Comparisons of territorial Brown Skua responses to intruder skuas and gulls indicate that both intruders elicited attack indiscriminately; less than 1% of all gull overflights (at any altitude), however, elicited long-call displays from territorial Brown Skuas.

Female Brown Skuas spent much of the time at the nest site engaged in either nest construction or incubation early in the season. Male energy investment in hunting and territorial defense was significantly greater than that of the female. Males took 90% of all penguin eggs and/or chicks taken ($\chi^2 = 38.095$, df = 1, $P < 0.001$), performed 67% of all long-call displays directed at intruding skuas ($\chi^2 = 5.952$, df = 1, $P < 0.025$), and were responsible for 88% of all attacks and/or chases of intruding birds ($\chi^2 = 33.754$, df = 1, $P < 0.001$).

Territory productivity and skua reproductive success.—The numbers of eggs produced, chicks hatched, and chicks fledged were determined for each of the pygoscelid colonies in the West rookery (Trivelpiece and Volkman, in prep.). Therefore, the number of eggs and chicks actually lost by each colony (and theoretically then available to territorial Brown Skuas) could be estimated. During the month of November, counts of penguin eggs returned to nest sites of four territorial pairs produced a mean of nine eggs per day per territorial pair. This count is in agreement with the behavioral data, indicating that territorial pairs took 0.6 eggs per h. Hence, during November (prior to the hatching of the first penguin chick on 1 December), territorial skua pairs required a mean of 270 penguin eggs. Brown Skua territories that had fewer than 270 egg losses were operationally defined as suboptimal. Suboptimal territories contained from 90 to 260 penguin nests, while optimal territories contained from 766 to 2,011 nests. In addition, suboptimal territories were apparently less attractive as food sources, as there were significantly fewer overflights by both intruder Brown Skuas ($\bar{x} = 2.9 \pm 0.6$; $t = 3.070$, df = 99, $P < 0.01$) and gulls ($\bar{x} = 1.0 \pm 0.4$; $t = 6.594$, df = 99, $P < 0.001$) when compared to overflights of optimal territories.

There were no significant differences in egg production (eggs laid per breeding pair) for Brown Skuas with optimal territories, Brown Skuas with suboptimal territories, nonterritorial Brown Skuas, South Polar Skua pairs, and Brown–South Polar Skua mixed pairs (Table 3). Brown Skuas that defended optimal feeding territories, however, fledged significantly more chicks than all other skua pairs ($H = 21.129$, df = 4, $P < 0.001$).

DISCUSSION

The results of this preliminary study indicate that Brown Skua feeding territories were defended primarily against conspecifics and Southern Black-backed Gulls, and this is consistent with observations made by Stonehouse (1956). Conspecifics and gulls were also the principal food competitors of territorial skuas within their feeding territories. Sheathbills were also attacked as they entered penguin colonies on foot to forage. Hence, it would seem that intra- and interspecific defense of feeding territories by Brown Skuas may be adaptive in that primary food competitors are excluded. Interactions between adjacent, territorial skua pairs were infrequent. Young (1972) has suggested that the stability and consistency of feeding territories from year to year in South Polar Skuas may be a function of the low replacement rate and long lifespans of these birds. The same explanation may be applied to the relatively low rate of conflict over territorial boundaries between Brown Skuas.

Skuas defended their territories against intruders that flew over at "hunting altitudes" (i.e. less than 3 m). Relatively little energy was expended on intruders flying above 3 m, and these overflights elicited a significantly higher percentage of long-call displays or no response from territorial skuas. Approximately 76% of all gull flights over 3 m resulted in no response from a territory holder. Although the long call was frequently directed at conspecifics, it is noteworthy that less than 1% of all gull overflights elicited this display from the territorial skua. Conceivably, more overt types of agonistic behavior (i.e. chases and attacks) are necessary in interspecific defense of feeding territories. Overt supplanting aggression is also common in interspecific interactions in mixed feeding flocks of other bird species (Recher and Recher 1969, Morse 1970).

The breeding skuas we monitored suggested that an adaptive advantage in maintaining a feeding territory appears to be increased reproductive success. Although there were no statistical differences in egg production, Brown Skuas defending optimal territories fledged significantly more chicks per pair than all other skuas (Table 3). The increased reproductive success of these pairs may be directly linked to the proximity of an abundant food source. Suboptimal and nonterritorial skua pairs were forced to invade the feeding territories of conspecifics or, in the case of South Polar Skuas, to forage at sea. We were not aware of any Brown Skua pairs that derived food items from sources other than the penguin colonies. Banded nonterritorial Brown Skuas were frequently observed hunting in the penguin rookery; no observations of these pairs were conducted at their nesting sites, however. It is therefore possible that these pairs exploited both the sea and the penguin rookery for food. Food regurgitated by their chicks during weekly weighings and remains of food items near the nest site of these pairs, however, suggested a totally penguin-dependent existence. Several more seasons of data will be necessary to clarify and confirm these findings.

To date, a similar reproductive advantage has not been established for territorial South Polar Skuas in other areas of the Antarctic. Although Trillmich (1978: 30) reported increased reproductive success for territorial South Polar Skuas at Cape Hallett, our contingency table analysis of these data failed to confirm his contention. Young (1963a) was also unable to observe differences in the numbers of chicks fledged by territorial South Polar Skuas at Cape Royds. Food available from the small Adelie rookery at Cape Royds was limited, however, and territorial birds began fishing by the end of the season.

Brown Skua pairs defending optimal territories fledged significantly more chicks per pair than skuas that maintained suboptimal territories (Table 3). Increased productivity of feeding territories has been related to the density of territorial pairs of Pomarine Jaegars (*Stercorarius pomarinus*; Pitelka et al. 1955) and increased reproductive success of Tawny Owls (*Strix aluco*; Southern and Lowe 1968). The adaptive advantage in maintaining a suboptimal territory might be more apparent in years of severe weather. Young (1963a) and Wood (1971) have indicated that seasons with severe storms depressed the reproductive success of South Polar Skuas. This may be due in part to the inability of skua pairs to forage at sea and adequately feed their chicks during periods of inclement weather. Possibly Brown Skuas that defend suboptimal territories realize their greatest benefit in "storm" years. Penguin chick mortality in the Antarctic peninsula may be correlated to heavy snowfall and storms (Sladen 1955, 1958), and during those years a suboptimal territory may offer more food than in years of mild conditions (and hence, lower penguin chick mortality). The proximity of such a food source would also be beneficial in years when animals could not forage at sea. Heavy sea ice eliminated the reproductive effort of the South Polar Skuas at Palmer Station in 1977–1978, because the animals had to fly too far out to sea to forage (Parmelee et al. 1978). Only Brown Skuas that maintained feeding territories produced chicks during that season (D. Neilson, pers. comm.). An alternative (but not mutually exclusive) explanation may be that skua pairs defending suboptimal feeding territories are young animals. Experience accrued by a skua defending a suboptimal territory may be of some value if the skua pair is able to acquire an optimal territory at some future data. Removal experiments with South Polar Skuas indicated that vacated territories are quickly claimed by new pairs (Young 1972), rather than being incorporated into extant territories. Finally, it should be noted that the suboptimal territories in this study contained only Gentoo Penguins. It is possible that Gentoos are less vulnerable to skua predation than Adelies or Chinstraps, and this question remains to be clarified.

The feeding territories of the Brown Skuas provide a good model for answering questions related to the adaptiveness of territoriality in general. The ability of the observer to quantify accurately the food resource (i.e. penguin eggs and chicks), the food consumed by territorial pairs, the intrusion rate, the time investment made by Brown Skuas in defense of their territories, and the reproductive success of pairs that defend territories versus those that do not should prove valuable in assessing the energetics of territorial maintenance and in testing hypotheses related to the economics of territorial defense (Schoener 1971). Problems to be clarified by future research should include comparisons of defense and foraging strategies of skua pairs with different sized, optimal territories; examination of seasonal changes in the utilization of the prey species by the Brown Skua related to either the penguin or skua reproductive cycles; investigation of differences in hunting strategies applied toward each penguin species; and the determination of the reproductive success of individually banded, territorial and nonterritorial Brown Skuas over the course of several years.

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