Wilson Bull., 107(2), 1995, pp. 317–327

AVIAN PREDATION AT PENGUIN COLONIES ON KING GEORGE ISLAND, ANTARCTICA

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ABSTRACT.—Predation at seven colonies that varied in size from 10 to hundreds of breeding pairs of Adelie (*Pygoscelis adeliae*) and Gentoo (*P. papua*) penguins was observed from a blind at King George Island, Antarctic Peninsula, from 21 Dec. 1993 to 3 Feb. 1994. We observed the colonies for 96 h to record foraging by Brown Skuas (*Catharacta lonnbergi*), Kelp Gulls (*Larus dominicanus*), and Giant Petrels (*Macronectes giganteus*) during the early chick through creche phase of the penguin breeding cycle. Activity rates by predators varied little with time of day or time of season for skuas and petrels. Kelp Gulls, however, showed significant variation in rates with time of season. Total activity and search rates were significantly higher for each predator species at larger versus smaller colonies. In addition, attempted predation and predation by skuas on penguin chicks were significantly higher, and from 4.1–7.9× more frequent, at colony edges rather than the center. Larger colonies probably receive greater attention by predators because of the larger number of prey, and by their greater circumference and edge area. Low breeding success by penguins in small colonies appeared to be partially attributed to predation losses, although predation rates were low. Penguin reproductive success may be significantly influenced by colony size and by the number and kinds of predators attending them. *Received 8 Sept. 1994, accepted 15 Nov. 1994.*

Predation at breeding colonies has received a great deal of attention by ornithologists interested in the evolution and adaptive significance of coloniality (e.g., Wittenberger and Hunt 1985, Kharitonov and Siegel-Causey 1988). In general, the number of predators and predation rates increase with colony size, but the proportion of prey killed usually decreases. This pattern suggests that large colonies provide greater protection for prey offspring due to the swamping effect of prey numbers on the predator. However, some studies have produced divergent results and indicate that the predator-prey relationship at colonies is complex and varies in different systems in relation to the number and kind of predators and the size and age of the colony (Davis 1982, Raveling 1989, Hunter 1991, Szep and Barta 1992). To test the hypothesis that larger rather than smaller colonies provide greater protection to penguin chicks, we examined predator activities at colonies of various sizes of Adelie (*Pygoscelis adeliae*) and Gentoo (*P. papua*) penguins in Antarctica. We determined activity rates in relation to time of day, time of season, and colony size and examined the effect of predation on reproductive success of penguins

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in small and large colonies. We compare our results with other studies to explain the predator-prey relationship in the Antarctic system.

METHODS

This study site is located at Llano Point on the western shore of Admiralty Bay, King George Island (Lat. 62°10′S, 58°30′W), South Shetland Islands (see Trivelpiece et al. 1990 for description of the study area). At Llano Point, colonies of Adelie and Gentoo Penguins have been censused and monitored for reproductive success each year since 1980. During the 1993/1994 breeding season, we estimated the breeding populations of these species at 6100 Adelie and 2200 Gentoo pairs. These estimates are based on nest counts conducted at peak egg laying in early and mid-November, respectively. Fledging success was based on chick counts completed in January and reproductive success, measured as chicks fledged per breeding pair, was calculated for each colony by dividing the number of chicks fledged by the number of nests. In addition, ten pairs of Brown Skuas (*Catharacta lonnbergi*), 120 pairs of Southern Giant Petrels (*Macronectes giganteus*), and approximately 20 Kelp Gulls (*Larus dominicanus*) comprised of 5–6 breeding pairs plus subadults and non-breeders occurred near these colonies.

We observed seven colonies of Adelie and Gentoo penguins from a blind between 21 Dec. 1993 and 3 Feb. 1994. Activities of Brown Skuas, Kelp Gulls, and Giant Petrels were recorded during 2-h observation periods that were sequentially alternated between 06:00 to 20:00 h each day. We continuously scanned the colonies during each period and recorded searches, attempted predation, predation, and scavenging on penguin eggs and chicks by these predators. Searches were recorded when birds hovered or flew low and circled slowly over the colonies or walked near the colony edges; a rapid, direct flight over the colonies was not considered a search. Attempted predation occurred when birds took and lost, or attempted to take, penguin eggs or chicks. Predation was recorded when a predator successfully removed a live chick or egg from the colony or creche and it died as a result of this removal. Scavenging occurred when birds began feeding on carcasses or spilled krill in or near the colonies. We recorded the location of predation and attempted predation events in the colony as either having occurred at the periphery (within three nests of the edge, see Ainley et al. 1983) or center (beyond three nests from the edge) of the colony. Local weather conditions also were recorded during each observation period; however, the relatively mild season in 1993/1994 precluded an analysis of predation rates with variations in weather conditions.

Activity rates for each predator species were calculated by dividing the number of events recorded by the number of hours of observation. These rates were determined for each species, and not individual predators, by time of day, time of season (divided into 5-day intervals that included at least 8 h of observations each), and colony. For Brown Skuas and Giant Petrels, we divided these rates into three categories: total activities (searches, attempts, predation and scavenging), searches and predation. We did not observe Kelp Gulls preying on guarded penguin eggs or chicks, but they frequently scavenged spilled krill from penguin feedings in and near the colonies. Thus, for Kelp Gulls, we substituted scavenging for predation rates. Data were analyzed using Chi-square goodness of fit, linear regression, and Spearman's Coefficient.

RESULTS

We completed 96 h of observations at the colonies. Brown Skuas and Giant Petrels had higher total activity rates than Kelp Gulls during the

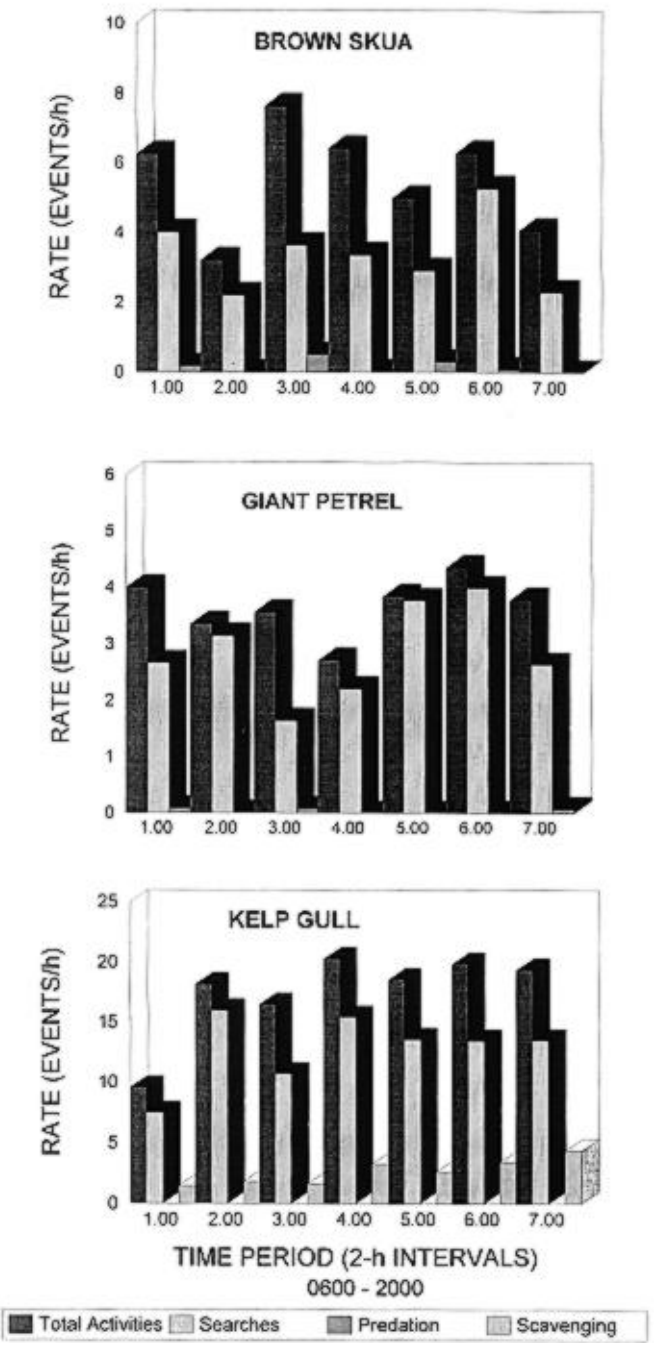
early morning (06:00–08:00 h), but there was no significant diurnal pattern for each species ($\chi^2 < 4.70$, df = 6, $P > 0.5$; Fig. 1). Predation rates were highest for skuas in the late morning and mid-afternoon and for petrels in the early morning and early evening. Kelp Gulls scavenged most frequently in the afternoon and early evening. Although these rates did not vary significantly, they suggest that these predators may partition their respective activities throughout the day.

Although there was a gradual decline in skua, and an increase in Giant Petrel, total activity and search rates throughout the season, no activity by each of these predators varied significantly with time of season (Fig. 2). However, there was a noticeable but non-significant increase in Giant Petrel total activity coincident with the hatching of the first Giant Petrel chicks, and a decrease in skua activities after peak creche (Fig. 2).

Total activities and searches by Kelp Gulls varied significantly ($\chi^2 > 29.3$; df = 8; $P < 0.05$) with time of season and were highest during period 6 (15–19 Jan.; Fig. 2). Except for scavenging which did not vary with time of season ($\chi^2 = 12.57$; df = 8; $P < 0.1$), all activities by this species declined steadily after period 6. Scavenging rates declined markedly in period 7 (20–24 Jan.), increased in period 8 (25–29 Jan.), but declined again thereafter.

All activities by each predator species were positively correlated with colony size (Spearman's Coefficient $R > 0.82$, N = 7, $P < 0.05$; Table 1). Search and scavenging rates by Kelp Gulls also were correlated positively with colony size ($R = 0.86$, $P < 0.05$). Predation rates by skuas, however, were not correlated with colony size ($R = 0.64$, $P < 0.11$), and predation rates by Giant Petrels were too low for statistical analysis. Predation events were rare but occurred most often at the larger colonies (Table 1). Small colonies were rarely visited by predators. Predation and attempted predation by skuas on penguin chicks was significantly higher and from 4.1–7.9× more frequent at the periphery of the colony than in the center ($\chi^2 = 27.6$, df = 1, $P < 0.005$; Fig. 3). Moreover, these activities were slightly, but not significantly, higher from the ground than from the air. All predation and attempted predation by Giant Petrels occurred from the ground and at the edge of creches.

We observed a non-significant increase in reproductive success with colony size in Gentoo Penguins ($R^2 = 0.53$; df = 5; $P < 0.1$). Reproductive success increased to a maximum of 1.3 chicks per pair for colonies with 34 or more nests; however, colony 9 with only 10 nests had no chicks surviving (Table 1). Although we did not witness predation at this colony, we did observe the same pair of skuas attempting to take chicks on several occasions, and we suspect that their efforts may have


BROWN SKUA
RATE (EVENTS/h)
0
2
4
6
8
10
1.00
2.00
3.00
4.00
5.00
6.00
7.00
GIANT PETREL
RATE (EVENTS/h)
0
1
2
3
4
5
6
1.00
2.00
3.00
4.00
5.00
6.00
7.00
KELP GULL
RATE (EVENTS/h)
0
5
10
15
20
25
1.00
2.00
3.00
4.00
5.00
6.00
7.00
TIME PERIOD (2-h INTERVALS)
0600 - 2000
Total Activities
Searches
Predation
Scavenging

removed many of the chicks from this colony. No pattern was observed with Adelie Penguin reproductive success and colony size.

DISCUSSION

A potential problem in these analyses is the attribution of most skua activities at the colonies to three pairs of breeding birds (recognized by their color bands) that held feeding territories in the study area. Although other skuas occasionally visited the colonies, these three pairs may bias the data toward individually learned behavior. Moreover, our study was of short duration and limited to the chick period of the penguin breeding cycle.

During our study, the weather was consistently mild, and we could not address the effect of severe weather conditions on predator activities. Young (1994) reported higher predation by South Polar Skuas (*Catharacta maccormicki*) on windy or stormy days when the adult penguins may be distracted or oriented in one direction, thereby facilitating prey capture. He also found variation in predation rates in relation to ice conditions and marine productivity in Antarctica. Similarly, predation of Common Murres (*Uria aalge*) and Brandt's Cormorants (*Phalacrocorax penicillatus*) by Western Gulls (*Larus occidentalis*) was higher in poor food years, causing additional constraint on the breeding effort by murres during those years (Spear 1993). We suspect predation rates will vary annually at King George Island because of these factors, but additional data are needed.

We found no variation in Brown Skua and Giant Petrel activity rates with time of day or season. Searches were the most common predator activity recorded during all observation periods. The ratio of searches to predation events was high, similar to those reported in other studies of South Polar Skua predation at Adelie Penguin colonies (Müller-Schwarze and Müller-Schwarze 1977, Young 1994). Müller-Schwarze and Müller-Schwarze (1977) suggested that frequent searches by predators at these colonies may facilitate predation by acclimating penguins to their presence, thereby causing them to be less alert. Equally possible is that skuas search the colonies continuously to locate vulnerable prey or to assess prey for future targets. We observed skuas returning to the same nest

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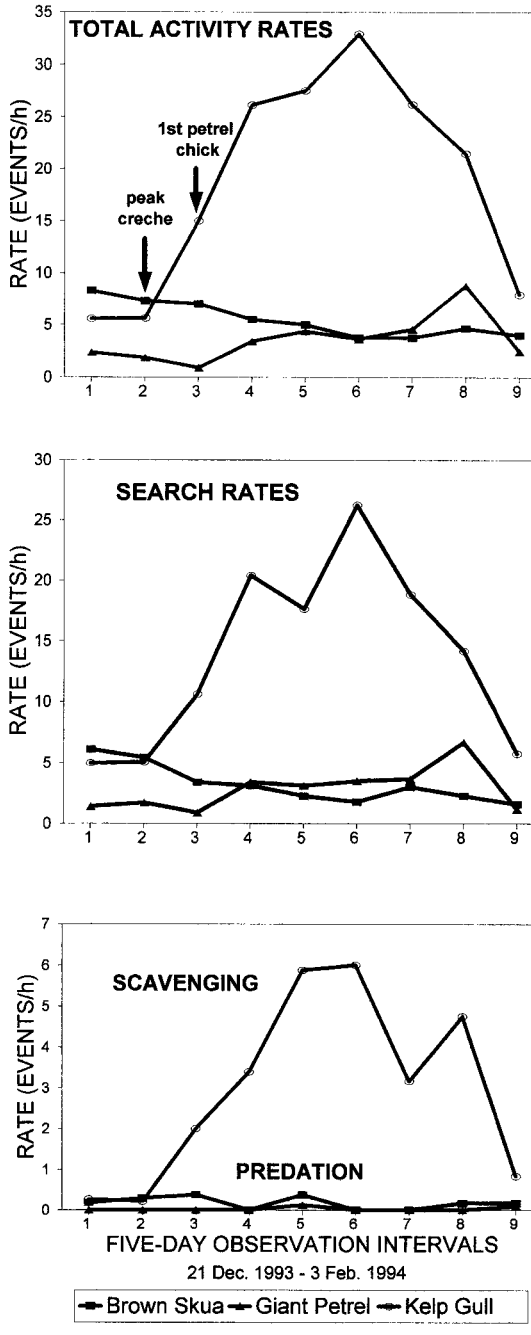
FIG. 1. Activity rates of predators with time of day at King George Island. Each time period represents a 2-h observational interval between 06:00 to 20:00 h. For each predator and each time period, activity rates are graphed for total activities and separately for searches and predation only. Scavenging rates, and not predation, are shown for Kelp Gulls only in the lower graph.


TOTAL ACTIVITY RATES
1st petrel chick
peak creche
RATE (EVENTS/h)
SEARCH RATES
RATE (EVENTS/h)
SCAVENGING
PREDATION
RATE (EVENTS/h)
FIVE-DAY OBSERVATION INTERVALS
21 Dec. 1993 - 3 Feb. 1994
Brown Skua
Giant Petrel
Kelp Gull

repeatedly until the prey was successfully taken. These nests usually contained small chicks or were more vulnerable to predation at the periphery of the colony.

Two species of Giant Petrels (*Macronectes giganteus* and *M. halli*) prey heavily on penguins, but have received less attention than skuas as their breeding range overlaps with penguins only in the Antarctic Peninsula and sub-Antarctic regions. Previous to our study, only Hunter (1991) has determined predation rates by Giant Petrels on penguins and at colonies of different sizes. Our observed predation rates by Brown Skuas and Giant Petrels are comparable to those reported for these species on King Penguins (*Aptenodytes patagonicus*) at Marion Island (Hunter 1991), and for South Polar Skuas on Adelie Penguins at Cape Crozier (Müller-Schwarze and Müller-Schwarze 1977) and Cape Bird (Davis 1982). These studies were based on systematic observations of penguins throughout the breeding period.

Our results agree with these studies in that predation was highest at larger colonies, although not significantly so. Davis (1982) found a significant and negative correlation between size of Adelie creches and the proportion of chicks depredated. Although the number of chicks lost was greatest at the largest creche, the proportion was smallest. He also attributed differences in reproductive success at penguin colonies to differential predation by skuas; colonies where the greatest number of South Polar Skuas foraged had the lowest reproductive success. We did not observe this pattern in our colonies where each had no more than two overlapping skua territories; Davis (1982) recorded from two to seven skua territories at each of his colonies.

Hunter (1991) counted corpses of chicks at colonies of King Penguins depredated by Brown Skuas and Giant Petrels. Similar to our results, he found daily predation rates determined from these counts to increase with colony size. He also found more corpses at the larger colonies, but the proportion of chicks lost (calculated from data in his Table 6) increased with size in some colonies (e.g., 11.5% in Kildalkey Bay A-D with 1457 chicks versus 19.8% at Prinsloomeer with 1848 chicks), the reverse pattern from that of Davis (1982). This difference may have been due to the greater number and diversity of predators at Marion Island (3 species) compared to Cape Bird (1 species). If so, variation in reproductive success

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FIG. 2. Activity rates of predators with time of season at King George Island for total activities (top), searches (middle), and predation (skuas and petrels) or scavenging (Kelp Gulls; bottom). The breeding season is divided into nine 5-day intervals, with from 8–14 hours of observations each, beginning 21 Dec. 1993.

TABLE 1

TOTAL ACTIVITY AND PREDATION RATES FOR BROWN SKUAS AND GIANT PETRELS AT THE SEVEN OBSERVATION COLONIES OF ADELIE (A) AND GENTOO (G) PENGUINS ON KING GEORGE ISLAND, ANTARCTICA, 21 DEC. 1993–3 FEB. 1994

Colony/species		No. nests	No. chicks	Chicks per pair	No. chicks seen killed	Skua total rates	Skua predation rates	Giant Petrel total rates	Giant Petrel predation rates
1	A	not counted	not counted	1.30[a]	11	4.21	0.083	2.92	0.031
4	A	36	39	1.08	2	0.15	0.021	0.052	0
5	A/G	71/45[b]	59/50[b]	0.83/1.11[b]	0	0.34	0	0.41	0
6	G	56	70	1.25	1	0.12	0.010	0.052	0
7	G	19	17	0.90	0	0	0	0	0
8	G	34	43	1.27	5	0.24	0.052	0.052	0
9	G	10	0	0	0	0.083	0	0.010	0

[a] Based on a monitored sample of 40 nests.

[b] Refers to Adelie/Gentoo penguins, respectively, that both bred in this colony. Data on colony size, number of chicks counted at fledging and reproductive success measured by the number of chicks fledged per pair at each colony also are given.

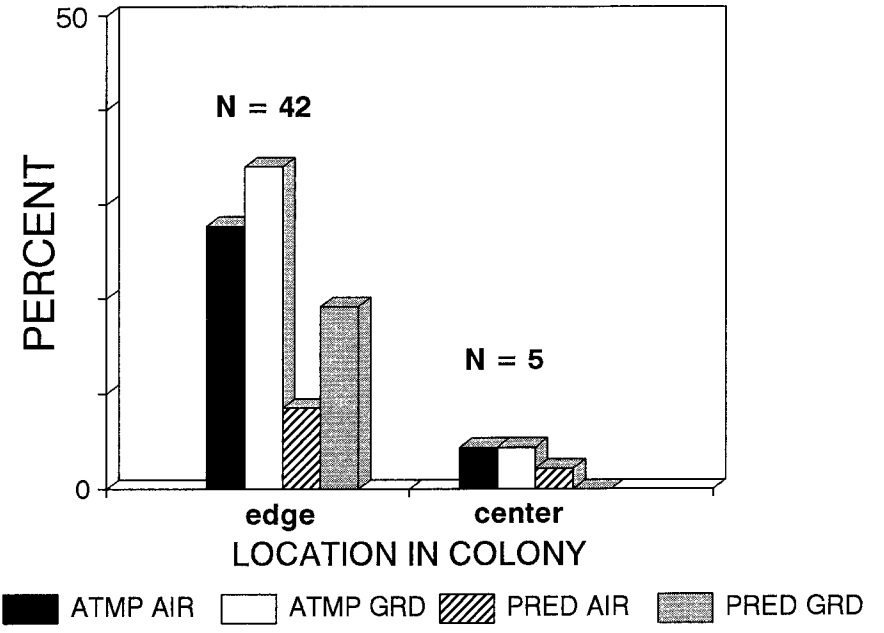

FIG. 3. Percent of total (N = 47) attempted predation and predation events on penguin chicks by Brown Skuas that were recorded from the air or ground and at colony edges or centers at King George Island.

by penguins of the same species, but at different colonies, may be due in part to the number and kinds of predators that attend them.

Increased predation with colony size is not difficult to explain. Larger colonies have a greater number, but small proportion, of nests on the periphery than smaller colonies (if their shape remains the same), and there is a greater variety of prey ages and sizes. Thus, predators should spend more time searching at large colonies where there is a better chance at finding a vulnerable target. Our findings that predation and attempted predation occur more frequently at colony edges supports this hypothesis. Spear (1993) also found higher predation by Western Gulls at the periphery of Common Murre colonies. However, colonial behavior is not adaptive as a means of reducing predation unless the proportion of prey taken by predators decreases with colony size. Our data on reproductive success with colony size also support this hypothesis. In addition, lower reproductive success in Adelie Penguin colonies may be due to a greater percentage of young or inexperienced breeders that may occur at the periphery of these colonies (Ainley et al. 1983). Small Gentoo Penguin colonies may be similarly biased with young breeders and this factor may account

for the lower success rates that we observed in colonies with less than 34 nests (Table 1).

Colonial-breeding penguins and their avian predators in the Antarctic represent a system in which both predator and prey are forced to co-exist due to lack of ice-free areas for breeding. One major predator, the South Polar Skua, often holds feeding territories that include penguin colonies but does not rely on this resource for successful breeding (Young 1994). Other studies, however, have indicated that both South Polar and Brown skuas with feeding territories have significantly higher reproductive success than pairs without feeding territories (Trillmich 1978, Trivelpiece et al. 1980, Trivelpiece and Volkman 1982, Pietz 1987, Young 1994). Spear (1993) had a similar finding for Western Gulls that held feeding territories within colonies of Common Murres and Brandt's Cormorants. Thus, life history strategy of skuas appears to benefit from the relationship whether it is obligate or opportunistic. For penguins, large colonies appear to be the best strategy for maximum reproductive success, but only for nests not located on the periphery. Our study indicates that the number and kinds of predators are important determinants in penguin reproductive success. Other studies suggest that variations in annual marine productivity also may be important (Spear 1993, Young 1994). Reproductive success in penguins should be interpreted in light of all these variables, especially when the impact of human disturbances or other unusual events are investigated.

ACKNOWLEDGMENTS

We thank R. Dilling and S. Klock for assistance in the field. Useful suggestions and discussions were provided by W. Fraser, M. Moulton, and S. Trivelpiece; M. Stiger assisted with graphics. The manuscript was improved by comments from G. Miller and an anonymous reviewer. This research was funded by NSF Grant DPP-9121952 to W. and S. Trivelpiece with supplemental funding to S. Emslie.

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